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## CHANGES IN CUTTLEFISH RETINAL SENSITIVITY DURING GROWTH

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CEPHALOPOD  
ALLOMETRY  
EYE  
VISION  
ACUITY

**ABSTRACT.** – We report here how the sensitivity of the eye of the cuttlefish (*Sepia officinalis*) to light changes with the growth of the animal. Measurements of body length and eye diameter show that cuttlefish hatch with relatively large eyes but these then grow throughout the animal's lifetime at a slower rate than the body, resulting in an allometric scaling coefficient of less than one. Electroretinograms (ERG) evoked by the application of controlled flashes of light were obtained from different sized animals and demonstrated that ERG amplitude decreased with increasing animal size and this appears associated with a small decrease in retinal sensitivity. However, increasing the stimulus flash duration increased the sensitivity of the retina; this result is similar to the situation in vertebrates but not that in most other invertebrates. The cuttlefish retina was found to be 100 times more sensitive to flashes of blue light than yellow; however animals of 7 cm mantle length demonstrated an enhanced sensitivity to blue light, when compared to smaller or larger animals. The results are discussed in relation to differences in the lifestyles of the juvenile and adult animals, particularly the tendency for the young animals to live in bright, shallow waters, and the older animals to migrate to deeper, darker waters.

### INTRODUCTION

The cuttlefish, like most other cephalopods, depends heavily on vision for prey capture, predator avoidance and intra-specific communication (Hanlon & Messenger 1996, Muntz 1999). The performance of its sophisticated visual system is comparable with that of the main competitors, the fishes and marine mammals (Land 1981, 1990). The cuttlefish eye is a single-chamber, camera-type eye that is regarded as a text-book example of convergent evolution because of the strong similarities it bears to the vertebrate eye (Packard 1972). Nevertheless, there are morphological and biochemical differences between vertebrate and cephalopod visual systems and these relate to performance; for example, colour vision in cephalopods is believed to be absent, or extremely rare (e.g. Messenger 1981, Seidou *et al.* 1990), whereas polarised light vision is considered the norm for all coleoid cephalopod species so far examined (Shashar *et al.* 1996, Shashar & Hanlon 1997).

In most vertebrate species there is little change in the morphology of the retina and eye, or in the overall performance of the visual system after maturity; although in later life, age-related deterioration will occur. However, in some species, particularly in fish, the animal continues to grow beyond maturation and hence the eye and lens continue to

increase in size; retinal neurogenesis may also continue and thus, new photoreceptors and associated neurons may be added to the retina (Johns 1982). These changes affect the animal's visual capabilities such as acuity and sensitivity (Shand 1997) but the precise effects are difficult to predict because of the range of inter-related factors involved; for example, a larger eye may increase image magnification onto the retina, but reduce the light intensity unless the pupil size also increases sufficiently. Similarly, additional retinal photoreceptors may imply an improvement in acuity but the larger surface area of the retina may increase the spacing between photoreceptors and hence reduce their packing density and hence spatial acuity (Land 1981, Van der Mee 1994, Nilsson & Warrant 2001, Land & Nilsson 2002).

Cephalopods also continue to grow in size throughout life and it has been shown recently, using behavioural response measurements, that visual acuity is better in large cuttlefish compared to small ones (Groeger *et al.* 2005). The mechanisms underlying this change in visual performance are not yet clear and so in this study we examine the retinal performance of the cuttlefish eye over a range of animal sizes looking particularly for age/size-related changes in visual sensitivity, i.e. changes in the sensitivity of the retina to light and also changes in its spectral response sensitivity.

## MATERIALS AND METHODS

**Animals and tissue preparation:** Cuttlefish, *Sepia officinalis*, of both sexes were used in this study. Animals were caught in the Plymouth area by bottom trawling or cultured from eggs at the Marine Biological Association of the UK and were kept in a semi-recirculating seawater system at temperature of 12-15°C. All animals were fed daily and kept on a 12 h light/dark cycle.

For the morphological studies, the animal was anaesthetised in a 2% solution of ethanol in seawater and then killed by decapitation. Measurements were taken of mantle length (ML), i.e. the body length from caudal to rostral tip excluding the head, and eye diameter of the excised eyes, as measured in the horizontal plane. In order to produce the retinal slices for the electrophysiological recording experiments, animals were dark adapted in dim red light for 30 min, then anaesthetized as before, and decapitated under dim red light. The eyes were then excised, the lenses removed, the retina washed in oxygenated, chilled artificial seawater (ASW) and then cut into 250 µm thick slices. Still under dim red light, the slices were allowed to recover for 10 to 15 minutes in chilled ASW and then a slice was selected and placed in the recording chamber, where it was fully submerged and superfused with oxygenated ASW at a flow rate of 2-3 ml/min. The temperature in the recording chamber was maintained at 12°C. The artificial seawater (ASW) contained: 470mM NaCl, 10mM KCl, 50mM MgCl<sub>2</sub>, 10mM CaCl<sub>2</sub>, and 10mM HEPES, buffered at pH 7.8. Care was taken to cut the retinal slices in a dorso-ventral direction such that the slices were cut perpendicular to the horizontal fovea area present in these animals (Young 1963); however, the small size of the tissue, its fragility, and working in low light, meant this could not be always guaranteed.

**Electroretinogram:** The electroretinogram (ERG) is the extracellular recording of the electrical field potential change resulting from activity in the retinal photoreceptors. To record the ERG, a borosilicate glass electrode, filled with ASW and having 1-2 Mohms resistance, was inserted into the inner segment region of the retinal slice, near the basal membrane, and manipulated to maximise the recorded ERG. An indifferent silver/silver chloride reference electrode was directly placed in the recording chamber. Data acquisition was performed with a CED 1401 computer-controlled laboratory interface, using the Signal 2 software suite (Cambridge Electronic Design LTD). The recording set-up was in a Faraday cage to reduce external, electrical noise from the ERG recordings.

**Sensitivity of the retina:** Once the electrode was placed in the retinal tissue, the preparation was stimulated with a 10 msec flash of 95 µW/cm<sup>2</sup> of light derived from an LED with peak emission wavelength at 590nm (RadioSpares, UK). This stimulus was repeated once every thirty minutes to check that the response amplitude of the evoked ERG had plateaued to a stable level. A light intensity series protocol was then performed, beginning with the lowest light intensity, keeping the flash duration and interval constant. In order to compare retinal sensitivity from different sizes of animals, Autrum's (1981) definition of absolute sensitivity was employed but modified to be the reciprocal of the intensity that

gave a 0.4 mV amplitude ERG response (also following Tasaki *et al.* 1963). This level was used instead of Autrum's half maximum value because maximum response amplitudes were rarely observed using our range of stimuli.

**Statistical analysis:** When studying the effect of flash duration, the different flash stimuli were separated by 60 sec intervals and an Analysis of Variance (ANOVA) for repeated measures used for analysis. SPSS (version 11.0.1; SPSS Inc, USA) was used in the statistical tests. Homogeneity of variance was always checked, using Levene's test, before a parametric ANOVA was carried out on the data. To determine if the mantle length of the cuttlefish affected the shape of the ERG, statistical analysis was performed on a test flash (i.e. 10 msec of 95 µW/cm<sup>2</sup> light) given before a light intensity series was performed. For investigating the difference in the parameters of the ERG shape a one-way ANOVA was employed.

## RESULTS

### *Change in eye size with growth*

Cuttlefish hatch from the egg as fully formed miniature adults with total body lengths of about 1.4 cm, and mantle lengths of about 1 cm. The eyes at this stage are quite large, measuring about 2.5 mm in diameter, and are functional – for the animal must feed within a few days, i.e. must be able to catch a moving prey item (Wells 1958). As the animal grows, the eyes increase in size such that a large adult animal of 40 cm mantle length has an eye 40 mm in diameter. Plots of mantle length against eye diameter for a range of animals (Fig. 1), show that the eye growth pattern can be well fitted by a standard allometric growth func-

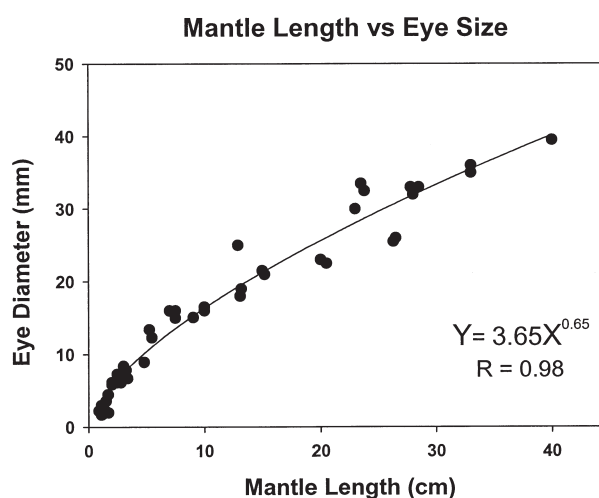


Fig. 1. – Plot of cuttlefish dorsal mantle length against the horizontal diameter of the eye showing the allometric growth relationship. The line of best fit is an exponential curve with equation as shown.

tion of the form  $y=ax^b$ , where “y”= eye diameter in mm, “x” = mantle length in cm, and “a” and “b” are constants. The regression line of best fit is good across the range, with an R value of 0.98 and parameters of “a” = 3.65 and “b”=0.65, indicating that the eye is relatively large at hatching and thereafter grows at a slower rate than the body.

### Electroretinogram

A typical electroretinogram (ERG) evoked by a flash of light onto the retina of an adult cuttlefish is illustrated in Fig. 2; this ERG can be characterised using five separate parameters: these are the response latency, duration, response amplitude, time to peak and finally the decay time constant. As has been found by others (Tasaki *et al.* 1963, Frank 1999), the amplitude of the ERG can vary between animals due to small changes in recording electrode placement and configuration. Although such variations are unavoidable, they were minimized by recording from the narrow inner segment of the retina. However, some of the variability here may also be due to small disparities in the fine morphologies of the retinal slices; for example, slices obtained from the more posterior part of the retina may contain photoreceptors with longer outer segments than those obtained from the central areas, due to the presence of the horizontal fovea (Young 1963); such morphological differences may influence the shape and size of the evoked ERG.

### Relationship between the mantle length and the sensitivity of the eye

In order to determine if the size of the cuttlefish influenced the absolute sensitivity of the retina, the isolated retinas were stimulated with flashes of different intensities and the recorded ERG's analysed;

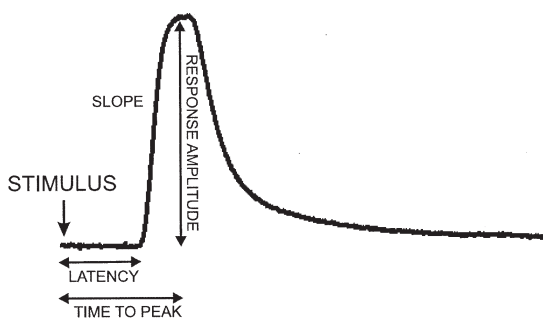


Fig. 2. – Representative electroretinogram (ERG) recorded from the eye in response to a single flash of light. Five separate parameters dealing with the shape of the response were measured and examined for any correlation with the animal's growth. The parameters were: response latency, duration, response amplitude, time to peak and the decay time constant.

this was done for five different sizes of animals (ML = 1, 2, 4, 12 & 22 cm) with 6 animals in each group (Fig. 3 top). An univariate ANOVA analysis of the data detected no statistical differences between the groups, although a regression analysis of the scatter plot produces a Pearson correlation coefficient of  $r = 0.8$ , which is just significant for  $p = 0.1$ .

To investigate further any differences in sensitivity during growth, an intensity-response ( $V/\log I$ ) plot was constructed for the different sizes of cuttlefish, where  $V$  is the amplitude of ERG evoked by a flash of light and  $I$  is the intensity of the stimulus flash. Such a plot for the different sizes of cuttlefish (Fig. 3 bottom) demonstrated

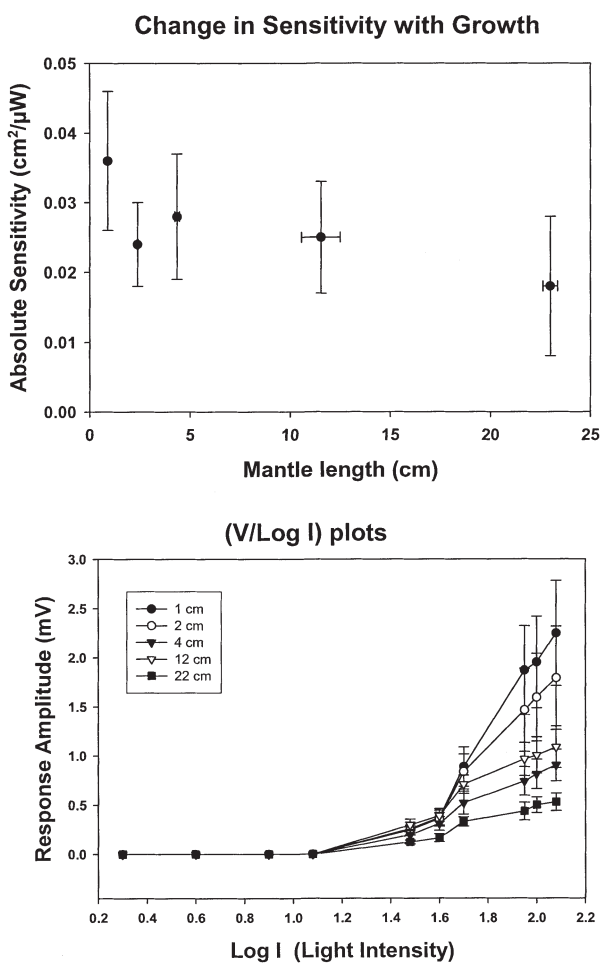


Fig. 3. – Top, Graph of cuttlefish mantle length against absolute sensitivity of the retina to light. Each point represents the mantle length values and absolute sensitivity values for 6 animals. The standard error bars show the variation in both sets of values. Pearson's correlation coefficient ( $r = 0.8$ ). Bottom, The  $V/\log I$  curves for animals of different mantle lengths. The interval between flashes (60 sec) and the flash duration (50 msec) remained constant while the intensity of the stimulus was increased. Five different sizes of animals were tested, with mantle lengths of 1, 2, 4, 12, & 22 cm, with five different animals in each group.

that the group of 1 cm mantle length animals had the largest ERG amplitudes, whereas the group of 22 cm mantle length animals had the smallest ERG amplitudes. The intermediate groups showed some degree of overlap in their ERG amplitudes. None of the plots show any indication of reaching a plateau demonstrating that, under our experimental protocols, the saturation intensity of these photoreceptors was not reached. Further analysis was achieved by fitting linear regressions to the mean response amplitude of each mantle length group to the five highest light intensities (Ziedins & Meyer-Rochow 1990). This showed that as mantle length (ML) increased, the slope of best fit line decreased – implying that smaller animals had a better contrast sensitivity than larger animals, for a steeper slope implies a greater threshold (Eguchi & Horikoshi 1984).

#### Relationship between growth and the ERG size and shape

To investigate the relationship between growth and the size and shape of the ERG, the parameters indicative of the ERG shape (see Fig. 2) were analysed for five animal size groups (i.e. 1, 2, 4, 12 and 22 cm). Each of the parameters was plotted against the increasing mantle lengths (ML) using

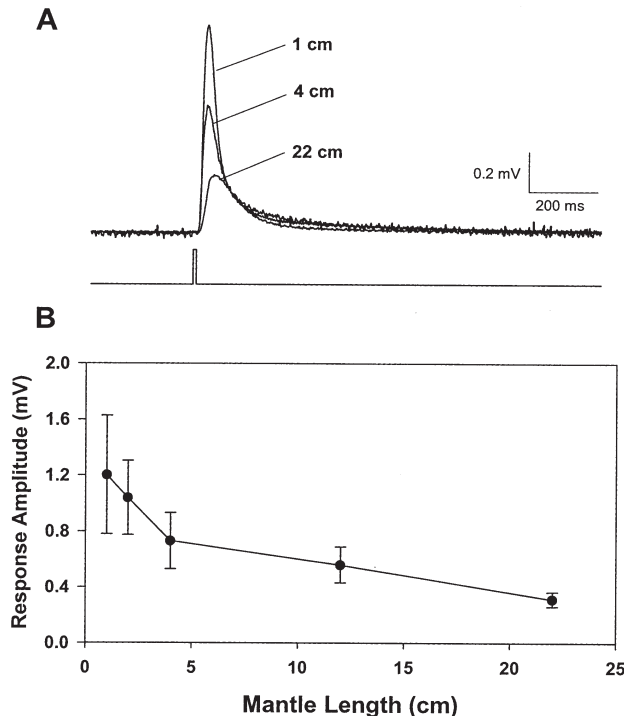


Fig. 4. – Relationship between ERG amplitude and animal size. A, Superimposed ERG responses from three different sized animals showing the responses to identical flashes of light. B, Graph showing the ERG response amplitudes to identical flash stimuli for five different sizes of cuttlefish (n=5 for each data point).

scatter plots to reveal any trends and the significance tested using a one-way ANOVA. The amplitude of the evoked ERG to a constant stimulus became progressively smaller for larger sized animals (Fig. 4A). The logarithm of response amplitude was the only one of the five ERG shape/size parameters that showed any statistically significant relationship with ML (Fig. 4B); none of the four other parameters showed any such relationship (data not shown).

#### The effect of stimulus wavelength on the sensitivity

The partial spectral sensitivities of the retinas of five medium sized animals (ML=6.9 ± 1.5 cm) were tested using light stimuli from yellow and blue Light Emitting Diodes (LEDs). The retina was found to be much more sensitive to blue light (absolute threshold = 1.33 ± 0.42 cm<sup>2</sup>/μW, for n=5) than yellow light (absolute threshold = 0.02 ± 0.002 cm<sup>2</sup>/μW, for n=5) and a paired *t*-test showed this to be significantly different, with *P* < 0.05. Thus, the cuttlefish retina is 100 times more sensitive to blue light than to yellow light. To examine this spectral sensitivity for a range of sizes of cuttlefish, three different sizes (MLs = 1, 7 and 22 cm) were further tested using the two LED's and their

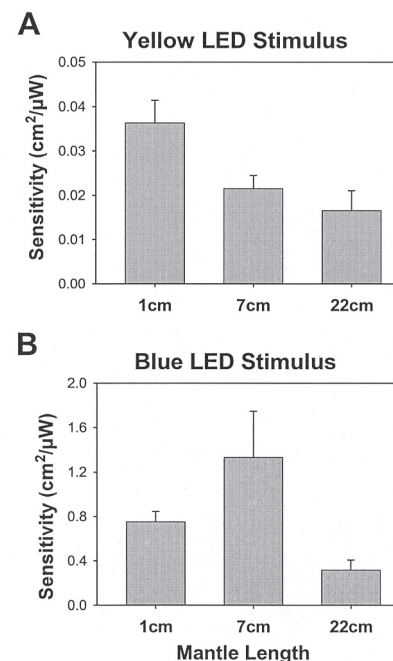


Fig. 5. – Histograms showing the absolute sensitivities of the retina to light flashes of yellow and blue light for different sized animals. A, Absolute sensitivities to flashes of yellow light for animals of 1, 7 and 22 cm mantle lengths. B, Absolute sensitivities to flashes of blue light for animals of 1, 7 and 22 cm mantle lengths. Error bars = ± standard error with n = 5.

absolute sensitivities measured (Fig. 5). For the yellow LED stimulus, a trend of decreasing sensitivity with increasing size of the animal (Fig. 5A) was found. However, when using the blue LED, the trend was unexpected, in that the group of middle-sized animals (ML=7 cm) showed an increased sensitivity (Fig. 5B) compared to the larger and smaller animals.

### ***The effect of varying flash duration on the sensitivity***

The absolute sensitivity of the retina increased significantly ( $p = 0.05$ ) as the duration of the stimulus flash was increased. Thus, the absolute sensitivity changed from  $0.022 \pm 0.008 \text{ cm}^2/\mu\text{W}$  for a 10ms flash of light, to  $0.028 \pm 0.012 \text{ cm}^2/\mu\text{W}$  for a 50 ms flash, to  $0.034 \pm 0.010 \text{ cm}^2/\mu\text{W}$  for a 500 ms flash; these were obtained from a 4 cm animal and are all means  $\pm$  standard deviations for  $n = 5$ .

## **DISCUSSION**

We report here how the light sensitivity of the cuttlefish eye changes with the growth of the animal and how the retina responds to changes in stimulus wavelength, flash duration and intensity.

### **The relative growth of the eyes in cuttlefish**

The data presented here show that the cuttlefish eye is relatively large at hatching compared to the body, about 25% of mantle length, but then grows at a lower rate than the mantle or body such that it is only around 10% of mantle length for a large, mature male. Allometric scaling coefficients of less than one have also been reported recently for eye growth in small squid (Packard 1969, Zeidberg 2004) as well as for many vertebrates, although an isometric relationship is found in some cyprinid fish (Fernald 1990) where vision plays an exceptionally important role in life style. Clearly, the lack of any parental care at hatching, and the necessity to avoid predators and catch the first meal within a very short time (Wells 1958), places a strong evolutionary pressure on having functional vision as soon as possible, if not immediately at hatching. This is different from the situation in many mammals where vision at birth is quite poor but then improves over a period of some months or years till maturity (e.g. humans: Atkinson 1984)

### **Mantle length and retinal sensitivity**

The absolute threshold of the cuttlefish retina to the light stimuli used in these experiments was around  $0.1 \mu\text{W}/\text{cm}^2$ ; this compares well with sensitivity levels measured for the photoreceptors of

other marine molluscs (Gillary 1974, Cobb & Williamson 1998), but is poorer than the value of  $2 \times 10^{-4} \mu\text{W}/\text{cm}^2$  obtained for the Antarctic fish *Pagothenia borchgrevinki* (Morita *et al.* 1997) – although differences in the experiment protocols may account for some of this.

The absolute sensitivity of the cuttlefish retina did not appear to change significantly with increasing animal size, although the scatter plot (Fig. 2) gave some indication of a slight decrease in sensitivity with age. Support for this latter finding was also seen in the “V/log I” plots (Fig. 3), where the steeper gradients of the plots for the small animals indicate greater contrast sensitivity, and also the reduction in sensitivity to yellow light stimuli with increasing body size (Fig. 5). It might have been expected that larger animals would have a greater absolute sensitivity to light for they have longer photoreceptors (Williamson unpubl observ) and hence a greater probability of photon capture (Land 1981, Van der Meer 1994, Nilsson & Warrant 2001). However, longer photoreceptors also have a greater level of inherent “dark noise” and this will act to reduce the sensitivity of the system (Laughlin & Lillywhite 1982, Baylor *et al.* 1980). In other animals, such as the goldfish, *Carassius auratus*, it is the increase in the density of rods in their retina which seems to be the key factor resulting in an increase in the visual sensitivity with the size of the animals (Powers *et al.* 1988).

It should be noted that the sensitivity data reported here need not necessarily correlate with the overall behavioural sensitivity of the animal, as has been demonstrated for the cuttlefish by Groeger *et al.* (2005), for additional mechanisms, including extra-retinal summing of photoreceptor inputs within the central nervous system, could be employed to improve the overall sensitivity at the expense of acuity.

### *Mantle length and the shape and size of the ERG*

Of the five ERG shape parameters investigated here, only the amplitude changed with cuttlefish size. This is probably related to the increased length of the receptor cells with increasing eye size, for this is likely to result in a change in the stimulus evoked, photo-current density across the tissue. Recordings from pre-hatchling *Sepiella* (Yamamoto *et al.* 1985) showed that the ERG first develops around developmental stage 34 and then increases in amplitude until near hatching at development stage 40. However, these recordings were from the whole eye and it is not clear if this ERG derives from the outer or inner retinal segments or a combination. Similar change in the amplitude of the ERG with growth to those reported here for *Sepia* have also been observed in humans (Westall *et al.* 1999) and other invertebrates, such as insects, which show a dramatic change in the ERG shape with growth and pupation (Autrum 1958).

### Flash duration and sensitivity

The absolute sensitivity of *Sepia officinalis* to light was found to be influenced by the stimulus flash duration. Thus, the slope of the V/log I curve increased with increasing stimulus duration (Fig. 3 bottom) as has also been found for vertebrate preparations (Kleinschmidt & Dowling 1975). However, other invertebrates do not appear to show this change (Matic & Laughlin 1981), implying that cephalopods are in this respect, more similar to vertebrates. As with the overall sensitivity response, this has been explained by the differences in the timings at which the peak response is reached, and when the feedback to termination of the transduction cascade is initiated. If the time to peak response is fast in relation to the termination of the cascade, then the pulse duration should not affect the V/log I curve (Matic & Laughlin 1981). This is probably the case in most invertebrates. However, if the peak amplitude is not reached before the shut down mechanism is begun, then the pulse duration will have an effect on the V/log I curve, as is found in vertebrate species.

### Spectral sensitivity of the retina

The cuttlefish retina was found here to be over 100 times more sensitive to blue light stimuli than similar stimuli of yellow light. This difference in physiological sensitivity can be related to the differential retinal absorption of the two wavelengths of light for it can be predicted, from the known absorption spectrum of cephalopod rhodopsin (Brown & Brown 1958), that light emitted by the blue LED should be better absorbed by the retina than light from the yellow LED, as the latter only partially overlaps the rhodopsin absorption spectrum whereas the former largely overlaps (data not shown). However, the improved sensitivity of the 7 cm mantle length animals to the blue light stimuli over both the smaller and larger animals was unexpected; this could, of course, represent a statistical exception, perhaps resulting from the small sample size, but may otherwise indicate a transient change in wavelength sensitivity with growth. The latter would be a novel finding for cephalopods but it would be useful to have this supported by microspectrometric measurements across the whole retina to test for variations in photoreceptor pigment absorption characteristics. A change in retinal spectral sensitivity towards the blue would be appropriate for animals moving into deeper water for there is better penetration of blue light at depth (Tett 1990).

### Further considerations on visual performance

These results indicate that the eyes of small, juvenile cuttlefish have a greater light and contrast sensitivity than those of adults. In other animals,

high spatial resolution and light sensitivity are often associated with comparatively brightly lit environments (Srinivasan & Bernard 1975) but these capabilities have a significant metabolic cost to the animal for both production and maintenance (Laughlin & Weckström 1993, Laughlin 1996). Cuttlefish eggs are usually laid and hatch in shallow waters where there is a high light environment and it is likely that as the animals increase in size and move into deeper and darker waters, especially during the winter months when seasonal light levels are reduced (Boletzky 1983), the cost of maintaining these visual capabilities increases.

Although the cuttlefish eye increases in size with growth and therefore the pupil widens and admits relatively more light, this will be countered by the increased magnification of the image onto the retina, thus reducing the amount of light falling per unit area of retina surface. There are a range of other mechanisms that could act to increase visual performance, for example: (1) lengthen the photoreceptors to improve the probability of photon capture, (2) increase the cross-sectional area of the photoreceptors to increase photon capture, (3) maintain the packing density of the receptors, despite the increase in retinal surface area, (4) sum the inputs from multiple receptors, either in the periphery or centrally, and/or (5) reduce the frequency response of the receptors to permit greater temporal summing of the input. Although there is limited evidence that (1) and (3) but not (2) occur in cephalopods (Williamson, unpublished observations, Packard 1969, Young 1963), and we now have data on the changes in retinal sensitivity with growth, these are not yet sufficient to account for the behavioural observation that cuttlefish spatial acuity increases with growth (Groeger *et al.* 2005) and hence further investigation is needed.

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