Form vision in the insect dorsal ocelli: An anatomical and optical analysis of the Locust Ocelli

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Abstract

The dorsal ocelli are commonly considered to be incapable of form vision, primarily due to underfocused dioptrics. We investigate the extent to which this is true of the ocelli of the locust *Locusta migratoria*. Locust ocelli contain thick lenses with a pronounced concavity on the inner surface, and a deep clear zone separating retina and lens. In agreement with previous research, locust ocellar lenses were found to be decidedly underfocused with respect to the retina. Nevertheless, the image formed at the level of the retina contains substantial information that may be extractable by individual photoreceptors. Contrary to the classical view it is concluded that some capacity for resolution is present in the locust ocelli.
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1. Introduction

The dorsal ocelli of adult insects are a set of simple lens eyes, present on the heads of many insects in parallel with the compound eyes. They consist of only a single, large aperture lens, followed by several hundreds of photoreceptors which converge onto a few tens of interneurons (Rev. Goodman, 1981). Ocellar interneurons project to target neuropils either directly, or through a small number of intervening synapses (Guy, Goodman, & Mobbs, 1979; Mizunami, 1994a; Reichert & Rowell, 1985; Strausfeld, 1976).

Despite their apparent simplicity, the function of the ocelli has remained elusive. Early studies were frustrated in their attempts to find clearly ocellar driven behavioural responses. Compounded by wide diversity in ocellar number

and morphology, this lead to the development of numerous and varied proposals of ocellar function (Cornwell, 1955; Goodman, 1965; Kastberger & Schuhmann, 1993; Lazzari, Reisman, & Insausti, 1998; Parry, 1947; Schricker, 1965; Schuppe & Hengstenberg, 1993; von Hess, 1920).

One morphological feature that has been consistently observed in a wide range of species is a lack of optical resolving power; ocellar lenses typically form focal planes well beyond the proximal limit of the retina (Cornwell, 1955; Homann, 1924; Parry, 1947; Schuppe & Hengstenberg, 1993; Warrant, Wallén, & Wcislo, 2006; Wilson, 1978). Poor spatial resolution is compounded by high convergence ratios from retinula cells to second-order neurons, which is presumed to preclude the possibility of spatial information processing by higher order neurons.

Based on these observations, Wilson (1978) proposed what is now widely considered to be the major function of the ocelli in flying insects. He suggested that the ocelli monitor global changes in illumination for the purpose of maintaining a stable attitude during flight. Flying insects typically have three ocelli, which are located on the apex

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of the head, and have fields of view that coincide with the position of the horizon when in level flight. The lateral ocelli are directed to the left and right of the head, respectively, while the median ocellus is directed straight ahead. During flight, differences in perceived illumination levels from each of the three ocelli encode information that can be used to maintain a level attitude about the pitch and roll axes. A roll to the left, for example, results in a darkening of the left lateral ocellus, and a brightening of the right lateral ocellus, while a pitch upwards results in a brightening of only the median ocellus. As each ocellus can essentially be considered as a single optical sensor rather than consisting of a number of individual pixels, this concept has been referred to as the single sensor hypothesis (Stange, Stowe, Chahl, & Massaro, 2002) and this convention is also retained here.

The attraction of the single sensor hypothesis lies in its simplicity and apparent applicability to several insect types. It is supported by several strands of evidence. First, the ocelli tend to be especially prominent in vigorously flying insects, and fields of view centred close to the equator result in the optimal detection of deviations about the pitch and roll axes (Neumann & Bülthoff, 2002). Second, ocellar photoreceptors and interneurons are predominantly sensitive to UV light (Chappell & DeVoe, 1975; Mobbs, Guy, Goodman, & Chappell, 1981; Kirschfeld & Lutz, 1977; Hu, Reichert, & Stark, 1978; Wilson, 1978), a wavelength range at which contrast between the sky and ground is very strong. Third, one of the two classes of ocellar second-order neurons have particularly large axonal diameters (L-neurons). In dragonflies, for example, the axonal diameter of L-neurons may approach or exceed 30 μm (Berry, Stange, Olberg, & van Kleef, 2006; Chappell, Goodman, & Kirkham, 1978; Patterson & Chappell, 1980). This suggests that these neurons are especially suitable for the conveyance of urgent information, such as would be expected from a system involved in flight control. Fourth, the relationship between ocellar interneurons and flight motor neurons is well established. Structural layering is not present in the ocelli, and the number of synapses between sensory input and motor output is small (Guy et al., 1979; Mizunami, 1994a; Reichert & Rowell, 1985; Strausfeld, 1976). In locusts, ocellar mediated signals may reach the thoracic ganglia in just 12 ms, which is less than half the latency of the fastest known compound eye driven unit (Reichert & Rowell, 1985). Lastly, reports of ocellar mediated behavioural responses soon followed the development of the single sensor concept. In tethered flying dragonflies, stimulating the ocelli with light results in dorsal light responses of the head (Stange & Howard, 1979; Stange, 1981), and Taylor (1981a) found similar head motions when rotating an artificial horizon around tethered locusts with the compound eyes ablated.

However, a growing body of evidence suggests that the single sensor hypothesis does not apply to a number of insects, but rather that some degree of spatial resolution is an integral part of the function of these eyes. An example is the dragonfly median ocellus, which has been shown to be capable of substantial spatial resolving power based on morphological, dioptric and eyeshine observations (Stange et al., 2002), as well as intracellular recordings of its photoreceptors (van Kleef, James, & Stange, 2005) and second-order neurons (Berry et al., 2006). An additional example is the ocelli of diurnal and nocturnal paper wasps, the lenses of which have recently been shown to form foci close to the proximal limits of the retinae (Warrant et al., 2006).

Additionally, it is now evident that even ocelli with highly underfocused lenses may still be capable of form vision. In the case of the blowfly *Calliphora erythrocephala*, Schuppe and Hengstenberg (1993) determined the spatial cut-off frequency of the ocellar lens at various locations and found that although the lens was decidedly underfocused, a poor quality astigmatic image was formed at the location of the retina. Objects of spatial wavelengths 56° or greater in the vertical plane, and 135° or greater in the horizontal plane were resolved by the lens at this location.

Given that the single sensor hypothesis was largely established from work performed on the locust ocelli, it is of interest to review the extent to which the morphology and dioptrics of these eyes limit their behavioural roles to single sensor type functions. In the present paper ocellar morphology is determined by traditional sectioning techniques, as well as three-dimensional reconstructions. The optical properties of the lenses are determined by direct observation using the hanging-drop technique (Homann, 1924). Image quality is assessed by determination of modulation transfer functions (MTFs), as has been used previously on biological lenses, for example, in humans (Campbell & Green, 1965), in fish (Jagger, 1996), and in skipper butterflies and agaristid moths (Land, 1984). MTFs are determined over a range of distances corresponding to locations normally covered by the ocellar retina. Possible functional roles for the locust ocelli are considered.

2. Method

2.1. Experimental animals

All experiments were performed on the locust *Locusta migratoria* (Acrididae). *Locusta* were either obtained from a supplier (Blades Biological, United Kingdom), in which case they were used for experimentation within two weeks of arrival, or obtained from a laboratory breeding colony.

2.2. Histology

Fresh heads were partially dissected in fixative (3.7% formaldehyde, 2.5% glutaraldehyde in 0.01 M phosphate buffered saline) by removing the mouthparts, frons and cuticle from the back of the head. Samples were then postfixed in 1% phosphate buffered osmium tetroxide, dehydrated through a graded alcohol series, and finally embedded in a hard Araldite 502 resin. Microwave radiation (Pelco BioWave 34700-230) was often used to greatly reduce processing times during the following steps; fixation: 1.8 min on, 1.8 min off, 1.8 min on at 150 W; osmication: 3.6 min on, 3.6 min off, 3.6 min on at 80 W; dehydration: 70 s at 250 W; infiltration: 5.4 min at 250 W. Semi-thin sections of 1 μm thickness were cut on a Reic-