



**Small Circuits for Large Tasks: High-Speed  
Decision-Making in Archerfish**

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vivo (23); however, increased quantal amplitude after SWE and pharmacological treatments in vivo identify a clear postsynaptic component for the plasticity observed. Although the in vitro pairing protocol is a crude approximation of the kind of activity that layer 2/3 neurons experience in vivo, it combines a physiological frequency (24, 25) of afferent stimulation (2 Hz) with NMDAR activation and predicts with remarkable accuracy the effects of in vivo SWE and pharmacological treatment.

Is this increase in synaptic strength correlated with learning behavior? To test this, we used an associative tactile conditioning task that pairs whisker deflection [conditioned stimulus (CS)] with a nonaversive, habituating air-puff stimulus [unconditioned stimulus (US); Fig. 4G and movies S1 and S2]. SWE mice showed increased mobility after whisker deflection as compared to controls, indicating that the SWE enhanced CS-US association (Fig. 4I). In parallel with their effects on synaptic strength in SWE mice, treatment with CPP and AIDA further enhanced or reduced associative learning (Fig. 4I). Analysis of changes in mobility over the course of task acquisition shows that SWE + CPP-treated animals acquired the CS-US association significantly faster than did SWE animals (Fig. 4J). These data indicate that increased synaptic strength in the barrel cortex is associated with enhanced performance in a whisker-dependent learning task, and that NMDAR and mGluR antagonists similarly affect synaptic strength and behavioral output.

Why doesn't normal sensory experience (that is, when all whiskers are intact) result in a similar

occlusion of NMDAR-dependent LTP? Compared to SWE, this stimulus may not be sufficiently strong to induce a switch in NMDAR and mGluR properties. However, in both our experiments and many others [see, for example (26, 27)], a fraction of neurons failed to demonstrate NMDAR-dependent LTP. It is tempting to speculate that in these cells, an mGluR-dependent form of LTP might be observed in the presence of NMDAR antagonists.

Our results indicate that after the initiation of LTP-like processes by sensory experience, a capacity for further synaptic strengthening is preserved and depends on mGluR activation. Because mGluR-mediated synaptic strengthening was observed both in vitro and in vivo, this is likely to be a physiologically relevant mechanism that may explain why an apparent "ceiling" for LTP does not negate the benefits of cumulative experience in enhancing response properties in the neocortex.

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#### Supporting Online Material

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Figs. S1 to S6

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Movies S1 and S2

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## Small Circuits for Large Tasks: High-Speed Decision-Making in Archerfish

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The enormous progress made in functional magnetic resonance imaging technology allows us to watch our brains engage in complex cognitive and social tasks. However, our understanding of what actually is computed in the underlying cellular networks is hindered by the vast numbers of neurons involved. Here, we describe a vertebrate system, shaped for top speed, in which a complex and plastic decision is performed by surprisingly small circuitry that can be studied at cellular resolution.

It is widely accepted that cognitive abilities such as making complex decisions require the enormous densities of highly interconnected cortical neurons. However, not all neurons within the areas labeled by functional magnetic resonance imaging (fMRI) as active during complex cognitive tasks [e.g., (1–4)] might be crucial for the performance, and perhaps much smaller "minimum circuitry" would suffice. Here, we provide evidence for this view in a vertebrate system, in which a highly

complex decision is made by surprisingly compact neural circuitry.

Archerfish are renowned for their ability to down aerial insect prey with precisely aimed shots of water. As soon as their successful shots dislodge their prey from the substrate, the fish must make an important decision (Fig. 1). On the basis of at least three independently varying initial parameters of prey motion, they must initiate an adapted open-loop start that, without requiring any further sensory information, rotates the fish toward where their prey will later land and pushes them off with a speed matched to distance (5–7). Due to heavy competition from peers and other surface-feeding fish, this decision must be made rapidly and accurately. The decision requires

learning and is absent when competition is lacking, and its tuning appears to involve high levels of generalization and abstraction (8–10).

In principle, archerfish could use a priori information to prime and speed up their decisions: Observing the shot would signal all school members when aerial motion needs to be responded to and could perhaps even signal the likelihood of particular trajectories. To test the importance of such contextual information, we completely deprived the fish of it. In these experiments prey was initially invisible to the fish, and the experimenter could at any time elicit a prey trajectory with speed and angle randomly selected from large ranges (matching the corresponding ranges in naturally dislodged prey) (fig. S1). Surprisingly, even when shooting-related information was thus not available for priming the decisions, the minimum and average latencies required for accurate responses were not longer than in the control, and average latency appeared to be even slightly reduced (by about 5 ms,  $P = 0.034$ ; Fig. 2B; table S1). Furthermore, with only target motion available, the fish were just as accurate as when additional contextual information was freely available ( $P = 0.212$ ; Fig. 2C; table S1). These findings show that motion cues are necessary and sufficient to trigger the archerfish's high-speed decisions and this, in turn, places full control over all decision-relevant parameters in the hands of the experimenter.

Prospective shooters must precisely pinpoint the location of their aerial prey (11) and could thus focus

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the processing of aerial motion signals to the region around their prey. To test whether such a focus, set a priori, was critical to the performance, we cued the fish to one of three platforms, but then started prey motion from any of the other platforms, a set distance from where the fish would assume motion to occur (Fig. 3A). Surprisingly, even substantial horizontal offsets of 20 cm—34° seen from below the cue platform—did not affect response latency ( $P = 0.103$ ; table S1). Latency increased only at an offset between expected and actual takeoff of 40 cm, or about 53° of visual angle (Fig. 3B;  $P < 0.001$ ; table S1). Minimum latency, observed in the fastest responses, was also only affected at this large offset (table S2). Furthermore, accuracy was completely unaffected by displacing the start point of the prey’s course (Fig. 3C;  $P > 0.3$  in all cases). Hence, the fish did not a priori limit or enhance the processing of target motion to a region of interest.

Yet the fish do exploit selective attention—however, not based on a priori information but rather as an integral part of their complex decision. To test whether the fish averaged motion signals over extended regions, as suggested by the findings of Fig. 3, B and C, we simultaneously blew off two similar-sized, initially invisible flies from the start platform. Both flies moved at approximately equal speed but in opposing directions (Fig. 3D), and averaging would make the fish choose the point of impact of the flies’ center of mass. However, when challenged in this way, the fish immediately and highly selectively decided which of the two conflicting motion signals to take into account. Starts were directed not at the point predicted by averaging or any intermediate point but right at the point of impact of the chosen fly (Fig. 3E; error distributions not significantly different in one-fly and two-flies conditions,  $P = 0.10$ ). Furthermore, the added decision which of the two targets to choose did not increase latency (Fig. 3E;  $P = 0.13$ ; table S1). The decision which fly to attend to was not made at random: Although the choices were not per se explained by differences in the speed

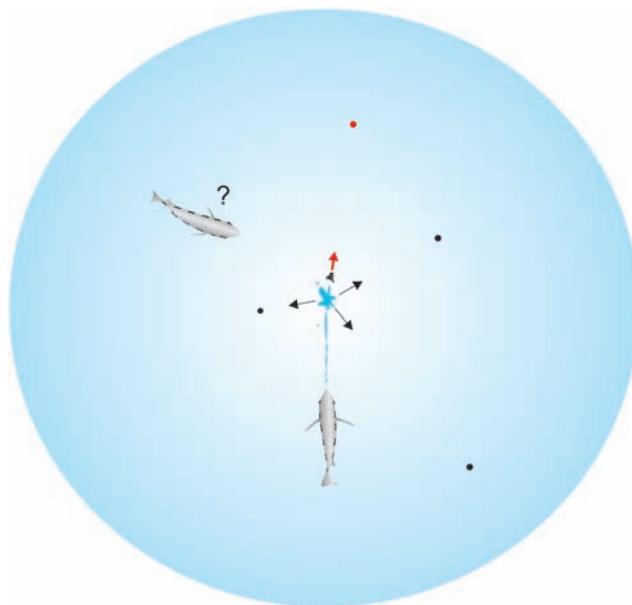
of the two flies or by the angle between the fly’s motion and the fish’s initial orientation, the fish significantly preferred that fly whose later landing point lay closer: Chosen flies had an average distance of 266 mm (SEM = 14.7 mm; range: 26 to 624 mm;  $n = 80$ ), whereas rejected flies were significantly ( $P < 0.001$ ) farther away (average distance: 353 mm; SEM = 12.6 mm; range: 73 to 597 mm,  $n = 80$ ). If it saved the fish at least 1 cm of travel (which it did in 77 cases), then the fish chose the closer fly with a probability of 68%.

The decisions showed a further interesting element of complexity. When changes in latency occurred, these were not accompanied by changes in accuracy. Figure 4A illustrates this finding for experiments in which changes in the visual contrast did affect latency (Fig. 4B) but not accuracy. This implies that latency is adjusted so as to guarantee a minimum in precision, thus avoiding energy being wasted with prematurely initiated inaccurate responses.

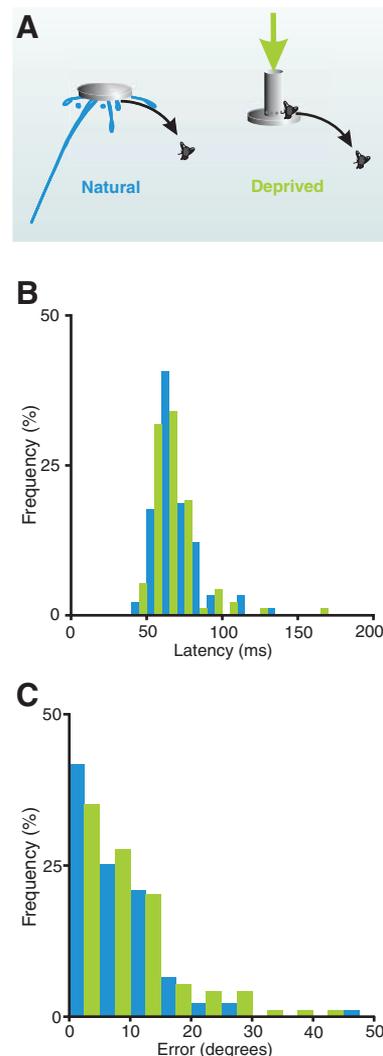
In the previous experiments, we noted accurately aimed responses at latencies down to 40 ms (table S2). To explore whether this value sets the limit of the archerfish’s decision-speed, we increased the visual contrast between the moving fly and its background (Fig. 4B). Average latencies obtained at lower visual contrast lay in the range reported previously (6, 7), but the highest contrast level produced a high proportion of precisely aimed predictive starts that were initiated after only a 40-ms latency (table S2 and Fig. 4A). However, the minimum decision time of about 40 ms could not be reduced further.

Our findings place a considerable upper bound on the neuronal circuitry that underlies the archerfish’s complex decision-making. The fish initiated adapted fast-starts as rapidly as 40 ms after the onset of the motion signals that were necessary and sufficient (Figs. 2 and 3) to trigger the decisions. The starts recruit the archerfish’s C-start escape network (5), which in most teleosts (12–14), including cichlids (15), consists of Mauthner’s cell-associated identified reticulospinal neurons and drives life-saving escapes

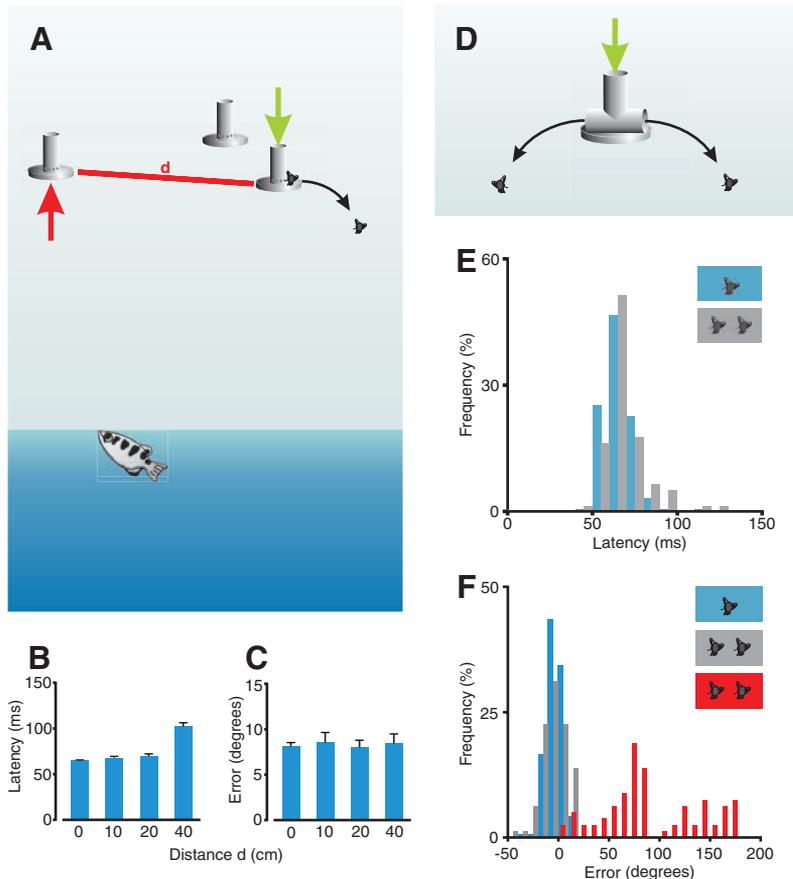
**Fig. 1.** High-speed decision-making in hunting archerfish. At the time a shot (blue) is on its way toward an insect prey, the insect’s later point of impact may be anywhere within a large area (blue circle; drawn to scale as appropriate for the present experiments). Previous work has shown that the fish quickly watch their prey’s initial motion to decide how much to turn and at what speed to start so as to be at the right spot at the right time. The decision is made on the basis of at least three variables that vary independently over large ranges: the initial speed, direction, and height of the insect prey. Arrows and dots indicate possible initial motion of the prey and corresponding impact points.



but also voluntary behaviors (16). In goldfish, the known path from the retina over the tectum to the ventral dendrite of the Mauthner’s cell to the onset of muscle contraction involves a sensorimotor delay of 35 ms (17, 18). Even if timing was slightly different in archerfish [and constrained mainly by photo-transduction (19–21)], to leave a more realistic 10 to 15 ms of sampling before the decision, the computations that underlie its decision must be done in the retina and the fastest output pathway. Retinal computations have already elegantly explained a range of



**Fig. 2.** Archerfish high-speed decisions do not require contextual a priori information. (A) In the “natural condition” (blue), fish dislodged a target fly from the bottom of a small disk. In the “deprived condition” (green), the fly was placed on top of the disk where it could not be seen by the fish. Motion then was triggered not by a fish’s shot but by an air-stream (green arrow) commanded by the experimenter. Depriving the fish from shooting-related contextual cues did not increase latency (B) nor decrease accuracy (C) of the responses (table S1). Histograms are based on  $n = 91$  (natural) and  $n = 94$  (deprived) responses. Binning starts at zero and counts relating to the natural (deprived) condition are shown in blue (green) in the left (right) half of each bin. Bin widths are 10 ms (B) and 5° in (C).



**Fig. 3.** Selective attention is part of the high-speed decision. (A) Fish were cued to one of three start disks (red arrow), but the initially invisible fly was started a set, randomly assigned, distance  $d$  from that disk. Response latency increased only at substantial distances (B), and the accuracy of the response was unaffected (C). Total of  $n = 556$  responses. (D) When two flies were simultaneously sent from the disk into opposing directions, the fish immediately and selectively attended to just one of the two flies. Latency (E) and aims taken (F) in the two-fly experiments were not statistically different from those in controls with just one fly leaving the start platform (blue). (E) Bins as in Fig. 2B. (F) Direction of aim relative to the later impact point of the chosen fly (gray; control: blue) and with respect to the point predicted by motion-averaging (red). Negative signs indicate errors in directions toward the start platform. First positive bin  $0^\circ$  to  $10^\circ$ , blue (gray) columns shown in first (second) half of bin, red columns placed in bin's center. Analysis of  $n = 163$  (80) single (two) fly starts.

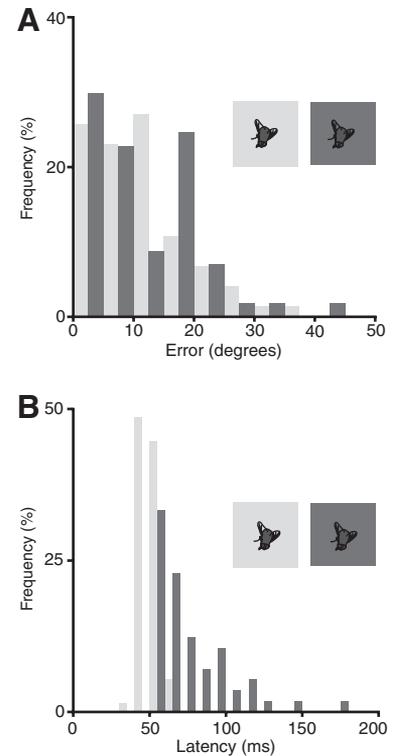
complex visual tasks (22–24) and could be the building blocks of the complex processing that would provide the archerfish's decision circuitry with quick and yet accurate estimates of speed, direction, and height of aerial prey. The later part of the circuitry must then combine the signals from the two eyes with signals coding for the fish's spatial position, accommodation, and gaze direction to transform them into an adapted motor pattern. Given our knowledge on teleost Mauthner's cell-associated C-start escape circuitry (12–18), it is likely that a small network of six identified neurons plays a key role in the initial decision, with the further (accessible) (12) set of serially repeated identified cells in the hindbrain contributing to its fine-tuning (10).

In conclusion, our data show that even complex decisions can be made rapidly and accurately by a relatively small number of neurons that are likely to offer outstanding opportunities for an approach at the cellular level (10, 12–14). Furthermore, because the circuitry does not require shooting-related inputs (Figs. 2 and 3), it can be studied *in vivo*, targeting both the ongoing processing and the ways in which the fish

tunes its decision-making circuitry to the laws of its outer world. Minimum circuits such as that used in archerfish decision-making might be much more widespread and could provide us with simpler systems to explore the neuronal mechanisms of decision-making and other “cognitive” computations, opening up a way of understanding how cognitive networks have evolved.

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**Fig. 4.** Top decision speed pins down the underlying network. Although changing the visual contrast between the prey and its immediate background did not significantly affect accuracy (A), it strongly affected latency (B). (A) Histogram showing the magnitude of the fish's error in aiming at high contrast ( $C = 0.51$ ) and low contrast ( $C = 0.061$ ). Both contrasts were different from the contrast used in the previous experiments. (B) High contrast shifts the distribution of latency and enables responses only 40 ms after the onset of prey motion. Binning as in Fig. 2, B and C, and based on  $n = 74$  starts at high (light) and  $n = 57$  at low (dark) contrast.

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**Supporting Online Material**

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