

for experimental analyses of the individuals and activities that are critical to the establishment and maintenance of social niches.

Flack *et al.* [2] observed that disputes between monkeys, for instance over access to food or mates, destabilised monkey societies, but that a small number of high-status individuals acted like police, physically intervening in conflicts, preventing escalation and preserving relationships. They carried out experiments in which such monkey policemen were temporarily removed, and found that their removal was associated with dramatic reductions in the size and connectivity of social networks related to grooming, play and so on. The presence of the police meant monkeys interacted with more individuals, and more diverse kinds of individuals, to generate big, integrated, cooperative societies. Their absence led to the breakdown of society into small cliques, with high levels of conflict. The authors argue that, by influencing the structure of social resource networks, policing is likely to have far-reaching consequences, for infant survival and the emergence of cooperation and cultural traditions.

Some questions regarding the study remain. For instance, it is not clear that it is policing activity, rather than some other characteristic of the police, that is critically responsible for the stability and connectedness of monkey societies, and the knock-on consequences of network structure for survivorship, cooperation and tradition are inferred rather than demonstrated. Nonetheless, Flack *et al.*'s [2] position is highly tenable. Theoretical studies support the hypothesis that policing, in the form of punishment of non-cooperators, can favour the evolution of large-scale cooperation [5], and that learned information diffuses more rapidly through an integrated than cliquey society [6].

More important, in my view, to the specific findings of the study, are the novel methods and theoretical constructs developed by these researchers, which are potentially widely applicable within the social and biological sciences.

Flack *et al.* [2] deserve credit for operationalizing the social niche, and showing how the factors instrumental to its structure can be rendered accessible to scientific inquiry. These researchers join a growing band of evolutionary biologists, ecologists, philosophers, archaeologists, anthropologists and psychologists who are using the new evolutionary framework provided by niche construction to gain insight into topics ranging from the cause of the demographic transition to the evolution of language [7–13]. Monkey policing not only builds stable macaque societies but may, in the fullness of time, play a part in the construction of a conceptual shift within the biological sciences.

#### References

1. Odling-Smee, F.J., Laland, K.N., and Feldman, M.W. (2003). Niche Construction. The Neglected Process in Evolution. Monographs in Population Biology, 37. Princeton University Press.
2. Flack, J.C., Girvan, M., de Waal, F.B.M., and Krakauer, D.C. (2006). Policing stabilizes construction of social niches in primates. *Nature* 439, 426–429.
3. Turner, J.S. (2000). The Extended Organism: The Physiology of Animal-built Structures (Cambridge, MA: Harvard University Press).
4. Lee, K.E. (1985). Earthworms: Their Ecology and Relation with Soil and Land Use (London: Academic Press).
5. Boyd, R., Gintis, H., Bowles, S., and Richerson, P.J. (2003). The evolution of altruistic punishment. *Proc. Natl. Acad. Sci. USA* 100, 3531–3535.
6. Cavalli-Sforza, L.L., and Feldman, M.W. (1981). Cultural Transmission and Evolution (Princeton, NJ: Princeton University Press).
7. D. Fragaszy and S. Perry, eds. (2003). The Biology of Traditions: Models and Evidence (Chicago: Chicago University Press).
8. Ihara, Y., and Feldman, M.W. (2004). Cultural niche construction and the evolution of small family size. *Theor. Pop. Biol.* 65, 105–111.
9. Borenstein, E., Kendal, J., and Feldman, M. (2006). Cultural niche construction in a metapopulation. *Theor. Pop. Biol.*, in press.
10. Kerr, B., Schwilk, D.W., Bergman, A., and Feldman, M.W. (1999). Rekindling an old flame: A haploid model for the evolution and impact of flammability in resprouting plants. *Evol. Ecol. Res.* 1, 807–833.
11. Schwilk, D.W., and Ackerly, D.D. (2001). Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94, 326–336.
12. Sole, R.V., Montoya, J.M., and Erwin, D.H. (2002). Recovery after mass extinction: evolutionary assembly in large-scale biosphere dynamics. *Phil. Trans. R. Soc. Lond. B* 357, 697–707.
13. Sterelny, K. (2003). Thought in a hostile world. *The Evolution of Human Cognition* (Oxford: Blackwell).

Centre for Social Learning and Cognitive Evolution, School of Biology, St. Andrews University, UK.  
E-mail: knl1@st-andrews.ac.uk

DOI: 10.1016/j.cub.2006.03.046

---

## Visual Motion: Homing in on Small Target Detectors

**Tracking moving targets is essential for animals that pursue prey or conspecifics. Recent studies in male and female hoverflies have described classes of neurons that detect the movements of small targets against a moving background but the mechanisms generating their responses remain unclear.**

### Jeremy E. Niven

Many animals detect and track small targets while hunting prey or pursuing conspecifics to secure territories or mates (for example [1–5]). For an animal perching or hovering watching a moving target, the target generates motion against a stationary background. Detecting moving targets under such conditions would be comparatively straightforward, but surprisingly few animals use such

a strategy and most of these are likely to be ambush predators, such as the praying mantis or the toad [4,5]. Usually, the detection of small moving targets is followed by a pursuit in which both the target and the pursuer move. For example, male hoverflies engage in visually guided tracking of females or other males in flight (Figure 1) [1,6].

During these bouts of tracking both target and pursuer are moving, so the pursuer must not

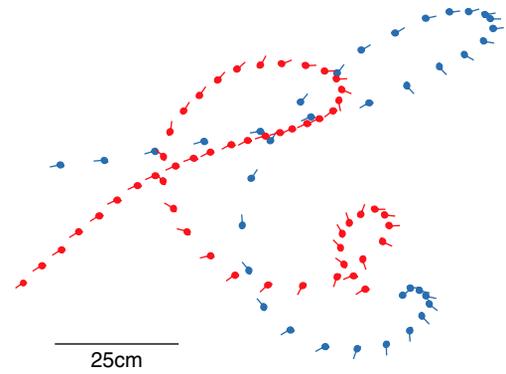
only track the target motion but also distinguish it from the panoramic background motion, or optic flow, induced by its own movements. For example, the optic flow generated by forward movement is different from that generated during rotation. Clearly some insects are capable of extremely accurate tracking, even when faced with complex movements of the target (Figure 1). Indeed, male dragonflies pursuing other males can not only manage this but can control their flight path and velocity making themselves appear stationary to the male being pursued [2].

Neurons that respond specifically to small moving targets have been identified in the visual systems of several insect species (for example [7,8]), but the interactions between target motion and optic flow remain unclear. A recent study [9] has described visual interneurons from the lobula complex of male hoverflies, *Eristalis tenax*, which respond to small target motion. Male hoverflies are able to track females or other males closely [1], making them ideal subjects for investigating the neural basis of small target detection. Nordstrom *et al.* [9] identified small target motion detector (STMD) neurons in intracellular recordings by their responses to a bar moving across their receptive field. Initially the bar was  $0.8^\circ$  wide by  $0.8^\circ$  high — a thumb's width at arms length is approximately  $2^\circ$  — the height was then systematically increased up to  $\sim 80^\circ$ . STMD neurons were defined as those responding with a greater number of spikes per second to bars  $<3^\circ$  than they do to bars  $>3^\circ$ .

Twenty distinct classes of STMD neuron were identified on the basis of their receptive field and their directional selectivity using this method. Of these, some classes, for example STMD 1 neurons, were responsive to small target movements in any direction, whilst others, such as STMD 2 neurons, were directionally selective [9]. Six classes of STMD neuron did not respond to background motion, which simulates optic flow, when it was presented alone. The responses of

Figure 1. An excerpt from a chase between two male hoverflies (*Volucella pellucens*).

The flight path of the chasing male is shown in red, the male being chased is shown in blue. (Adapted from [6].)



five of these six classes of STMD neuron to small target motion were unaffected by the presence of background motion, even when the background velocity was matched to that of the target, though STMD neurons from the other class were affected by background motion [9]. Remarkably, many of the STMD neurons were extremely sensitive even at relatively low contrasts, responding to the movements of targets smaller than the receptive field of a single photoreceptor.

What neural mechanisms underlie these responses? Neural circuits underlying responses of visual neurons to object motion have been suggested in the blowfly, *Calliphora vicina*, as well as in the rabbit and salamander retina [7,10]. In the blowfly, the figure detection 1 (FD1) neuron responds to the movements of a bar from the front to the back of the eye. These responses are suppressed in the presence of global motion due to inhibitory inputs from the ventral centrifugal horizontal (VCH) neuron [7]. Similarly, in the vertebrate retina, object-motion-sensitive (OMS) ganglion cells are responsive to object motion against a stationary background or incoherent background motion. When background motion is coherent — object motion is the same as background motion — however, the responses of the OMS ganglion cells are suppressed [10]. This suppression is thought to be mediated by polyaxonal amacrine cells that respond to global motion and inhibit the OMS ganglion cells.

In both the blowfly visual system and the vertebrate retina, therefore, background motion suppresses

the response of object motion sensitive neurons (Figure 2A). This may be important for target detection, because the motion of the target on the retina of the pursuer is a combination of the target motion and optic flow induced by the movements of the pursuer. Therefore, a circuit in which self-motion induced optic flow inhibited object motion detectors would theoretically allow the true motion of the object to be detected (for example, by the relation retinal image shift minus self-motion-induced optic flow equals target motion).

In male hoverflies, however, at least five classes of STMD neurons are not inhibited by background motion, even when both target and background motion are matched, and consequently their responses to target motion are not suppressed [9]. Indeed, the only clear inhibitory inputs in these STMD neurons are generated by the movements of bars within their receptive field larger than the preferred target size (Figure 2B). One possible explanation is that in hoverflies target motion is calculated using a mechanism based on changes in local contrast. Such a mechanism would account for the sensitivity of the STMD neurons even at low contrasts [9]. In addition, calculation of the target motion may not be entirely dependent on feedback from visual interneurons that detect optic flow, because it is self-generated and therefore may be predictable if the output of the flight motor system (an efferent copy) is relayed back to the visual system.

Whatever the mechanism, the robustness of the STMD neurons to small target motion in the presence

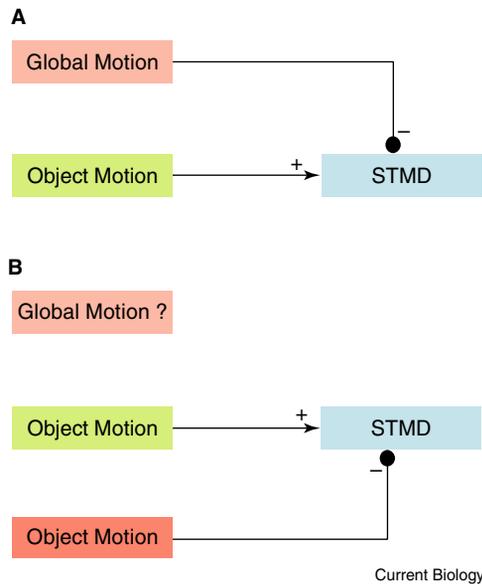


Figure 2. Schematic representation of neural circuits for detecting object motion against a moving background.

(A) In blowfly lobula [7] and rabbit and salamander retina [10] background motion (red) inhibits object motion (green) sensitive neurons. (B) Potential mechanisms shaping the responses of the STMD neuron. Object motion within the receptive field (green) evokes depolarising inputs leading to spikes in a STMD neuron but, as the object increases in size, inhibitory inputs to the STMD are evoked (red, lower). Background motion (red, upper) does not evoke direct inhibitory inputs to at least five classes of STMD neurons.

of background motion suggests that the neural circuits in the hoverfly are different from those described in blowflies. This is not that surprising, however, as hoverflies and blowflies are separated by ~82 million years of evolution [11]. Moreover, the neural circuits in male insects specifically designed for tracking females during courtship (for example [12–15]) may have evolved independently numerous times. Surprisingly, STMD neurons have also been found in the lobula of female hoverflies [16]. Three classes of STMD neuron were described all of which respond selectively to small moving targets. Interestingly, female STMD neurons had larger receptive fields than those of males and, with the exception of one class, their object height tuning was much broader [16]. The functional role of these neurons, however, remains unclear.

Although an elaborate system for tracking the motion of small objects against background motion seems to be present in

many animals, a simpler solution would be to stop periodically during a pursuit, calculate the target motion against a stationary background and then continue the pursuit. This type of behaviour is observed in the tiger beetle, *Cicindela repanda* [3]. Whilst pursuing prey on the ground, tiger beetles pause periodically to detect the motion of their prey (Figure 3). The duration of each pause is reduced as the angular velocity of the prey increases. This is an effective strategy for tiger beetles, which hunt on the ground and can easily outrun their prey.

The results of all these studies emphasise that a variety of both behavioural and neural strategies are used by animals to enable them to track prey or conspecifics. Comparison of object motion sensitive neurons in blowflies and hoverflies suggest that they are using different neuronal mechanisms, even when they show similar behaviours. Moreover, the discovery of STMD neurons in female hoverflies, which show no obvious tracking behaviours,

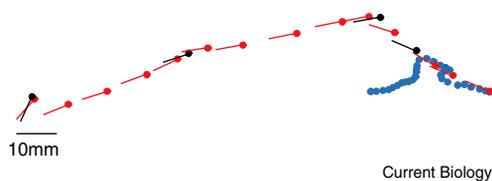


Figure 3. An excerpt from a pursuit of live prey (*Drosophila melanogaster*) by a tiger beetle (*Cicindela repanda*).

The path of the tiger beetle is shown in red, points at which it paused are shown in black and the path of the prey being pursued is shown in blue. (Adapted from [3].)

should emphasise that the relationship between single neurons and behaviour is not always straightforward. Further studies will be needed not only to determine the neural mechanisms underlying the response properties of STMD neurons but also to begin to understand how information about target movements is transformed into a motor output for tracking.

#### References

1. Collett, T.S., and Land, M. (1975). Visual control of flight behavior in the hoverfly *Syrirta pipens*. *J. Comp. Physiol. A* 99, 1–66.
2. Mizutani, A., Chahl, J.S., and Srinivasan, M.V. (2003). Insect behaviour: Motion camouflage in dragonflies. *Nature* 423, 604.
3. Gilbert, C. (1997). Visual control of cursorial prey pursuit by tiger beetles (*Cicindelidae*). *J. Comp. Physiol. A* 181, 217–230.
4. Ewert, J.P. (1974). The neural basis of visually guided behaviour. *Sci. Am.* 230, 34–42.
5. Collett, T.S. (1996). Vision: Simple stereopsis. *Curr. Biol.* 6, 1392–1395.
6. Collett, T.S., and Land, M.F. (1978). How hoverflies compute interception courses. *J. Comp. Physiol.* 125, 191–204.
7. Warzecha, A.K., Egelhaaf, M., and Borst, A. (1993). Neural circuit tuning fly visual interneurons to motion of small objects. I. Dissection of the circuit by pharmacological and photoinactivation techniques. *J. Neurophysiol.* 69, 329–339.
8. Collett, T.S. (1971). Visual neurons for tracking moving targets. *Nature* 232, 127–130.
9. Nordstrom, K., Barnett, P.D., and O'Carroll, D.C. (2006). Insect detection of small targets moving in visual clutter. *PLoS Biology* 4, e54. DOI: 10.1371/journal.pbio.0040054.
10. Olveczky, B.P., Baccus, S.A., and Meister, M. (2003). Segregation of object and background motion in the retina. *Nature* 423, 401–408.
11. Grimaldi, D., and Engel, M.S. (2005). *Evolution of the Insects* (Cambridge: Cambridge University Press).
12. Gilbert, C., and Strausfeld, N.J. (1991). The functional organisation of male-specific visual neurons in flies. *J. Comp. Physiol.* 169, 395–411.
13. Strausfeld, N.J. (1980). Male and female visual neurones in dipterous insects. *Nature* 283, 381–383.
14. Vallet, A.M., and Coles, J.A. (1993). The perception of small objects by the drone honeybee. *J. Comp. Physiol. A* 172, 183–188.
15. Burton, B., and Laughlin, S.B. (2003). Neural images of pursuit targets in the photoreceptor arrays of male and female houseflies *Musca domestica*. *J. Exp. Biol.* 206, 3963–3977.
16. Nordstrom, K., and O'Carroll, D.C. (2006). Small object detection neurons in female hoverflies. *Proc. R. Soc. B* DOI: 10.1098/rspb.2005.3424.

Smithsonian Tropical Research Institute, Roosevelt Avenue, Tupper Building – 401, Balboa, Ancón, Panama City, Republic of Panama.

E-mail: [nivenj@si.edu](mailto:nivenj@si.edu)

DOI: 10.1016/j.cub.2006.03.044