

# Current Biology

## Visual Threat Assessment and Reticulospinal Encoding of Calibrated Responses in Larval Zebrafish

### Highlights

- Fast looming stimuli produce short-latency escapes or freezing behavior
- Slow looming stimuli produce longer-latency, more kinematically variable escapes
- Mauthner cell recruitment is more likely during responses to fast looming stimuli
- Alternate reticulospinal circuits drive responses to less urgent visual stimuli

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### In Brief

Bhattacharyya et al. demonstrate that larval zebrafish use the approach rate of looming visual stimuli to assess the potential level of threat and act accordingly.



# Visual Threat Assessment and Reticulospinal Encoding of Calibrated Responses in Larval Zebrafish

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<http://dx.doi.org/10.1016/j.cub.2017.08.012>

## SUMMARY

All visual animals must decide whether approaching objects are a threat. Our current understanding of this process has identified a proximity-based mechanism where an evasive maneuver is triggered when a looming stimulus passes a subtended visual angle threshold. However, some escape strategies are more costly than others, and so it would be beneficial to additionally encode the level of threat conveyed by the predator's approach rate to select the most appropriate response. Here, using naturalistic rates of looming visual stimuli while simultaneously monitoring escape behavior and the recruitment of multiple reticulospinal neurons, we find that larval zebrafish do indeed perform a calibrated assessment of threat. While all fish generate evasive maneuvers at the same subtended visual angle, lower approach rates evoke slower, more kinematically variable escape responses with relatively long latencies as well as the unilateral recruitment of ventral spinal projecting nuclei (vSPNs) implicated in turning. In contrast, higher approach rates evoke faster, more kinematically stereotyped responses with relatively short latencies, as well as bilateral recruitment of vSPNs and unilateral recruitment of giant fiber neurons in fish and amphibians called Mauthner cells. In addition to the higher proportion of more costly, shorter-latency Mauthner-active responses to greater perceived threats, we observe a higher incidence of freezing behavior at higher approach rates. Our results provide a new framework to understand how behavioral flexibility is grounded in the appropriate balancing of trade-offs between fast and slow movements when deciding to respond to a visually perceived threat.

## INTRODUCTION

When an animal perceives an oncoming predator, it is critical to correctly choose whether, when, and how to move to survive the

impending attack. Looming visual stimuli, simulating an approaching predator, provide an opportunity to investigate the underlying mechanism of threat assessment involved in this set of decisions [1, 2]. The current consensus across a variety of vertebrate and invertebrate organisms is that an approaching predator triggers a ballistic escape response once it reaches a certain subtended angle threshold [3–6]. Given the constraints on predator size, this angle threshold is equivalent to a proximity threshold.

Within vertebrates, this theory of a proximity-based response aligns well with findings from a bilateral pair of giant fiber interneurons in the brainstem of fish, called Mauthner cells (M-cells) [7]. M-cells collect sensory information from one side of the body and transmit it to the other side via a large caliber axon [8, 9], resulting in a strong contraction of body muscles opposite to the stimulus that generates a short-latency evasive turn. M-cells respond to visual, tactile, vestibular, auditory, lateral-line, and electric field stimuli [10–15] and are difficult to excite [16–18]. The conclusion from these studies across various modalities is that the decision to escape is a result of reaching the M-cell firing threshold due to strong sensory input, as would arise from an approaching predator that has traversed the proximity threshold.

However, with a proximity mechanism, there is no way to distinguish between an object that passes the proximity threshold rapidly versus slowly, corresponding to threats of differing urgency. Moreover, while M-cells expedite signal propagation and ensure quick reflexes, the power and relatively stereotyped reactions they produce can exact energetic costs and be exploited by predators [19–21]. It would therefore be beneficial to encode speed of approach as an additional means to decide whether to engage the giant fiber escape systems or alternate, less costly strategies, such as no response or a less rapid, more flexible response. Currently, it is unknown whether vertebrates use approach rate to inform the trade-off between short-latency, ballistic movements, and long-latency, more variable movements.

Here, we test the hypothesis that approach rate modulates escape behavior in larval zebrafish by using virtual looming stimuli with naturalistic sizes and approach rates, high-speed kinematic analysis in free swimming animals, and in vivo calcium imaging in partially restrained fish to assess the contribution of M-cells to the observed behavior. While zebrafish larvae did

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