2.9 The Resolution of Lens and Compound Eyes

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2.9.1 Introduction

Two distinctly different types of eyes have been highly developed in evolution: lens eyes (= camera eyes) in vertebrates, some molluscs and arachnids and compound eyes in arthropods. Based on his comparative studies of the optical properties of compound and lens eyes, Exner (1891) concluded that both types of eyes are optimally adapted for different functions: lens eyes with their high angular resolution seem to more useful for pattern recognition, whereas the compound eyes, with their poor resolution, are thought to be specialized for movement perception. This view is still generally accepted (see the textbooks of Scheer, 1969, Kaestner, 1972). Furthermore, the small facet diameters of the ommatidia in compound eyes seem to cause a poor absolute sensitivity (Exner, 1891; Barlow, 1952; Kirschfeld, 1966; Prosser and Brown, 1969; Snyder et al., 1973). Some insects are said, however, to have higher temporal resolution than humans (Autrum, 1948).

Irrespective of the mentioned disadvantages of compound eyes - poor resolution and sensitivity - many more individual animals as well as animal species are equipped with compound rather than with lens eyes, since even the number of known insect species (~ 10^6) is at least 10 times larger than that of vertebrates (Weber and Weidner, 1974). Though primitive lens eyes (the ocelli) are also common to many insects, these must not be as useful as compound eyes since evolution has clearly favored the latter.

If it is true that both types of eyes are adaptations for different functions, we expect that the world as seen through a compound eye looks different from the world observed by a lens eye. Information on the optical environment available from both types of eyes should be different at the receptor level.

We will consider in this chapter if this is really the case. In order to illustrate the situation we will answer the questions of what would a compound eye look like if it had the optical performance of a human eye, and how a lens eye with the performance of the compound eye of a fly would need to be constructed.

2.9.2 Subjective Resolution

There is no doubt that the absolute resolution of compound eyes is far inferior to that of lens eyes. The angular distance between stripes of a striped pattern that is just able to induce an optomotor turning response must be larger than approximately 2° in the fly (Eckert, 1973), whereas under optimal conditions the "minimum separabile" in man is $0.6\text{-}1.8 \times 10^{-2}$ degrees (Buddenbrock, 1952).

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These variations in performance do not necessarily reflect differences between the various principles according to which lens and compound eyes are realized. It might be due rather to the fact that the eye of such a small animal as a fly is just much smaller than a human eye. It may be more germane in terms of function to compare acuity relative to eye size or, biologically relevant as well, to animal size instead of absolute resolution, since, as we will see below, physical dimensions of an animal's eye place severe restraints upon its performance.

Angular resolution as determined by physiological methods apparently is dependent on the quality of the dioptrics of an eye ("optical resolution") as well as on the angular separation $\Delta\varphi$ of the receptors ("anatomical resolution"). The resolution of the whole visual system has been determined with physiological methods. Test objects have been striped patterns or two point sources, the critical distances of which have been determined. These numbers, here called "physiologically resolution ε", have been measured for many animal species. They characterize the performance of eyes sufficiently well for our purpose and will be used for comparison, even if they do not give such a precise description as the modulation transfer or linespread functions which are known only for a few species.

Fig. 1 relates experimentally determined values of anatomical ($\Delta\varphi$) and physiological (ε) resolution to body height, H, for several species of animals.

We find in the first order a simple interrelationship between resolution ($\Delta\varphi$ or ε) and body height H:

$$\Delta\varphi \approx \varepsilon = k\frac{1}{H} \text{ [deg]}, \quad (1)$$

where k is a factor of proportionality. For most of the animals listed in Fig. 1, k is between 0.2 and 3 deg x cm.

Whereas $\Delta\varphi$ and ε in degrees are measures for an <u>absolute</u> spatial resolution, we may use k in deg x cm as a measure for "subjective resolution", the resolution being the better the smaller k. If two animals have the same subjective resolution, this means that for the same "subjective distance" of an object the same number of points per object area are scanned or resolved, where subjective distance is measured not in units of centimeters but in units of body height. For example, if we ($H \approx 2$ m) look at a fly in a distance of 5 m we resolve this fly into the same number of points as a fly ($H \approx 2$ mm) looking at another fly from a distance of 5 mm.

Eq. (1) is only a first-order approximation of the data of Fig. 1. There are, in fact, interesting deviations from this relationship. For instance, of all the larger animals, birds have the smallest value of k, that is the highest subjective resolution. The bat <u>Myotis</u> and the jumping spider <u>Metaphidippus</u> represent two extreme cases of low and high "subjective resolution". These facts will be considered again when we have developed a concept that allows an interpretation of the data on the basis of the performances of idealized lens and compound eyes.

The data suggest that smaller animals are adequately endowed even with a smaller absolute resolution because they have sufficient "subjective resolution". This is reasonable because small animals are concerned with objects in closer proximity than are large animals. At these shorter distances, a small animal can then resolve the same objects as well as can a larger animal at a greater distance. On the other hand,