

Efference copies: Context matters when ignoring self-induced motion

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Across the animal kingdom, efference copies of neuronal motor commands are used to ensure our senses ignore stimuli generated by our own actions. New work shows that the underlying motivation for an action affects whether visual neurons are responsive to self-generated stimuli.

Did you ever wonder why you cannot tickle yourself? Or why you are not startled by your own hands even if they move rapidly and animatedly in front of your face? The neurophysiological reason for this is something called an ‘efference copy’: when you perform an action, an efference copy is sent to your sensory organs to warn them of the imminent sensory input specific to your actions. Efference copies of motor signals seem to be ubiquitous across senses and species (for an excellent review see¹), and to have the timing and amplitude required to abolish the sensory signal that would be generated by the perceiver’s own actions^{2–5}. A new study reported in this issue of *Current Biology* by Fenk, Kim, and Maimon⁶ shows that, in the fly *Drosophila melanogaster*, an efference copy can be affected by the underlying motivation for the action dictated by the respective motor signal.

Our senses help us understand what is going on in the world around us. We humans depend strongly on vision, whereas other animals may rely more on other senses, such as echolocation in bats³ and the lateral line system⁷ in fish and amphibians. Visual motion can be generated by our own actions or be generated by motion in the environment. Our own movement generates something called optic flow, which can be described as widefield visual motion across the retina. In humans, such optic flow can be generated by movement of the entire body, of the head, or of just the eyes. This optic flow informs us about where we are heading and how to navigate within our environment. But sometimes it is optimal to suppress the perception of optic flow. For example, if your eyes move rapidly

from one part of a scene to another to perform a saccade, the scene during the saccade becomes blurred, as the movement is too fast for our photoreceptors⁸; however, the signal sent to the eye muscles to induce the saccade is also copied and forwarded to the visual centres, where it inhibits the visual signal⁹. This efference copy thus momentarily inhibits our visual perception of the blurred scene¹⁰.

Similarly in flies, optic flow is important for stabilizing flight paths and navigating through the environment. Furthermore, there is strong evidence that optic flow in flies is also suppressed via efference copies in certain circumstances^{5,6}. Optic flow sensitive neurons in the fly optic lobes¹¹, which synapse with motor centre neurons that control flight^{12,13}, have long been believed to play a role in stabilizing optomotor responses¹⁴. For example, if the fly is involuntarily moved to the right by a gust of wind (black arrow, Figure 1A), this creates optic flow to the left (‘exafference’; green input arrow, Figure 1A). The optic flow sensitive neurons process this information leading to an optomotor turn in the direction of the optic flow (green output arrow, Figure 1A). The resulting optomotor response itself induces self-generated optic flow which is again processed by optic flow sensitive neurons (‘reafference’; Figure 1A). The optomotor response thereby ensures that the fly continually corrects for any unintended deviations from its flight course. Given the optomotor response keeps the fly on the straight and narrow, how then can flies ever turn?

Previous fly work⁵ showed that during voluntary turns (efference; red input,

Figure 1B) an efference copy (purple, Figure 1B) is sent to inhibit optic-flow-sensitive neurons in the visual centre. The timing and magnitude of the efference copy is matched to the timing and magnitude of the saccade, so that the inhibition cancels out the reafference⁵ (grey, Figure 1B). We know that this inhibition is an efference copy as it occurs even in blind flies⁵, and is thus not a result of the visual stimulus itself. This is thus all very convincing, and similar to the efference copies described during human saccades^{1,9}.

In their new study, Fenk *et al.*⁶ asked the following: is the efference copy the same if the action is the same (outputs, Figure 1), but the underlying motivation different (inputs, Figure 1)? The original studies⁵ looked at saccades that were voluntary and thus occurred at an apparently random time. In the new study they added turns that were of similar amplitude and timing, but were induced either by a looming stimulus, or a rapid pulse of widefield motion. The author found that, besides being suppressed during voluntary saccades⁵, the optic-flow-sensitive neurons in the visual centre were also suppressed if the fly was turning away from a looming stimulus (Figure 1C), such as would be seen when for example pursued by a predator. But the same visual neurons were not suppressed during rapid pulses of optic flow (Figure 1A), even if the resultant behaviour — a very quick turn — was the same in the two scenarios.

This finding, backed by exquisite, technically demanding recordings of single visual neurons in flying animals, together with cleverly designed stimuli, while at first peculiar, makes sense from a

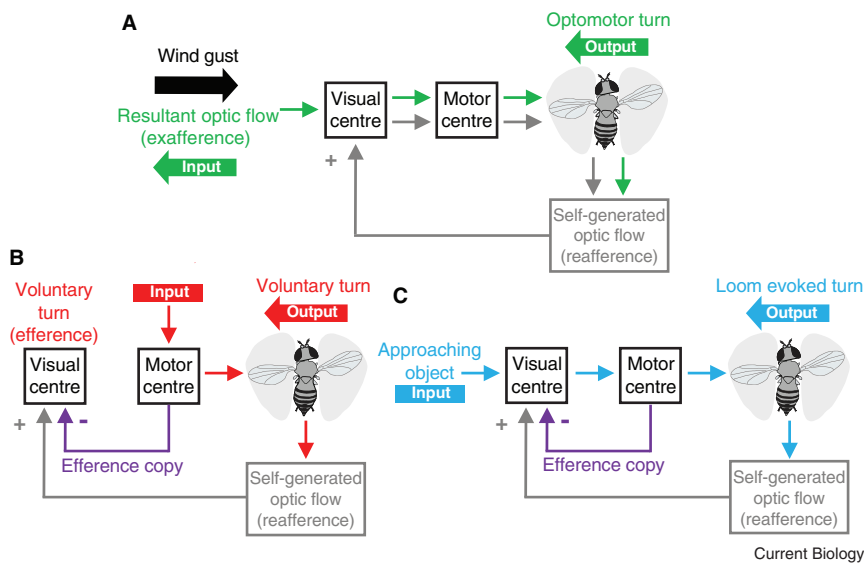


Figure 1. Motivation modulation of efference copies in the fly *Drosophila melanogaster*. (A) If a flying animal is moved to the right by, for example, a gust of wind (black arrow), this generates optic flow to the left (exafference, green input arrow). This stimulates optic flow sensitive neurons in the visual centre¹¹, which in turn activates motor command neurons in the motor centre, resulting in a leftward turn (green output arrow) to correct for the unintended flight deviation¹⁴. This turn itself generates self-generated optic flow (reafference, grey), which activates other optic flow sensitive neurons in the visual centre. (B) If the fly instead performs a voluntary saccadic turn (efference, red input), an inhibitory efference copy (purple) is sent from the motor centre to optic flow sensitive neurons in the visual centre. The strength and timing of the efference copy (purple) cancels out the reafference signal (grey)⁵. (C) If the fly turns away from a rapidly approaching object (blue input), the inhibitory efference copy (purple) functions as during voluntary saccades⁵. (Fly by Gaby Maimon.)

control theory perspective. Indeed, in two of the cases the fly is turning voluntarily, either randomly or in an attempt to avoid a predator. Thus, suppression of the optomotor response is required so as not to counteract these turns. Indeed, a long-standing conundrum in insect motion vision has been how to suppress the strong optomotor response¹⁴ so as not to counteract voluntary turns, for example during target pursuit¹⁵.

In contrast, Fenk *et al.*⁶ found that if the fly was exposed to a rapid pulse of optic flow, as would be experienced if for example it were moved by a strong gust of wind, the visual neurons involved in the optomotor response were not suppressed. This makes sense if thinking about the role of these neurons: as they control the optomotor response¹⁶, the fly should not suppress them, because generating a corrective flight maneuver of the right magnitude and duration is precisely their role.

Fenk *et al.*⁶ convincingly demonstrate that we can think of this in a course-changing *versus* course-stabilizing

context. Indeed, the neurons involved in the optomotor response need to be suppressed during *course-changing* turns, to stop them from inducing an optomotor response that could otherwise counteract the voluntary turn¹⁵ (Figure 1B, C). In contrast, they need to remain active during *course-stabilizing* manoeuvres to ensure that the resulting flight correction restores the intended flight path (Figure 1A).

Fenk *et al.*'s study⁶ thus opens up a new way to look at activity modulation of sensory neurons, where the context of the action is just as important as the action itself, even for something as seemingly simple as a turn. This is important as efference copies are found in many systems. For example, when bats produce their loud echolocation sounds they simultaneously suppress their auditory pathways², so they are not temporarily deafened and thus unable to detect the much fainter echoes³. Similarly, in crickets the pattern motion generator producing singing simultaneously inhibits the auditory pathway⁴. Furthermore, in the

lateral line system, where efference copies have been studied for a long time⁷, the hair cell suppression is adjusted to the swimming behavior. Indeed, in zebrafish only the subset of hair cells that would be activated by a swimming behavior are inhibited, while leaving others unaffected¹⁷, thereby still allowing the detection of potential predators.

Importantly, flies are extremely useful for scientific research as we have access to identified neurons at each stage of the sensori-motor transformation cascade^{13,18,19}, as well as a range of genetic tools that allow for real-time activation and inhibition of single neurons in active animals. *Drosophila* thereby provides an excellent and powerful system for investigating the cellular basis for efference copies. In future work it will be interesting to determine the extent to which the context of the action affects efference copies across the animal kingdom.

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Biodiversity: Monitoring trends and implications for ecosystem functioning

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Systematic, long-term monitoring provides crucial evidence regarding the vulnerability of biodiversity to environmental change. New research shows that trends in taxonomic diversity do not necessarily match trends in functional diversity. Interpreting the implications of different kinds of diversity change for ecosystem functioning remains a key priority.

The modern era has been defined as a period of rapid environmental change¹. Some ecologists have raised concerns that this environmental change occurs in the form of apocalyptic species declines², whereas others have emphasized a re-organization of species akin to a game of musical chairs³. The social, economic, and environmental implications of biodiversity change have been the focus of interdisciplinary research for the last three decades^{4,5}. For example, influential experiments have revealed that species loss can reduce the productivity and stability of plant communities. Similarly, declines in biological diversity can also translate into reductions in multiple important ecological functions and services such as pest control, pollination, and breakdown of organic matter⁶. Outside of controlled experiments, however, attributing real-world

biodiversity changes to changes in ecosystem service has proven to be considerably more complicated⁷. This has led to the suggestion that multifaceted approaches are needed to interpret and predict the potential implications of diversity change⁸. Indeed, a new study by Greenop *et al.* in this issue of *Current Biology* shows that, for taxa associated with at least four key ecosystem services or disservices, temporal trends in taxonomic diversity do not parallel changes in functional diversity⁹.

Greenop *et al.* tracked roughly 225 species associated with three desirable ecosystem services (crop pollination, pest control, and organic matter breakdown) and one ecosystem disservice (crop damage)⁹. They evaluated national-scale diversity trends for Great Britain using several million spatially and temporally explicit records

collected by naturalists from 1970 to 2015 and deposited in the UK Biological Records Centre⁹. From these records, they discovered that variability in ecosystem vulnerability depended on the focal ecosystem service (or disservice) considered, as well as the metric used to assess diversity (taxonomic diversity or functional diversity)⁹. Aquatic invertebrates associated with organic matter breakdown (specifically, caddisflies) showed a decline and recovery for both functional and taxonomic diversity⁸. In contrast, bee species associated with pollination of oil rapeseed crops increased in taxonomic diversity, but showed a dip followed by a rise in functional diversity⁹. Both pests and pest-control agents (specifically, predatory beetles) showed increases in taxonomic diversity but comparatively stable patterns of functional diversity⁹.