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The pupillary response of cephalopods

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Summary

This paper provides the first detailed description of the time courses of light-evoked pupillary constriction for two species of cephalopods, *Sepia officinalis* (a cuttlefish) and *Eledone cirrhosa* (an octopus). The responses are much faster than hitherto reported, full contraction in *Sepia* taking less than 1 s, indicating it is among the most rapid pupillary responses in the animal kingdom. We also describe the dependence of the degree of pupil constriction on the level of ambient illumination and show considerable variability between animals. Furthermore,

both *Sepia* and *Eledone* lack a consensual light-evoked pupil response. Pupil dilation following darkness in *Sepia* is shown to be very variable, often occurring within a second but at other times taking considerably longer. This may be the result of extensive light-independent variations in pupil diameter in low levels of illumination.

Key words; pupil, eye, cephalopod, squid, octopus, *Eledone cirrhosa*, cuttlefish, *Sepia officinalis*.

Introduction

Invertebrates display a plethora of eye designs, most of which are very different from those of vertebrates (Land, 1981; Land and Nilsson, 2002). However, although the eyes of cephalopod molluscs and fish are different in some important respects, they share enough similarities, such as the possession of a single near spherical lens with a graded refractive index, the ability to accommodate and similar eye movements, that they represent a good example of convergent evolution (Packard, 1972). One of the aspects in which the eyes of teleost fish and cephalopods do differ, however, is in the mobility of their pupils. While the majority of elasmobranchs (Kuchnow, 1971; Gilbert et al., 1981) and cephalopods (Hurley et al., 1978; Muntz, 1977) have pupils that respond to changes in illumination, teleost fish, with a few exceptions (Douglas et al., 1998, 2002), have irises that remain fixed.

Although it has been known for over 100 years that the pupils of most cephalopods are able to change size on illumination (Beer, 1897; Bateson, 1890; Magnus, 1902; Weel and Thore, 1936), the detailed dynamics of the response are virtually undescribed. Perhaps surprisingly, most is known about the pupil of the 'primitive' pinhole eye of *Nautilus pompilius*, whose area decreases on illumination from 4 mm² to 0.2 mm² over a period of 90 s (Hurley et al., 1978). The only quantitative investigation of the pupil response in coleoid cephalopods examined the response of *Sepia officinalis* and suggested pupil constriction occurred in around 5 s and dilation

in about 30 s (Muntz, 1977). Although faster than *Nautilus*, this is still considerably slower than many other animals, and the speed of the pupil response in coleoid cephalopods is therefore generally quoted as being much less rapid than that of, for example, mammals (e.g. Hurley et al., 1978; Messenger, 1981). However, the temporal resolution of this earlier work was poor as digital video technology was not available. Here we provide the first detailed description of the timecourse of light-evoked pupillary constriction for two species of coleoid cephalopod, *Sepia officinalis* (a cuttlefish) and *Eledone cirrhosa* (an octopus), and show that the response, especially in *Sepia officinalis*, is not only much faster than hitherto reported but is in fact among the fastest in the animal kingdom.

We also describe the dependence of the degree of pupillary constriction in both *Sepia* and *Eledone* on the level of irradiance, and show considerable individual variation in sensitivity. Pupil dilation following the cessation of a light stimulus is also shown to be very variable. Such variation may be the result of extensive light-independent changes in pupil diameter within an individual over short periods of time, which are especially apparent in lower levels of illumination.

Simple observation suggests that the two pupils of individual coleoid cephalopods respond independently to light (Magnus, 1902; Weel and Thore, 1936). This lack of a consensual response in cephalopods is described quantitatively here.

Materials and methods

Animals were caught by shallow water trawl off the coast of southwest England and maintained in recirculating seawater tanks at the Marine Biological Association of the UK. They were exposed to the normal daily light cycle and kept at a water temperature of 12–15°C.

Direct pupil response to illumination

Five adult *Sepia officinalis* L. and three adult *Eledone cirrhosa* Lamarck were removed from their home tanks during the light phase of their light/dark cycle and placed in darkness in a jar with a perforated lid within a shallow aquarium. Their pupils were filmed under infrared illumination for 11–50 min using a camera positioned perpendicular to the plane of the eye. Animals were subjected to a series of diffuse overhead white light exposures from a Kodak slide projector and sufficient time was allowed between exposures to allow redilation of the pupil. The light intensity, which was adjusted by neutral density filters, was measured at the end of each experiment where the animal's eye had been. As each animal was in a slightly different position relative to the light source, the precise intensities that each animal was exposed to varied. Pupil area was determined by digitising individual video frames and analysing with Scion Image software. To compensate for changes in image size due to refocusing of the camera between light exposures, pupil area is expressed as a percentage of the dark-adapted pupil area immediately prior to a given light stimulus.

Consensual pupil response

Both eyes of a single adult *Sepia officinalis* and an adult *Eledone cirrhosa* were filmed separately in darkness under infrared illumination and following a series of white light exposures ($10 \mu\text{W cm}^{-2}$) from a 1500 fibre optic light source (Schott; Mainz, Germany), to the right eye only. The pupil area of each eye was compared before and 2–5 s after stimulation of the right eye.

Results

Direct pupil response

The dark-adapted pupils of *Eledone cirrhosa* and *Sepia officinalis* were close to circular. On exposure to bright light the pupil of *Eledone* became a horizontal slit with two small pinholes at either end, while that of *Sepia* assumed a W shape. In response to the highest intensities, the pupils of both species constricted to less than 3% of their dark-adapted areas. The precise extent of pupil constriction was difficult to determine as the final area was often too small to measure accurately, although at times the pupil, especially in *Sepia*, seemed almost completely closed.

In *Eledone*, full constriction took just over 1 s, while the response of *Sepia* was faster (Fig. 1). Since pupil closure was initially very rapid, before

approaching maximal constriction more slowly, a more accurate estimate of the speed of contraction is given by the time taken to attain half the final pupil area (t_{50} ; Douglas et al., 1998). In *Eledone* this occurred on average after 0.65 s, while the equivalent time in *Sepia* was only 0.32 s. The degree of constriction was related to the intensity of the light in both species, although different animals varied greatly in their sensitivity (Fig. 2).

Although the pupil always responded to illumination, it also showed light-independent movements. This was especially apparent for *Sepia* in low levels of illumination, when pupil diameter varied extensively despite no change in the ambient illumination. Possibly as a consequence of this, the rate of pupil dilation following cessation of the light stimulus was also very variable. Usually it was immediate, the pupil opening within 1 s in *Sepia*, while at other times it was considerably delayed (Fig. 3).

Absence of a consensual response

When the right eye alone was illuminated there was never any contraction of the left pupil in either *Eledone* or *Sepia* (Fig. 4). Thus, these coleoid cephalopods do not possess a consensual pupil response.

Discussion

Direct light-induced pupillary constriction

Previous quantitative studies of the cephalopod pupil response to light suggest that it is relatively slow in comparison to that of many other animals (Hurley et al., 1978; Muntz, 1977). However, here we show that the time required for pupil closure in coleoid cephalopods, especially *Sepia officinalis*, is in actual fact much less than in most other animals. For example, the pupil of *Porichthys notatus*, the teleost fish with the fastest iris response measured to date, takes around 0.75 s to reach half its final area in response to illumination under comparable conditions, a value similar to that of humans

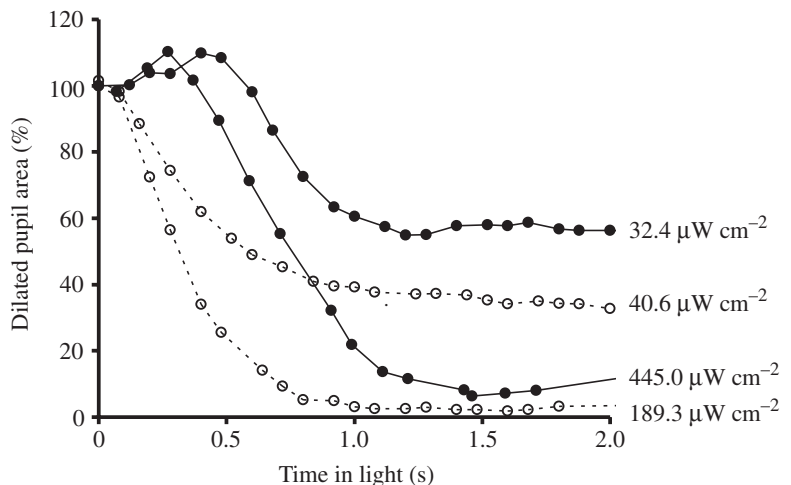


Fig. 1. Relative pupil area of an eye in *Eledone cirrhosa* (solid lines and symbols) and *Sepia officinalis* (broken lines and open symbols), following exposure to different intensities of white light.

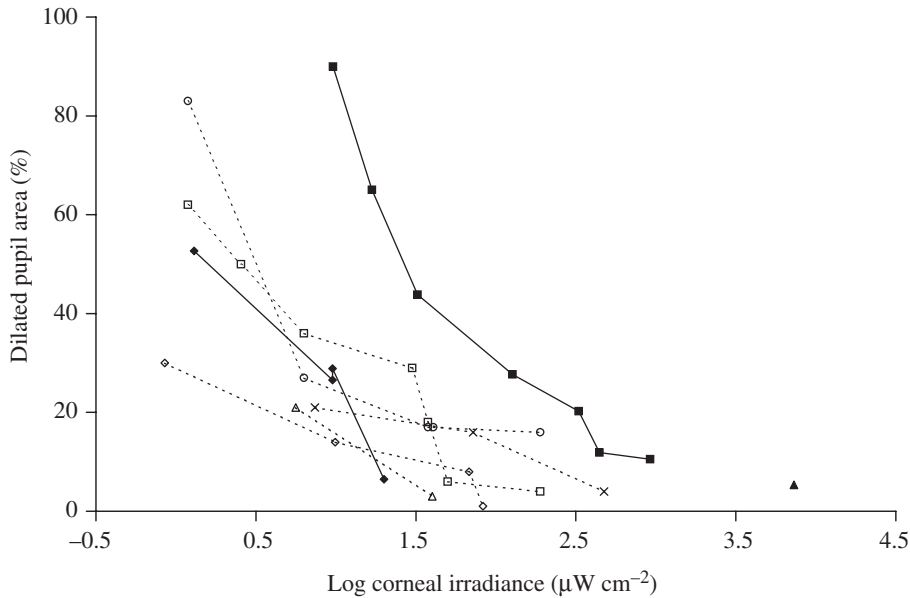


Fig. 2. Relative pupil area of individual eyes in three *Eledone cirrhosa* (solid lines and symbols) and five *Sepia officinalis* (broken lines and open symbols) exposed to different intensities of white light.

(Douglas et al., 1998). The pupils of *Sepia*, on the other hand, take only 0.32 s to attain half maximal constriction. The only group of animals with a similarly rapid pupil response are birds (Barbur et al., 2002).

Pupil dilation

Previous work (Muntz, 1977) suggested the pupil of *Sepia officinalis* takes around 30 s to dilate following a decrease in illumination. Here we show that full dilation can in fact be achieved within 1 s (Fig. 3). However, this can vary significantly, most probably due to the confounding effects of non-light-related factors on pupil size (see below), possibly

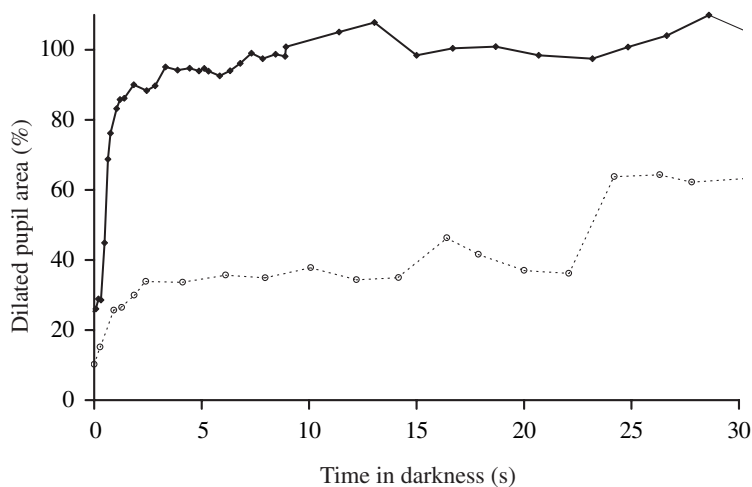


Fig. 3. Relative pupil area of individual eyes from two *Sepia officinalis* on cessation of exposure to white light of $40.6 \mu\text{W cm}^{-2}$ (solid line) and $7.4 \mu\text{W cm}^{-2}$ (dotted line), showing the variable off-response of this species.

explaining the large difference between our work and that of Muntz (1977).

In most vertebrates pupil constriction is caused by a sphincter muscle encircling the pupillary margin, while dilation is caused by radial fibres forming a dilator muscle. Although it is probable that cephalopods also possess both of these muscles (Magnus, 1902), the presence of a dilator has yet to be clearly demonstrated anatomically (Froesch, 1973). The fast rate of dilation noted here, however, is strongly suggestive of the presence of such a muscle.

Lack of a consensual pupillary light response in coleoid cephalopods

In many animals illumination of one eye causes constriction in the other. Mammals generally have such a consensual pupil response (Lowenfeld, 1993), as do some amphibia (von Campenhausen, 1963), teleost fish (Douglas et al., 1998) and most rays (von Studnitz, 1933). However, in other teleosts (Nilsson, 1980) and amphibia (Henning et al., 1991), as well as in most sharks (Kuchnow, 1971), reptiles (Werner, 1972) and birds (Schaeffel and Wagner, 1992), the pupils act independently. Among cephalopods the situation appears equally varied. While the pin-hole eyes of *Nautilus* display a consensual response (Hurley et al., 1978), here (Fig. 4) we confirm previous observations (Beer, 1897; Magnus, 1902; Weel and Thore, 1936; Hanlon and Messenger, 1988) suggesting that the pupils of coleoid cephalopods respond independently to light.

Cephalopods have laterally placed eyes and thus see much of their world monocularly. Consequently, their two eyes will often see quite different things. Interestingly, *Octopus vulgaris* often uses only one eye when viewing objects (Muntz, 1963) and, like many vertebrates, especially birds, display a degree of lateral asymmetry in eye use (Byrne et al., 2002). If the pupil responds not only to the overall level of illumination but also to other, more specific, stimuli, as will be suggested below, it seems reasonable that the pupils of the two eyes should behave independently.

The function of light-induced pupil constriction in cephalopods

The most obvious function of changes in pupil size is to regulate the light flux incident on the retina. However, even a pupil constricted to 1% of its dilated area, only decreases retinal illuminance by 2 log units, which is significantly less than the total range of ambient illumination that a shallow living cephalopod will experience throughout a day, indicating that, as in

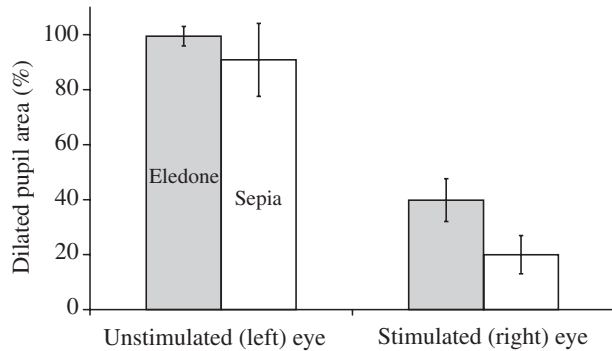


Fig. 4. Relative pupil area for both eyes of a single *Eledone cirrhosa* and one *Sepia officinalis*, following stimulation of the right eye alone with $10 \mu\text{W cm}^{-2}$ white light. Data are averages of 6 and 7 responses for the octopus and cuttlefish, respectively. Error bars show 2 standard deviations.

other species, additional mechanisms of light adaptation are important.

Pupillary constriction will also enhance image quality. Light traversing most lenses at different points is focussed at varying distances behind it, resulting in a degraded image. Constricting the pupil will restrict the passage of light to a smaller portion of the lens, thus decreasing the amount of such longitudinal spherical aberration. In teleost fish, most of which have a fixed pupil, spherical aberration is minimised by a refractive index gradient within the lens (Sivak, 1990). If the lenses of cephalopods have significantly more spherical aberration than those of fish, it may offer an explanation for why the former have a variable pupil and the latter generally do not (Sivak, 1982, 1991). Although some studies do suggest that the lenses of cephalopods may suffer from more spherical aberration than those of fish (Sivak, 1982, 1991; Sivak et al., 1994), others indicate this is not always the case (Jagger and Sands, 1999).

We have previously noted that among teleosts, pupil mobility is largely restricted to species that attempt to blend in with the substrate (Douglas et al., 1998, 2002). In such animals a large circular dark pupil would be very visible, and a contractile iris is most likely part of the animal's camouflage mechanisms. Pupillary constriction in cephalopods, many of whom have well developed camouflage strategies, may, at least in part, serve a similar function (Hanlon and Messenger, 1988).

Light-independent pupillary movements

Although the degree of pupil constriction is related to the intensity of the light in both *Sepia* and *Eledone*, different animals vary greatly in their sensitivity (Fig. 2). Several previous studies (Beer, 1897; Magnus, 1902; Weel and Thore, 1936) have noted that different animals within the same tank, and therefore exposed to very similar light levels, can have pupils constricted to varying degrees. Thus, factors other than the overall illumination clearly influence pupil size. Not surprisingly, therefore, we often observed extensive pupil movements, especially in low light levels, despite the lack of any change in light level.

In several species the pupil is known to reflect the 'emotions' of an individual (Lowenfield, 1993). In humans, for example, the pupil often dilates when confronted by an attractive member of the opposite sex. Similarly, chickens give a much larger response to the presentation of a red stimulus (possibly indicating blood) than they do to a simple change in light level (Barbur et al., 2002). The pupil of cephalopods also dilates when they are 'aroused' during fighting, mating or viewing food (Beer, 1897; Bateson, 1890; Packard and Sanders, 1971; Muntz, 1977; Wells, 1966, 1978; Hurley et al., 1978; Messenger, 1981).

A dilated pupil in relatively bright light may serve a number of functions. It could, for example, be an intraspecific signal during courtship displays (Wells, 1966; Packard, 1972). It might also be one of a series of deimatic displays that help 'create the illusion of larger size' when facing a potential predator (Wells, 1966; Hanlon and Messenger, 1988, 1996; Messenger, 2001). A dilated pupil may also aid in the judgement of distances, something cephalopods are able to do with accuracy (Wells, 1966; Muntz and Gwyther, 1988).

Many animals with laterally placed eyes use monocular cues, such as the accommodative state of their eye, to determine their separation from an object (Collett and Harkness, 1982). However eyes with a single small aperture have a large depth of field, minimising the need for accommodation. Consequently animals with constricted pupils cannot use the refractive state of the eye as a cue to distance. Not surprisingly therefore, cephalopods, like chameleons (a species known to use accommodation as cue to distance; Harkness, 1977) but unlike most animals, maintain a wide pupil when viewing close objects (Wells, 1966), making accommodation a more useful cue to distance.

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