

## Dispatches

# Visual Neuroscience: How Flies Segregate Moving Objects from the Optic Flow Field

Moving animals often have difficulty detecting moving objects because self-generated optic flow patterns confound image motion. The new hypothesis of 'regressive motion salience' reveals simple rules used by fruit flies.

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Separating self-generated sensory stimulation, termed reafference, from externally generated stimulation, exafference, presents challenges to sensory systems [1,2]. Stationary viewers can detect moving objects with comparative ease, reliably categorize such stimuli as exafferent, and respond adaptively. On the other hand, an animal moving through a stationary environment experiences reafferent optic flow, the fluctuating pattern of apparent motion of stationary objects in the visual field [3]. Complex animal movements generate optic flow patterns that cannot be completely predicted unless the animal knows the spatial layout of objects in its environment [4]. Thus, reafferent retinal stimulation, which provides information about the stationary environment and ego motion [5], becomes confounded with exafferent stimulation, which may signal the motion of a predator or prey or a potential mate, to which the viewer should respond differently. Some simple types of animal motion, such as pure translation or pure rotation, do, however, generate reafferent optic flow fields in which the moving retinal images are predictable in terms of their direction, if not their velocities. Thus, any image moving in a direction different from the predicted one must have an external source and could be responded to if the animal's nervous system is able to compare the predicted directional stimulation with the total retinal stimulation [6].

In this issue of *Current Biology*, Zabala *et al.* [7] present results from a technically clever experimental protocol to show that walking fruit flies, *Drosophila melanogaster*, are able to respond to a mismatch between predicted reafferent retinal motion

and externally caused motion. Single flies walking straight in an arena with patterned walls generate optic flow in which images move progressively from front-to-back across their retinas. When a *Drosophila*-sized magnet manipulated by an elegant robotic control system moved regressively from back-to-front through the walking fly's visual field, the fly stopped walking (Figure 1A). Conversely, when the magnet moved progressively through the fly's visual field, its motion was confounded with the progressive flow field and the fly barely altered its behavior. The authors describe this simple mechanism for recognizing exafference as 'regressive motion salience'.

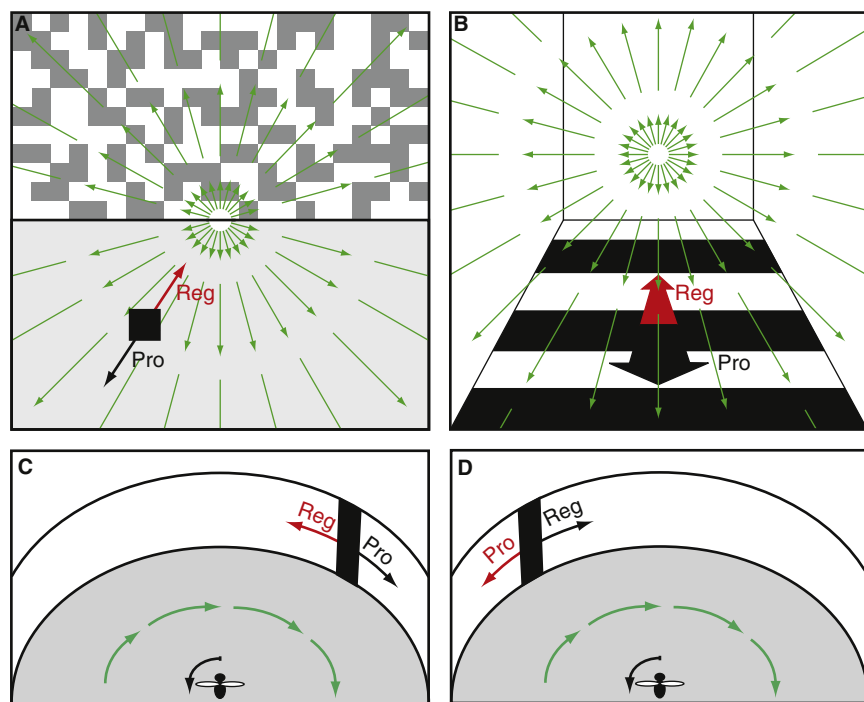
The robustness of this simple mechanism depends upon the fly's movement. As noted above, as an animal's movements combine translation and rotation in complex ways, the less predictable the optic flow field. Separation of reafference from exafference becomes an ill-posed problem, *sensu* Poggio and Koch [8], in which there is no unique solution to the source of the retinal image velocities. Thus, straight walking fruit flies generated a completely predictable progressive flow field and had a high probability of stopping (>75%) when they saw regressive motion. Conversely, as the walking flies mixed rotation, which generates regressive reafference on the inside of the turn, with straight walking the salience of the regressively moving image of the magnet declined and they hardly altered their behavior.

Regressive image motion may also have salience in behavioral contexts other than the dyadic interaction investigated by Zabala *et al.* [7]. In flight, flies executing certain maneuvers may also generate predictable optic flow and respond

adaptively when their expectations are not met. Forward translatory flight is somewhat similar to the walking scenario — environmental contrast elements should produce progressive image motion across the retina. *Drosophila hydei* in straight free flight in a wind tunnel respond more strongly to experimental regressive motion of a patterned floor at almost all velocities than to progressive motion (Figure 1B) [9]. While a wide-field stimulus of the floor pattern is not interpreted as another individual, the fly's two-fold stronger response to regressive motion similarly indicates that it recognizes something caused by an external agent, rather than by its own reafference. In the natural case, the regressive motion would be caused by a headwind.

For flies flying with a combination of translation and rotation we would not expect 'regressive motion salience' to apply generally, as the authors point out [7]. Flying flies making body saccades [10], which are rapid angular rotations around the yaw axis, generate reafferent visual stimulation that is again more predictable with respect to directionality. Experimentally tethered fruit flies flying in closed loop with a visual surround demonstrate that they are aware of the expected direction of reafference [11,12]. When the coupling between the fly's torque and motion of the visual surround is inverted, for example, a fly generating torque to the left moves the visual world leftward instead of rightward as predicted, flies notice that their directional expectation is not met and begin immediately to compensate for the mismatch. This occurs when incorrect motion of the visual surround generates regressive or progressive motion (Figure 1C,D) [11]. In this context, flies respond well to regressive motion, but it is not more salient than progressive motion in an unexpected direction.

One previous study [13] investigated responses of walking fruit flies to regressive and progressive motion



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Figure 1. Salience of progressive and regressive movement of different objects experienced by a moving fly.

Green arrows represent reafferent optic flow. Red arrow indicates movement direction that is more salient. (A) Fly is walking in a straight line, translating forward with no rotational velocity. A small object moving regressively is more salient than when moving progressively. (B) Fly is flying through a wind tunnel with a moving pattern on the ground. Pattern is more salient when moving regressively. (C,D) Tethered fly in a circular arena carrying out a yaw turn to the left. (C) Again, when a stripe is moved regressively against the optic flow, the movement is more salient. (D) However, progressive motion of the stripe can be more salient when it is moved against the optic flow.

of a  $5^\circ \times 5^\circ$  image, which is equivalent in the current protocol to the fly being separated from the magnet by about 18 mm. Tethered male and female flies walked in open loop on a trackball and viewed the image moving back and forth around them. Flies presented with regressive motion turned toward it to fixate the image when it was in the caudal visual field, and tracked the image when it moved regressively across the frontal visual field. When the stimulus image moved progressively, flies tracked it regardless of its position in the visual field. These results differ from those of the present study, but the depauperate experimental environment (no visual surround) and the open loop nature of the protocol serve to highlight the importance of the 'regressive motion salience' hypothesis proposed by Zabala *et al.* [7]. When an animal is in closed loop with its surroundings it generates expectations about how its actions

influence image flow across its retina. If the animal's predictions are not met, it performs an adaptive behavior to allow clarification of the mismatch. As the predictions become less precise, as Zabala *et al.* [7] show with increasing amounts of angular rotation added to the walking fly's translation, the animal's nervous system can no longer provide reliable information about the mismatch and the animal no longer responds to it.

'Regressive motion salience' may have generality beyond flies simply detecting objects moving in reafferent optic flow fields. The current project originated during development of an automated tracking system [14] to investigate social interactions among groups of flies. Such interactions occur in a complex milieu, so the context was reduced to the pair-wise fly-magnet interactions of the present study. Could the simple rule of 'regressive motion salience' scale up to social contexts of larger numbers of moving

individuals and perhaps help regulate inter-individual position? There are few relevant data in the literature, but several applicable systems offer opportunities for further investigation. Position in swarms of locusts is regulated visually with a flying locust generating forward thrust when it sees regressive motion of locust-sized images in its lateral visual field [15] and nymphs are much more likely to march forward when they see another individual in their posterior visual field [16], but whether regressive motion was more salient was not explicitly tested.

Even some vertebrate animals may use this simple rule for regulating their position in moving groups. Shoaling fish are a possible candidate, as regressive motion of nearest neighbors can influence the behavior of a focal fish [17]. Lateral line, rather than visual, information is necessary and sufficient for cohesion of fish schools [18], but swimming fish generate a progressive hydrodynamic flow field and perhaps 'regressive motion salience' may also apply to this sensory modality. Birds flying in flocks tightly control their position relative to specific flockmates [19] and could rely on regressive visual motion.

Finally, whether 'regressive motion salience' influences movements in human crowds is unclear. A few simple visual heuristics based on collision avoidance suffice to capture movement dynamics of small numbers of pedestrians [20]. Regressive motion in the visual field, however, does not indicate collision, but rather that the detected moving object will pass in front of the observer's trajectory. Precisely which visual information forms the basis for movement decisions in groups remains unclear, but simple yet powerful mechanisms such as 'regressive motion salience' could be a basic element that is used across phyla.

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## Cell Polarity: Overdosing on PCPs

Several spatial cues combine to influence cell polarity within the plane of the *Drosophila* wing epithelium, orienting two separable mechanisms of short-range intercellular communication, one utilizing the ‘core’ polarity proteins, and another utilizing the protocadherins Dachsous and Fat, and the atypical myosin Dachs.

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The polarization of cells within the plane of an epithelium can orient cell divisions, tissue growth, cell migration and differentiation events, both cell autonomous and multicellular; you need planar cell polarity (PCP) to do everything from elongating your embryonic axis to lining up the stereocilia in your inner ear [1]. Yet for all that is known about the molecular mechanisms regulating PCP, in even the best-studied systems there are debates about everything from the nature and number of the orienting cues, the links to and between various downstream pathways, and the molecular details of intercellular signaling. Four recent studies [2–5] using an important model of PCP, the epithelium of the developing *Drosophila* wing imaginal disc, provide important new information on the ways that several cues combine to orient PCP via two pathways with important roles in both fly and vertebrate PCP.

The best-studied PCP system involves the so-called ‘core’ PCP proteins; these are required within cells for normal wing hair polarity, and a subset help transmit polarity

information to neighboring cells. There is still a lively debate about how, exactly, they work. In ‘vector’ models, both the intracellular and intercellular PCP information is thought to be mediated by the polarized redistribution of the core proteins in each cell [6] (Figure 1A). In the wing, for instance, just before each cell produces a single, distally oriented hair, specific core proteins are dramatically polarized to the proximal, distal or both cell faces. In vector models, interactions between the core proteins amplify the polarization within each cell, and polarized transmembrane proteins signal in a way that attracts or repels proteins on adjacent cells. Intercellular signaling is thought to depend on distal Frizzled (a Wnt receptor), proximal Van Gogh/Strabismus, and proximal and distal Starry night/Flamingo, a homophilic cadherin; several proposals exist for how these bind and communicate [7,8].

Vector models have been questioned, however, because some mutations that disrupt detectable core protein polarization do not obviously affect intercellular signaling. Moreover, PCP proteins are apparently required

prior to their dramatic polarization in older pupal wings. An alternative model therefore proposed a gradient of Frizzled activity across the wing that does not directly polarize cells [9] (Figure 1B). Individual cells establish PCP by comparing their own Frizzled activity to that of the adjacent cells in a way that, although requiring the presence of the transmembrane core proteins, does not require their polarization within a cell. In this view, the polarization of the core proteins is a late end-point of the PCP process, not a mechanism.

Two recent studies [2,3], both appearing in *Current Biology* (Sagner *et al.* [2] in this issue), are therefore important in part because they demonstrate subtle core protein polarization at quite early stages of wing development, early enough to account for the timing of activity, and subtle enough that it might easily be overlooked. The data thus support, although do not prove, the existence of vector-like intercellular signaling at early stages, and it is easy to imagine how this weak polarization might be stabilized and amplified by subsequent interactions.

But in vector models something must orient the local vector with respect to the tissue, and this has also been the subject of much debate. The core PCP system contains not only a Wnt receptor but also its effector Dishevelled, and there is evidence in other systems for PCP orientation by extracellular gradients of diffusible Wnts [10]. But in the fly wing there was