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Vision Research

journal homepage: www.elsevier.com/locate/visres

Small fruit flies sacrifice temporal acuity to maintain contrast sensitivity

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ARTICLE INFO

Keywords:

Acuity
Sensitivity
Development
Plasticity
Drosophila
Fruit fly

ABSTRACT

Holometabolous insects, like fruit flies, grow primarily during larval development. Scarce larval feeding is common in nature and generates smaller adults. Despite the importance of vision to flies, eye size scales proportionately with body size, and smaller eyes confer poorer vision due to smaller optics. Variable larval feeding, therefore, causes within-species differences in visual processing, which have gone largely unnoticed due to ad libitum feeding in the lab that results in generally large adults. Do smaller eyes have smaller ommatidial lenses, reducing sensitivity, or broader inter-ommatidial angles, reducing acuity? And to what extent might neural processes adapt to these optical challenges with temporal and spatial summation? To understand this in the fruit fly, we generated a distribution of body lengths (1.67–2.34 mm; $n = 24$) and eye lengths (0.33–0.44 mm; $n = 24$), resembling the distribution of wild-caught flies, by removing larvae from food during their third instar. We find smaller eyes (0.19 vs. 0.07 mm²) have substantially fewer (978 vs. 540, $n = 45$) and smaller ommatidia (222 vs. 121 μm^2 ; $n = 45$) separated by slightly wider inter-ommatidial angles (4.5 vs. 5.5°; $n = 34$). This corresponds to a greater loss in contrast sensitivity (< 50%) than spatial acuity (< 20%). Using a flight arena and psychophysics paradigm, we find that smaller flies lose little spatial acuity (0.126 vs. 0.118CPD; $n = 45$), and recover contrast sensitivity (2.22 for both; $n = 65$) by sacrificing temporal acuity (26.3 vs. 10.8Hz; $n = 112$) at the neural level. Therefore, smaller flies sacrifice contrast sensitivity to maintain spatial acuity optically, but recover contrast sensitivity, almost completely, by sacrificing temporal acuity neurally.

1. Introduction

In general, larger animals have eyes that are larger in absolute terms but smaller relative to body size (Hughes, 1977; Rensch, 1948; Stevenson, Hill, & Bryant, 1995). Because optical quality is limited by the eyes' absolute and not relative size (Land & Nilsson, 2012), progressively smaller animals face an increasingly difficult optical challenge. Substantial comparative work has demonstrated evolutionary adaptations in the optics and neural processing of visual systems to cope with small apertures (Hughes, 1977; Krapp, 2000; Land & Nilsson, 2012; Theobald, Warrant, & O'Carroll, 2010). However, though body and eye size can also vary substantially within species (Shingleton, Estep, Driscoll, & Dworkin, 2009; Shingleton, Frankino, Flatt, Nijhout, & Emlen, 2007), little is known about what developmental adaptations smaller-eyed conspecifics employ.

The fruit fly, with two neural superposition compound eyes, each about 0.15 mm² in area, exemplifies this small-eyed developmental challenge. Limited food availability during the fruit fly's late larval stages, a common condition in nature, results in smaller adults with

smaller eyes (Callier & Nijhout, 2013; Shingleton et al., 2007, 2009). Each eye is an approximate hemisphere composed of about 800 nearly identical ommatidia, each containing 1 lens that focuses light upon 8 photoreceptors (Ready, Hanson, & Benzer, 1976). This geometric arrangement dictates that smaller eyes must confer poorer vision due to a decrease in the size of each ommatidial lens, an increase in the angle between ommatidia, or some combination of both. Neural summation processes might compensate for some of this loss, but only at the expense of some form of acuity (Warrant, 1999). Although small adults are common in nature where larval food availability and other environmental factors are highly variable, fly vision is mostly studied with uniformly large, lab-reared adults, and how small adults cope with small optics is unknown. Here we measure the sacrifices made by smaller flies at the optical level, and the summation processes they employ at later stages.

1.1. Limited larval feeding leads to adult flies with small eyes

The size of a holometabolous insect in general, and a fruit fly in

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particular, is determined by the size it achieves as a larva (Shingleton, Mirth, & Bates, 2008). Fruit fly larval development is divided into a sequence of 3 instars and allocates much of its nutrient intake towards growth. During the last instar, a larva eats until it reaches a critical size, eventually stops feeding, and wanders away from the food source in search of a place to pupate (Callier & Nijhout, 2013; Edgar, 2006; Shingleton et al., 2007). Importantly, there is a delay between when the larva reaches critical size and when it begins wandering, called the ‘interval to cessation of growth’ or the ‘terminal growth period’ (TGP; Callier & Nijhout, 2013; Edgar, 2006; Shingleton et al., 2007). During the TGP, larvae will continue to feed if possible but exposure to starvation or limited nutrition results in smaller but otherwise normal adults (Callier & Nijhout, 2013; Edgar, 2006). This developmental plasticity allows feeding that may be suboptimal for growth but necessary for survival (Edgar, 2006; Shingleton et al., 2008; Stevenson et al., 1995).

The effect of larval feeding on the developing eye is similar to and affected by the development of the overall body. Each kind of imaginal disc (eye-antenna, leg, and so on) has its own critical size and TGP. Limited nutrition during the TGP of an imaginal disc results in slower rates of growth and proliferation and, eventually, a smaller adult organ. (Shingleton et al., 2007) In the case of the fruit fly’s eye imaginal disc, limited nutrition during the third instar results in small adult eyes (Callier & Nijhout, 2013; Edgar, 2006; Shingleton et al., 2009; see Fig. 1A and B).

1.2. Smaller eyes must sacrifice spatial acuity, contrast sensitivity, or some combination of both

A general principle of vision is that spatial acuity, or visual sharpness, and contrast sensitivity, or the ability to discriminate luminance levels, trade off (Land, 1997; Land & Nilsson, 2012; Theobald et al., 2010). Contrast sensitivity is determined by the amount of light absorbed by each photoreceptor, which is limited in the fruit fly by ommatidial diameter (Fig. 1C, labeled D). The contrast sensitivity, S , of an

eye to an extended light source is calculated by: $S = \left(\frac{\pi}{4}\right)^2 D^2 \left(\frac{d}{f}\right)^2 \left(\frac{kl}{2.3 + kl}\right)$, where D is ommatidial diameter (μm), f is ommatidial focal length (μm), and d , l , and k the diameter (μm), length (μm), and absorption coefficient (photons μm^{-1}) of each photoreceptor rhabdomere (Warrant & Nilsson, 1998). Spatial acuity is inversely determined by the angle between adjacent ommatidia, the inter-ommatidial angle (Fig. 1C, labeled $\Delta\phi$; Land & Nilsson, 2012). The highest discernible spatial frequency, ν_{max} , of a hexagonal lattice like the fruit fly’s eye is given by: $\nu_{\text{max}} = \frac{1}{\sqrt{3}\Delta\phi}$. The fundamental acuity-sensitivity tradeoff is demonstrated by the eye’s geometry, such that decreasing $\Delta\phi$, which increases spatial acuity, necessarily decreases D , which decreases contrast sensitivity, and vice versa (Land & Nilsson, 2012). Likewise, reducing eye size necessarily decreases D , increases $\Delta\phi$, or some combination of both. As a result, smaller flies, who have smaller eyes, must sacrifice at least one of the two visual properties, acuity or sensitivity, and the overall image quality.

Because the development of the imaginal discs is largely influenced by feeding, and this effect can vary between the different imaginal discs (Shingleton et al., 2009), it is unknown how limited larval feeding will affect the optics of small eyes. For most imaginal discs, nutrition limits both cell proliferation and cell growth, resulting in adult organs that are smaller due to both fewer and smaller cells (Robertson, 1963; Shingleton et al., 2009). If this holds for the eye imaginal disc, then smaller flies could have fewer and smaller ommatidia, necessarily reducing contrast sensitivity and possibly reducing spatial acuity.

1.3. Neural summation can improve contrast sensitivity, but only at the expense of spatial or temporal acuity

Low light absorption due to smaller ommatidia presents the same problem as that faced by all animals viewing images in dim light: how to resolve an accurate image with fewer photons? Both vertebrate and invertebrate visual systems improve the visible range of ambient light intensities by increasing the receptive field of visual interneurons, via

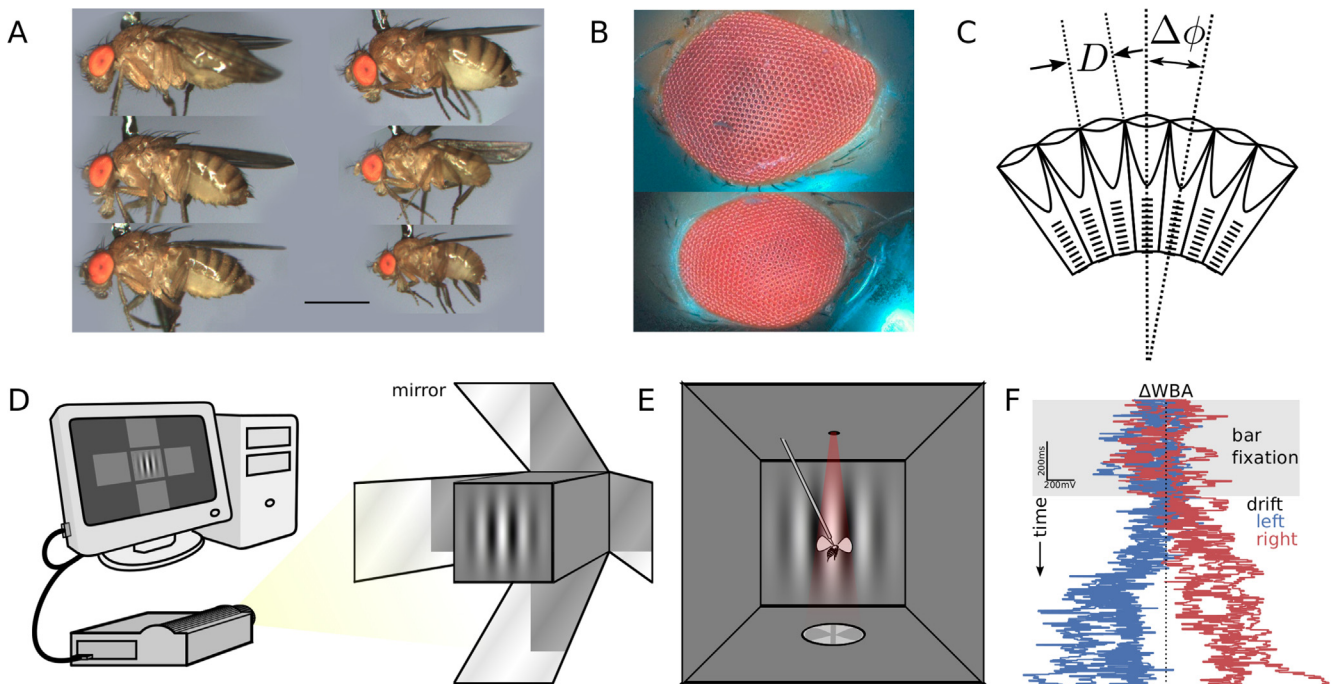


Fig. 1. (A) Lab-reared adults that were abundantly fed as larvae (left) are generally larger than those who had limited larval food availability (right). (B) Eyes are proportionate to the size of the overall body. (C) Ommatidial diameter, labeled D , limits contrast sensitivity, while inter-ommatidial angle, labeled $\Delta\phi$, inversely limits spatial acuity. Because ommatidial diameter is directly proportional to inter-ommatidial angle, the two visual properties of sensitivity and acuity trade off. (D) A computer generates visual stimuli projected onto 5 surfaces of the flight arena via 4 mirrors. (E) In the flight arena, each of the fly’s wingbeats are captured by an infrared light and two receivers. (F) The difference in wing beat amplitudes, ΔWBA , signals the fly’s steering effort.

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