particularly provocative and informative. First, there is a growing consensus acknowledging the critical role of cortical processing for echo suppression and its related behavioral consequences for spatial hearing [18,19]. To the extent that cortical regions are necessary, then echo suppression becomes a relatively slower and higher-order process than traditionally thought. Second, the findings of Bishop *et al.* [15] show that a relatively 'slow' sensory modality like vision can influence a relatively 'fast' sensory modality like audition. Responses to sound in primary auditory cortex have been shown to onset at ~10–15 ms, whereas responses to light in primary visual cortex have been shown to onset at ~40–50 ms [3]. Thus, cortical processing of sounds has a head start over visual stimuli, even if such appear together simultaneously in the external world.

What Bishop *et al.* [15] have shown is that the 'slow' visual modality provides information-rich as well as spatio-temporally coupled signals to the 'fast' auditory processing pathway that in turn alter perception and behavior. While their results are undoubtedly a harbinger of continued research on multisensory influences on nominally unisensory low-level functions, there is already a degree of neuroscientific support for the pervasiveness of visual signals during auditory processing, particularly during the treatment of communication signals (speech) and objects. In a study that focused on the effects of musical training, Musacchia *et al.* [14] showed there to be visual influences on auditory brainstem evoked responses. More recently in a study appearing in *Current Biology*, Kayser *et al.* [20] showed that visual signals can increase the information content of neural activity within auditory cortices of rhesus monkeys by reducing response variability.

The upshot is that if you want to find the 'snooze' button and get back to sleeping, you might consider opening your eyes first.

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Oogenesis: Matrix Revolutions

The mechanism of egg-chamber elongation during *Drosophila* oogenesis has always been mysterious. A new study shows that the egg chambers spin around their long axis laying down polarised extracellular matrix, which acts as a molecular corset to restrict radial expansion.

Rebecca Bastock and Daniel St Johnston*

Tissue elongation is a central feature of all embryonic development. Underlying this deceptively simple process is a complex variety of cell behaviours, such as shape changes, polarised division, directed migration and intercalation [1]. The mechanism of tissue elongation has been well studied during convergent extension in vertebrate gastrulation and *Drosophila melanogaster* germband extension. Both processes involve cell rearrangements that are directed and coordinated by planar polarity across the extending tissue, although different molecular mechanisms underlie the polarisation in each case. In vertebrates, the core planar cell polarity (PCP) pathway downstream of Frizzled signalling is responsible, driving lateral cell intercalation [2,3], whereas in the *Drosophila* germband, polarised localisation of myosin II and Bazooka/Par-3 directs junctional remodelling [4,5]. Apart from these two model processes, the mechanism of

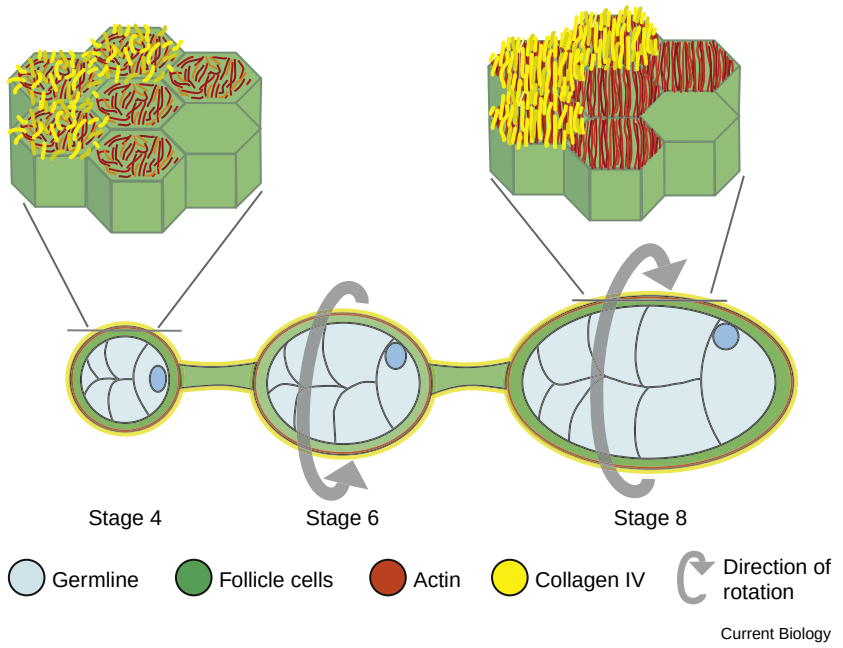

Figure 1. Elongation of the *Drosophila* egg chamber.

Between stages 5 and 9 the egg chamber elongates from a spherical to an ellipsoid shape. During this process the entire chamber spins around its long axis (grey arrows) within a static layer of collagen IV matrix (yellow). It can rotate either clockwise or anticlockwise (grey arrows). As the egg chamber spins, the collagen fibrils become polarised and form a molecular corset, restricting radial expansion of the egg chamber and forcing it to elongate.

elongation in many other tissues remains unknown. In a recent study, Haigo and Bilder [6] observed tissue elongation *in vivo* during *Drosophila* oogenesis. They uncovered a new and unprecedented morphogenetic movement, in which elongating egg chambers spin around their lengthening axis, laying down polarised extracellular matrix (ECM) as they travel.

The *Drosophila* egg chamber consists of a germline cyst surrounded by a single-layered epithelium of somatic follicle cells. The egg chamber buds off from the germarium and grows as it passes down the ovariole, to be mature by the time it reaches the oviduct. When the egg chamber leaves the germarium it is spherical. During oogenesis stage 5 it begins to elongate in the anterior-posterior axis and by stage 9 has formed an ellipsoid shape (Figure 1). This shape change is important to allow the mature eggs to be laid. It has been known for some time that elongation depends on the polarised basal actin cytoskeleton of the follicle cells. This was thought to form a molecular corset restraining radial expansion [7–9]. However, the nature of the cell behaviours underlying this elongation remained unclear.

Haigo and Bilder [6] now report that the entire egg chamber spins during elongation, completing approximately three revolutions at a speed of about 0.5 μm/min. The egg chamber always rotates around the elongating axis, although it can move either clockwise or counterclockwise. Interestingly, rotation occurs within a static ECM of circumferentially polarised collagen IV fibrils.

To investigate the link between rotation and elongation, the authors imaged egg chambers containing cells mutant for the ECM receptor integrin, which had previously been shown to be required for elongation [7]. They found that these egg chambers either rotate around the wrong axis or fail to rotate at all. Similarly, mutants lacking collagen IV begin to rotate, but quickly stop and fail to elongate. To address the function of this rotation, Haigo and Bilder [6] generated egg chambers in which only a subset of the outer follicle cells could make collagen IV and observed that as the epithelial cells move they lay down polarised collagen fibrils. When elongated egg chambers were treated with collagenase, they rounded up, and this effect was significantly greater than that produced by disrupting the basal actin cytoskeleton with latrunculin. This suggests that the polarised ECM is the key component of the molecular corset that restricts egg chamber growth. The authors also examined collagen IV in *integrin* mutant egg chambers, which fail to spin. They found that although fibrils are present and of the correct density and length, their polarised distribution had been lost. Thus, the rotation of the egg chambers spins out a polarised ECM, which then constrains the growth of the egg chamber in the circumferential direction, so that it grows in the orthogonal direction (Figure 1).

One intriguing question raised by these results is the purpose of the highly polarised basal actin network. Although recent work by another group [10] suggests that polarised contractions of the basal actinomyosin restrict egg chamber width from stage 9 onwards, Haigo and Bilder [6] also found that the shape changes produced by direct disruption of the actin cytoskeleton late in oogenesis are relatively subtle. However, if actin plays only a minor role, why do mutations that alter the polarity of the actin network lead to a dramatic failure of elongation? Although most mutations of this type are in proteins that link actin to the ECM, mutants in the atypical cadherin Fat2 also produce round eggs and disrupt basal actin polarity at later stages [11]. This fits with Haigo and Bilder's [6] suggestion that the actin network may be required for motility during stages 5–9, rather than mechanical restriction at later stages, and raises the intriguing question of where the force is generated to move the egg chambers. This could depend on the movement of ECM receptors along polarised basal actin, or may involve some other type of actin-dependent motility, such as pulling on actin-rich protrusions. However, it could also occur by some other mechanism, and one of the major questions for future research will be to determine what drives egg chamber spinning, as well as the origin of the planar polarity that determines the axis of rotation.

Haigo and Bilder [6] have described a new type of morphogenetic behaviour in which movement of the follicle epithelium across a stationary matrix leads to spinning of the entire egg chamber and polarisation of the ECM. The function of the ECM as a

molecular corset also highlights its role in shaping tissues, and raises the possibility that the polarised arrangement of ECM fibrils will be important in other morphogenetic processes.

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Sexual Selection: Do Flies Lie with Asymmetric Legs?

A newly described species of empidid or 'dance fly' shows a bizarre polymorphism in their forelegs, which presumably serve as a mating lure. This trait may have evolved by frequency-dependent deceptive male signalling.

Michael G. Ritchie[1,*] and Karim Vahed[2]

Empidid flies are well-known for the extraordinary variation in their mating systems. To increase their chances of securing a mating, the males of most species donate prey items, captured flies of other species, as nuptial gifts to females [1]. However, empidid flies show a remarkable extent of apparently deceptive sexual signals in both sexes [2,3]. The nuptial gift often leads to reversed sex-roles, such that females compete for the attention of choosy males [4]. This role reversal can be reflected in sexually selected body parts. The females of some species, for instance, possess flattened scales on their legs which, when held against the body, increase the apparent girth of the female's abdomen — males show a preference for rotund females [5]. In *Rhamphomyia longicauda*, females take this trick a step further by inflating their abdomen using specialised abdominal sacs [2,6]. Male empidids, however, can be especially devious: in some species, males present the female with a real nuptial gift, an edible insect, while the males of other species present their mates with dried insect remains or inedible items wrapped in silk. In some species, the males take this deceit further and entice females using an entirely empty balloon of silk [7,8]. Even in species which offer genuine prey gifts, males sometimes cheat by using an inedible ball of willow fluff as a substitute gift, such as in *Empis opaca* [9]. Female *Rhamphomyia sulcata* can be experimentally induced to mate with males whose nuptial gift has been replaced by a cotton ball [10].

Now, a recently discovered species of empidid fly from the slopes of Mount Fuji, *Empis jaschhoforum*, provides an extraordinary addition to the list of apparently deceptive traits in empidid flies [11]. The new species shows remarkable and previously undescribed variation in a male sexual ornament, with some males being unornamented while others can sport ornaments on either or both forelegs [11]. How this extraordinary variation is maintained by evolution in this species is currently not understood, but one intriguing possibility is that it could reflect antagonistic frequency-dependent evolution between males and females in a sexual system driven by cheating.

When collecting exemplars of the new species, Daugeron *et al.* [11] found that some males of *E. jaschhoforum* possess greatly enlarged tarsi ('foot' segments) on the first pair of legs, fringed with long hairs, which probably mimic a prey gift. Other species of empidids are also known to have clubbed feet which resemble males holding prey items. However, what is remarkable about the new species is that the possession of enlarged foreleg tarsi was found to vary greatly between individual males: in one of 33 males sampled, both tarsi were enlarged; in 14, only one, either right or left, was enlarged, while the remaining 18 males showed no modification at all (Figure 1).

How could such an unusually high level of polymorphism and asymmetry be maintained? The authors ruled out the possibility that the asymmetrical males were gynandromorphs (mosaic animals containing male and female parts of the body), as no males possessed other female characters. Partial feminisation due to infection by parasitic nematodes was also thought unlikely. Moreover, differences in body size between males did not appear to account for the extent of expression of the secondary sexual traits, as occurs in some species [12] — males with modified legs were no larger than those with un-modified legs. Daugeron *et al.* [11] thus suggest that a type of disruptive selection could favour both males with the enlarged tarsi, which may be better at attracting females from a distance, and males with unmodified legs, who may be subject to less drag and be able to impress females at close range with better aerobatic skills [8]. Alternatively, if the tarsi do mimic males carrying genuine nuptial gifts, frequency-dependent selection might act. In general, mimicking strategies work better when the mimics occur at a lower frequency than the model they are mimicking, as in classic Batesian model–mimic systems,