Changes of Acuity during Light and Dark Adaptation in the Dragonfly Compound Eye

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Intracellular recordings of angular sensitivity from the photoreceptors of Aeschnid dragonflies (*Hemianax papuensis* and *Aeschna brevistyla*) are used to determine the magnitude and time course of acuity changes following alterations of the state of light or dark adaptation. Acuity is defined on the basis of the acceptance angle, $\Delta\varrho$ (the half-width of the angular-sensitivity function). The maximally light-adapted value of $\Delta\varrho$ is half the dark-adapted value, indicating greater acuity during light adaptation. Following a change from light to dark adaptation, $\Delta\varrho$ increases slowly, requiring at least 3 min to reach its dark-adapted value. In contrast, the reverse change (dark to light) induces a rapid reduction of $\Delta\varrho$, and at maximal adapting luminances, this reduction takes place in less than 10 sec.

Introduction

When a compound eye experiences a change in the level of ambient illumination it undergoes certain physiological and anatomical modifications which alter the sensitivity of the eye to light, thus optimising visual performance in a new photic environment. These modifications are known collectively as *adaptation* (reviewed in [1]). At the neural level a change in ambient illumination causes changes in the transduction processes and intrinsic membrane properties of the photoreceptor which alter its "gain". These processes are termed *photochemical* and *neural* adaptation. In addition, anatomical changes within the ommatidium (especially by light-induced migrations of pupilliary screening pigments) can alter the rate of photon absorption by the rhabdom. This is termed *photomechanical* adaptation. The effect of both types of adaptation is to alter the sensitivity of the eye to light. However, photomechanical adaptation also has the potential to alter the *spatial acuity* of the eye by altering the angular field of view of the photoreceptor. Photomechanical changes tend to reduce the field of view during light adaptation and increase it during dark adaptation, producing a concomitant increase and decrease in acuity respectively [1]. Except for two brief accounts [2, 3], the time courses of adaptational changes in acuity have not, to our knowledge, been documented. These changes are reported here for dragonfly photoreceptors.

Materials and Methods

Aeschnid dragonflies of two species (*Hemianax papuensis* and *Aeschna brevistyla*) were caught in Canberra and used the same evening. Dragonflies were mounted at the centre of a cardan arm arrangement which supported a moveable point source (subtending 0.6° at the eye). This *test* stimulus delivered monochromatic light of wavelength 480 nm (bandwidth 5 nm) obtained by passing light from a xenon-arc lamp through a monochromator. The test stimulus was at the centre of a white reflective card which could be illuminated from the front by white light produced from a 150 Watt quartz-halogen bulb. This *adapting* source subtended 17° at the dragonfly eye and when used was set at one of four intensities (surface luminances): 0.3, 3, 28 or 225 cd/m^2. A glass, potassium-acetate-filled microelectrode was lowered through a tiny hole made in the dorsal region of the eye. Intracellular recordings of the graded responses of retinula cells (with dorsal fields of view (35°–55° above horizontal) and peak sensitivity to blue light of wavelength 480 nm) were amplified by a Grass P-16 preamplifier and collected on a chart recorder. While recording from a cell, step changes from a state of dark adaptation to one of the four states of light adaptation were made. Step changes from light to dark were also made. Following the experiments associated with a step change, the imposed state of adaptation was maintained for at least 10 min prior to the next step change. The point source and surrounding adapting source were moved together in 0.5° or 0.25° steps in horizontal arcs through the receptive

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field of the cell. At each position a dim 100 msec test flash was delivered to the cell. Angular steps and accompanying flashes were separated by about 1.5 sec. In this way continuous forward and reverse sweeps through the receptive field (each taking 8 – 10 sec) were maintained for several minutes following a step change in adaptation state. Thus, the time course of changes in the receptive field width caused by the subsequent adaptation could be monitored. As the point source is moved along the arc away from the visual axis of the cell (the point of highest sensitivity), the amplitude of the graded response becomes progressively smaller. The profile thus obtained by a single sweep through the receptive field is known as the angular sensitivity of the cell, and when responses are transformed through the cell's non-linear intensity-response function, curves like those of Fig. 1 are obtained [4]. The half-width of these curves is called the acceptance angle, $\Delta\varrho$, and is a useful measure of the acuity of the cell. $\Delta\varrho$ sets the limit for two-point discrimination by the eye and also the highest spatial frequency resolvable [5].

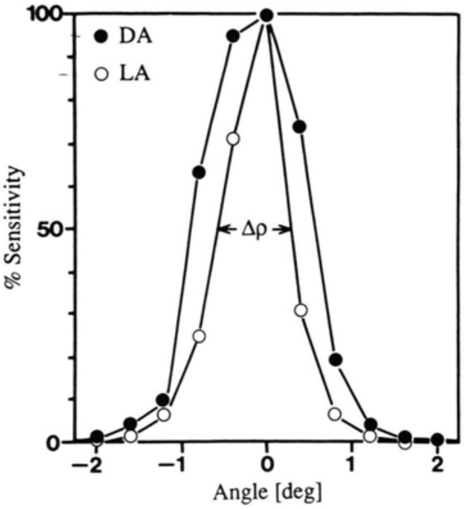

Fig. 1. Light-adapted [○] (225 cd/m^2) and dark-adapted [●] angular-sensitivity functions from a retinula cell of *H. papuensis*. These profiles are equivalent to the receptive fields of the cell in the light- and dark-adapted state, and their half-widths are defined as the acceptance angle, $\Delta\varrho$. Each function was taken from the 225 cd/m^2 light-adapted to dark-adapted run displayed in Fig. 2*B* (see arrows). Acceptance angles are 0.86° and 1.54° for light- and dark-adapted profiles respectively. LA = light-adapted; DA = dark-adapted.

Results

The receptive field profiles of retinula cells from dorsal ommatidia were found to be considerably broader in dark-adapted conditions than when adapted with light of intensity 225 cd/m^2 (Fig. 1). In the light-adapted state, however, the minimum values of $\Delta\varrho$ obtained were only about one-and-a-half times larger than the minimum practicable point source used for stimulation (0.6°). This means that the smallest values of $\Delta\varrho$ are probably overstated by about 0.2° [6].

For both species, the maximum ratio of $\Delta\varrho$ obtained in the dark-adapted state to that obtained in the light-adapted state was found to be approximately 2. This ratio is about average for apposition eyes (reviewed in [7]).

When a fully dark-adapted retinula cell is subjected to a sudden onset of an adapting luminance, the angular-sensitivity function narrows rapidly (Fig. 2A, 2C), especially if the imposed adapting luminance is intense (*i.e.* 28 or 225 cd/m^2). In such cases, essentially all change takes place before the first angular-sensitivity function can be measured, that is, within the first 10 to 20 sec. At the lowest adapting luminance (0.3 cd/m^2) the rate of narrowing is slowest, taking up to 90 sec for completion. The steady-state value of $\Delta\varrho$ attained is lower for higher adapting luminances. Dark-adapted values of $\Delta\varrho$ were found to be 1.80° ± 0.05° (3 cells) for *A. brevistyla* and 1.50° ± 0.06° (8 cells) for *H. papuensis*.

When the reverse experimental procedure is employed (*i.e.* a sudden onset of dark adaptation after light adaptation at a set intensity), the angular-sensitivity function begins to widen (Fig. 2B, 2D). Widening, however, proceeds much more slowly than the narrowing described above. This is especially evident in *A. brevistyla* (Fig. 2D) where no appreciable widening has taken place even after 5 min of dark adaptation. The process is slightly faster in *H. papuensis* (Fig. 2B) where the dark-adapted value of $\Delta\varrho$ (*i.e.* 1.5°) is approached after about 3 min. This is about twice as fast as found in the apposition eye of the locust, using comparable methods [2].

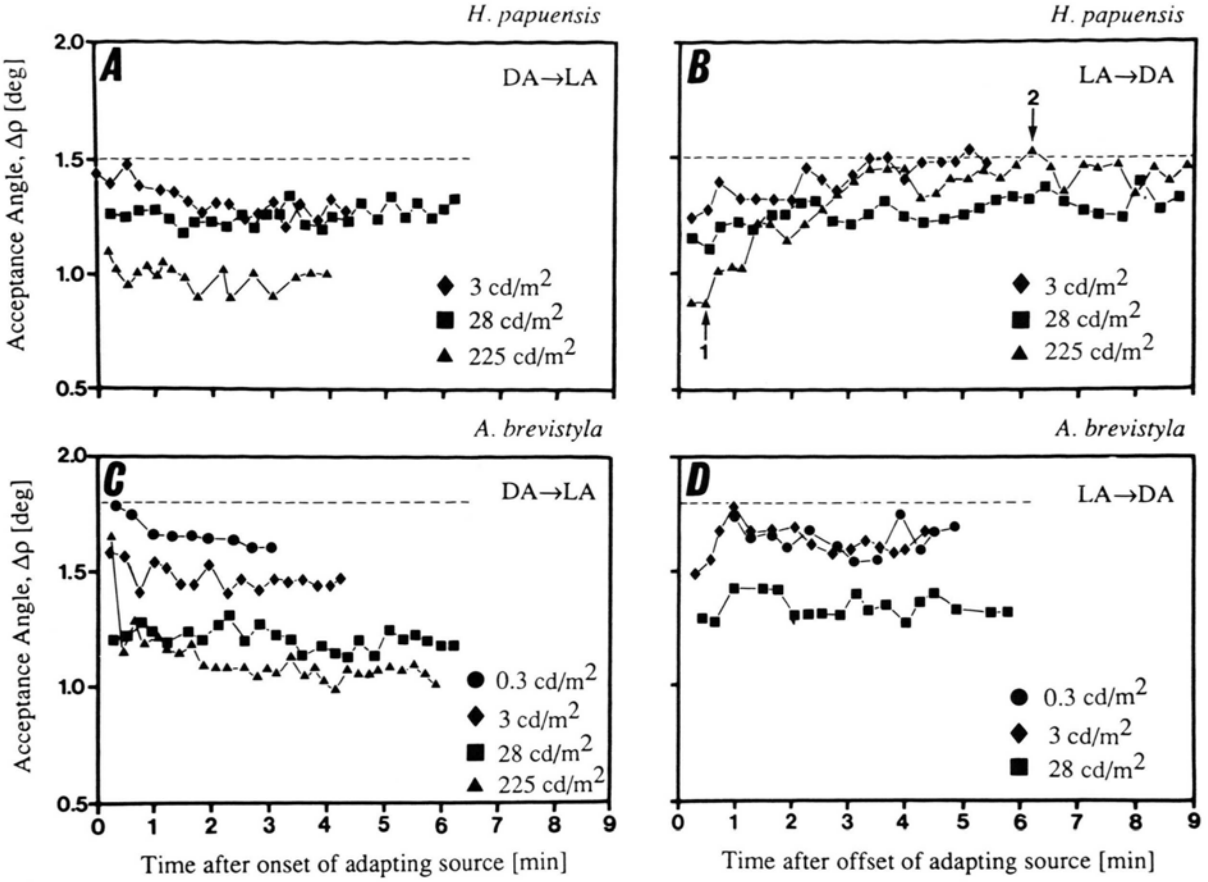

Fig. 2. Adaptational time courses of photoreceptor angular sensitivity for step changes in adaptation state from dark (DA) to light (LA) (*A* and *C*) and from light to dark (*B* and *D*), for *H. papuensis* (*A* and *B*) and *A. brevistyla* (*C* and *D*). Step changes were made to or from states of light adaptation whose intensities are indicated in each panel. The dashed lines indicate the fully dark-adapted values of Δϱ. The results represent intracellular recordings from a single, typical cell of each species (totally, 8 cells were studied for *H. papuensis* and 3 cells for *A. brevistyla*). The arrows in *B* indicate the light-adapted (1) and dark-adapted (2) angular-sensitivity functions displayed in Fig. 1.

Discussion

Photomechanical effects are the most widely documented cause of acuity change following an alteration in adaptation state [1, 5, 8]. These effects include migration of screening pigments and the morphological alteration of the rhabdom and its surrounds.

Primary screening pigment granules, forming a moveable "iris pupil" around the crystalline cone-rhabdom junction, are found in some crabs [7] and ants [9] and commonly in locusts [10] and dragonflies [4]. Dark-adapted outward migrations of this pupil take somewhere between 15 and 60 min to attain maximum displacement [8]. In many flies, butterflies, wasps, bees and cockroaches, screening pigment granules resident within each retinula cell migrate toward the rhabdom during light adaptation and away during dark adaptation. This "radial pupil" is very fast and often completes its full migration within a few seconds [8, 11, 12]. In some insects, notably locusts, dragonflies and cockroaches, dark adaptation leads to the formation of a "palisade" immediately around the rhabdom. This palisade is an offshoot of the endoplasmic reticulum and is considered to have significantly lower refractive index than the regular cellular matrix. In many insects, the formation of the palisade is accompanied by an outward migration of mitochondria and pigment granules which possess a higher refractive index than the rhabdom interior. In locusts the entire process requires 15 min to complete [2]. Dark adaptation also results in a reversible widening of the rhabdom in many insects [10]. All, some or none of these photomechanical changes may occur in a given species, and in addition, the changes may be under the influence of a circadian rhythm.

A startling outcome of our experiments is the speed with which $\Delta\varrho$ narrows following a step change from dark to light adaptation. If a photomechanical change is responsible for this rapid narrowing (which is probably the case), then an inspection of the examples listed above indicates that a radial pupil mechanism is probably the most likely explanation. All other photomechanical changes which are capable of changing $\Delta\varrho$ are apparently too slow, at least during dark adaptation (the only situation documented). However, according to a study on the Corduliid dragonfly *Hemicordulia tau* [13], retinula cell pigments are almost absent in the dorsal ommatidia, and this implies the absence of a radial pupil. It is possible, however, that the histological procedures used in that study washed out the pale yellow pigments present in the dorsal eye, thus rendering them invisible (D.-E. Nilsson, personal communication). Reflection measurements from ommatidia of the Libellulid dragonfly *Sympetrum vulgatum* (D. Stavenga, unpublished data) indicate a fast pupil mechanism but the data are insufficient to say with certainty that retinula pigments are responsible. In our Aeschnids the time course of dark adaptation is quite slow, as supported by studies of sensitivity increase in other dragonfly species [14, 15]. In *S. vulgatum*, however, dark adaptation is quite fast (but still slower than light adaptation), with a half time of 15–30 sec. Other reflection measurements on *Sympetrum* sp. (D.-E. Nilsson, unpublished data) indicate a much slower time course for dark adaptation (in the order of minutes), which agrees well with data presented here. In locusts, Tunstall and Horridge [2] correlated the time course of $\Delta\varrho$ widening (following dark adaptation) with growth of the palisade.

Insufficient evidence is available to say with certainty, however, that a radial pupil is responsible for the changes in acuity reported here. It is even possible that the combined action of several photomechanical mechanisms are responsible, and exactly which may depend on adaptation state. Nevertheless, whatever the mechanism(s), the results reported here indicate they are much faster during light adaptation than during dark adaptation. A careful study of photomechanical changes in the dragonfly eye is needed to clarify the situation.

When a dragonfly experiences a change in the ambient illumination, the modifications of acuity which take place in the retina must have some effect on acuity at higher levels in the visual pathway. Whether or not these retinal changes can account for the spatial properties of higher-order interneurons provides the basis of an accompanying study [16].

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