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Neurobiology: Imaging Prey Capture Circuits in Zebrafish

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Two recent studies used a virtual hunting assay and functional imaging to identify prey-capture circuits in zebrafish. Together they show that the optic tectum and a pretectal region are two retinorecipient areas important for the recognition and capture of prey.

In many species certain visual stimuli can trigger specific behaviours. For example, a change in light levels will cause compensatory changes in pupil diameter. For simple behaviours, such as the pupillary light reflex, we understand in some detail the neural circuits that underlie and link perception of the stimulus to execution of the behaviour [1]. For more complex visually-guided behaviours, such as hunting prey or avoiding predators, we know far less about the underlying circuitry. Two recent studies [2,3] have used larval zebrafish as a model system to reveal some of the circuitry involved in hunting, a behaviour that appears when larvae reach five days of age. Prey capture at this stage is highly dependent on vision and occurs through a number of distinct locomotor behaviours: a unilateral bend of the tail into a J shape, which orients larvae towards their prey; convergent saccades, which create a region of binocular overlap and which may provide a mechanism for judging prey distance; a capture swim; and finally a bite [4–7].

J turns and convergent saccades are motor behaviours that are fairly unique to hunting and can therefore be used to distinguish hunting from other behaviours, such as escaping or simply navigating from A to B. Importantly, J turns and convergent saccades can be triggered by artificial stimuli, such as moving dots projected onto a screen, and

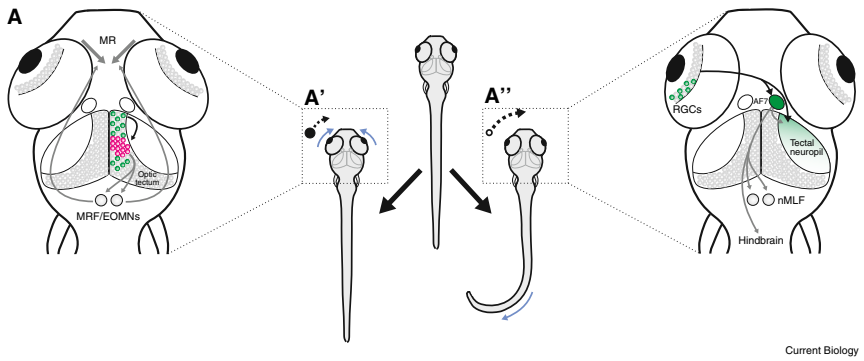

Figure 1. Visual neural circuits activated during virtual prey capture in zebrafish larvae.
(A) Schematic diagram showing the prey-like stimuli used to elicit convergent eye movements (left) and J-turns (right) according to Bianco and Engert [2] and Semmelhack *et al.* [3], respectively. The optimal stimuli found in these studies differed in size, speed and contrast polarity (see text for details). (A') Inset depicting neurons in the optic tectum (green cells) that are candidates for the perception of prey, the recruitment of tectal assemblies (magenta cells) that may trigger saccades following prey perception, and the hypothesized downstream circuits (grey arrows) which control eye movement. In particular, activity of the tectal assemblies activates circuits in the mesencephalic reticular formation (MRF) which control saccadic eye movements through the activation of motorneurons innervating extraocular muscles (EOMNs). Medial rectus (MR) muscles are controlled by ipsilaterally projecting EOMNs to produce a convergent saccade. (A'') Inset showing prey-responsive retinal ganglion cells (green cells in the retina) and their arbourization patterns in the brain, which include the pretectal area AF7 and the superficial layers of the tectal neuropil. Grey arrows indicate the potential downstream circuitry involved in the release of locomotor behaviours such as J turns.

in larvae that are partially restrained [4,8]. Bianco and Engert [2] and Semmelhack *et al.* [3] used this virtual hunting assay for restrained larvae to identify the stimulus most effective at triggering hunting behaviour (Figure 1). They then combined presentation of the optimal stimulus, high-speed video recording of behaviour and *in vivo* functional imaging of larvae expressing a genetically-encoded calcium sensor (GCaMP5G or 6s) throughout the brain in order to identify the neurons involved in prey recognition or release of hunting behaviours.

In the study by Bianco and Engert [2], reported in this issue of *Current Biology*, convergent saccades were used as a readout of hunting behaviour. Convergent saccades were triggered quite rarely, but the probability of eliciting a saccade was dependent on specific combinations of stimulus features — the most effective stimulus from the set tested was a dark spot, 13° in size, and moving at 30° per second (Figure 1). Using functional imaging, the authors then identified populations of neurons in the optic tectum that were tuned non-linearly to the same combination of stimulus features. The authors have thus identified neurons in the zebrafish tectum that are excellent candidates for being part of a circuit that mediates perceptual recognition of prey.

To find such neurons in the optic tectum is perhaps not unexpected. The retinotopic organisation of retinal inputs to the tectum creates a map of visual space in the brain which is used to direct orientating behaviours, such as those involved in hunting. Furthermore, neural activity within the larval zebrafish tectum has been observed in response to live paramecia and ablation of the tectum severely impairs the ability of larvae to catch prey [9,10]. Bianco and Engert [2] went a step further, however, by asking which neurons might trigger convergent saccades following the perception of prey. Because convergent saccades occurred quite rarely the authors could compare the activity of tectal neurons during hunting and non-hunting episodes in order to identify neurons whose activity specifically preceded the initiation of saccades. This approach revealed assemblies of neurons that met these criteria and, strikingly, these assemblies contained very few of the neurons involved in prey recognition (Figure 1). Thus, the perception of prey and release of hunting behaviours appear to be mediated by separate populations of tectal neurons.

Bianco and Engert [2] have thus captured the tectum's role in perception *and* action selection. An important point demonstrated by the authors is that action does not automatically follow perception. Activation of the 'prey-detecting' neurons only occasionally leads to activation of the 'prey-capture neurons' and hence a hunting response. Why would this be the case? Firstly, it may be that at larval stages prey capture circuits are still under development and that the mechanisms linking prey-perception to prey capture are not fully formed at this stage. Even in fully mature circuits, however, attention, internal states such as hunger and recent experience can all influence stimulus preference and behavioural choice. The findings of Bianco and Engert [2] allow them to propose a model circuit for hunting behaviour (Figure 1), and the assay they have developed will provide the means with which to probe how factors such as motivational state modulate the function of these circuits.

Bianco and Engert [2] have thus demonstrated tuning for prey-like stimuli in the tectum, but — perhaps motivated by classic literature demonstrating retinal ganglion cells in the frog that respond to prey-like objects [11] — Semmelhack *et al.* [3] hypothesised that such tuning is first generated in the retina. To test this, they performed functional imaging of GCaMP6-expressing retinal ganglion cell axons within retinorecipient areas of the larval brain. Aside from the tectum, which is the largest retinorecipient area, there are nine other areas, or arbourisation fields (AFs), in which retinal ganglion cell axons terminate [12]. Currently, very little is known about the function of these areas. To find the optimal stimulus for triggering hunting Semmelhack *et al.* [3] also used a virtual hunting assay for tethered zebrafish, but instead of saccades they used the J turn as an indicator of a hunting episode (Figure 1). The authors found that bright spots of 3° in size, moving at 90° per second, were most effective at triggering J turns.

Using functional imaging Semmelhack *et al.* [3] found that retinal ganglion cell axons terminating in AF7, a pretectal area, and the optic tectum responded well to the optimal stimulus and that the tuning of retinal ganglion cell axons in AF7 closely matched the behavioural tuning curves for stimulus size and speed. Furthermore, retinal ganglion cell axons within AF7 responded to real prey (paramecia) and the frequency of prey capture bouts was reduced, but not

eliminated entirely, by laser ablation of the retinal ganglion cell axons within AF7. These data suggest that selectivity for prey-like stimuli is already present in retinal ganglion cell axons targeting AF7, and that AF7 plays a role in regulating hunting behaviour. Anatomical reconstruction of singly labelled cells showed that two morphological subtypes of retinal ganglion cell innervate AF7, and that these cells also send collateral branches to the superficial layer (*stratum opticum*) of the tectum, consistent with the fact that some responses to prey-like stimuli were also seen in RGCs innervating the tectum.

By labelling single neurons in the vicinity of AF7, Semmelhack *et al.* [3] reconstructed the anatomy of potential postsynaptic partners of retinal ganglion cell axons targeting AF7. They identified cells that projected to the optic tectum and a second type of neuron that projected to the nucleus of the medial longitudinal fasciculus (nMLF) and hindbrain, areas that are important for controlling swim direction and speed (Figure 1) [13–15]. In future studies, it will be important to establish that these cells are *bone fide* targets of retinal ganglion cells within AF7 and to determine their tuning properties and neurotransmitter identity. Addressing these questions will provide valuable insight into how retinally-derived information about the presence of prey is transformed by circuits within AF7 to modulate prey capture.

Bianco and Engert [2] and Semmelhack *et al.* [3] reach different conclusions about the optimal stimulus for triggering hunting. This may be because the two groups did not explore exactly the same stimulus space, or that important experimental conditions were not identical in each study. An alternative explanation is that the two studies focussed on different stages of the visual pathway, Semmelhack *et al.* [3] on retinal ganglion cells, and Bianco and Engert [2] on tectal neurons. The differences they see may reflect the different response properties of neurons at different stages of the sensorimotor pathway. The two studies may therefore be complementary rather than contradictory. Together they certainly provide significant new insight into the circuitry underlying a complex visually-driven behaviour and raise some fascinating questions for the future. How do the tectum and AF7 together coordinate the various aspects of prey capture, and how are prey capture circuits modulated by attention, motivational state and input from other sensory modalities are questions to keep the field busy for quite some time.

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Epithelial Cell Division: Keeping Aneuploidy Levels in Check

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Aneuploidy is deleterious at the cellular and organismal level and can promote tumorigenesis. Two new studies in *Drosophila* imaginal discs underscore the cellular and tissue-wide mechanisms that prevent the accumulation of aneuploid cells in symmetrically dividing epithelial tissues upon changes in centrosome number.

Aneuploidy — an abnormal number of chromosomes or parts of chromosomes — is deleterious at the cellular and organismal level from yeast to man [1,2], and maintenance of highly aneuploid cells in a tissue can cause

