

# What pops out for you pops out for fish: Four common visual features

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Visual search is the ability to detect a target of interest against a background of distracting objects. For many animals, performing this task fast and accurately is crucial for survival. Typically, visual-search performance is measured by the time it takes the observer to detect a target against a backdrop of distractors. The efficiency of a visual search depends fundamentally on the features of the target, the distractors, and the interaction between them. Substantial efforts have been devoted to investigating the influence of different visual features on visual-search performance in humans. In particular, it has been demonstrated that color, size, orientation, and motion are efficient visual features to guide attention in humans. However, little is known about which features are efficient and which are not in other vertebrates. Given earlier observations that moving targets elicit pop-out and parallel search in the archerfish during visual-search tasks, here we investigate and confirm that all four of these visual features also facilitate efficient search in the archerfish in a manner comparable to humans. In conjunction with results reported for other species, these findings suggest universality in the way visual search is carried out by animals despite very different brain anatomies and living environments.

## Introduction

Visual search, the ability to find a target amidst distractors, is vital for animals' survival, since it can serve to search for prey or conspecifics and avoid predators. The animal's reaction time—that is, the time it takes to detect the target among distractors—is affected by the features of the target, the distractors, and their relations (Eckstein, 1998; Treisman & Gelade, 1980). In a typical visual-search experiment in the lab, the subject is requested to detect as fast as possible a target in a field of distractors. The change in the reaction time and accuracy as a function of the number of distracting objects is of great interest, since it helps to quantify the search and the efficiency of a feature (Wolfe, 1998a).

A fundamental estimate of visual-search performance is the slope of the reaction time as a function of the number of distracting objects (Wolfe, 1998a, 2016). When visual search is efficient (Figure 1A), the observer can scan the entire visual scene virtually in parallel and the target “pops out” immediately and automatically from the background. In such cases, reaction time does

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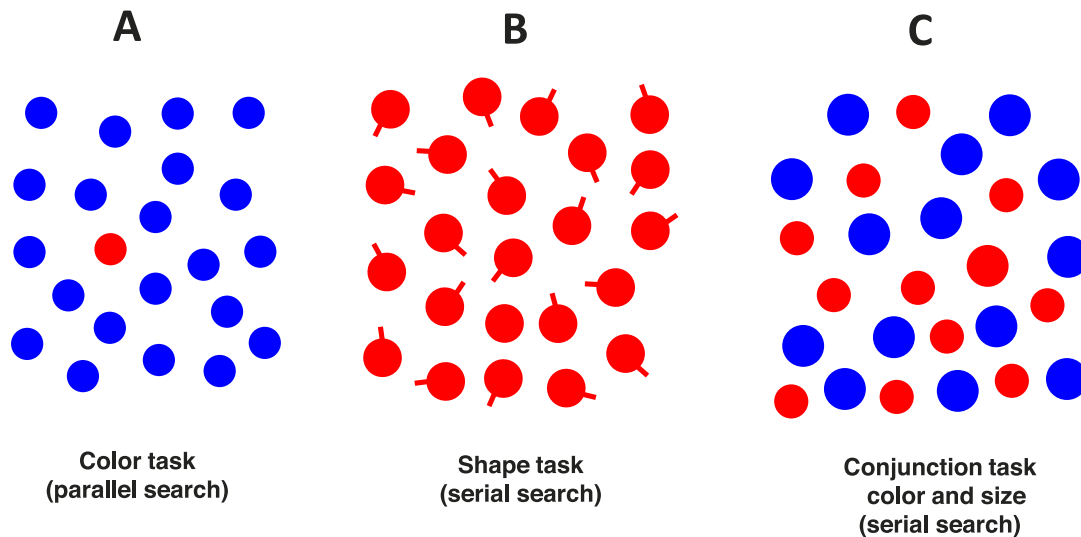


Figure 1. Visual-search task examples. (A) The color feature is very efficient, since it causes the target to “pop out,” making the search task easy (the target is the red disc). (B) An example of a shape task where the target does not pop out (the target is the red disc without the line). (C) Search task for a target characterized by two efficient features, such as color and size, is hard to detect, and the reaction time increases as a function of the number of distractors (the target is the large red disc).

not increase as a function of the number of distractors, and the slope of the function is near zero. In contrast, if the visual search is inefficient (Figure 1B), reaction time increases linearly, on average, as a function of the number of distractors, making the slope of the function positive and indicative of a search mode that scans the items serially one by one.

Many studies have been devoted to investigating the behavioral aspects of visual search in humans (Eckstein, 1998; Treisman & Gelade, 1980; Treisman & Gormican, 1988; Wolfe, 1998a, 1998b; Wolfe & Horowitz, 2017). Specifically, in the past 50 years, researchers have sought to explore which visual attributes guide attention—that is, which features elicit an efficient, fast visual-search mode. Wolfe and Horowitz (2004) concluded that there is considerable evidence that color, size, orientation, and motion guide attention in humans, causing the target to pop out in visual-search tasks. Taking into account the bulk of findings in the literature, it has been demonstrated that there is a continuum of search slopes from highly efficient to inefficient searches (Haslam, Porter, & Rothschild, 2001; Wolfe, 1998b, 2003, 2016). This observation complements the original observation and categorization of visual search into parallel and serial search modes (Treisman & Gelade, 1980), and places these search modes as part of a continuum of search efficiency. These two extremes, however, can serve as anchor modes when performance is unmistakably characteristic of either.

There is an extensive body of research devoted to investigating other animals' ability to search visually (Amo, López, & Martín, 2004; Hamilton & Winter,

1984; Schultz & Fincke, 2013; Schwarz, Mangan, Zeil, Webb, & Wystrach, 2017; Sztatecsny, Strondl, Baierl, Ries, & Hödl, 2010; Théry & Casas, 2002). Nevertheless, in contrast to humans, little is known about what features guide attention in the context of visual-search tasks—that is, which features elicit efficient visual search and which do not. For example, it has been reported that color helps bees identify flower species with high pollen and that they can find a target among distractors when it is distinguished by its color. However, this type of search is not efficient, since as the set size of distracting objects increases, so does the bees' reaction time (Chittka & Spaethe, 2007). Other examples include flies that are able to choose a target based on saliency of color and shape (Tang & Guo, 2001) and spiders that rely on the saliency of motion direction to capture prey (Bartos & Minias, 2016). However, these types of saliency findings do not demonstrate pop-out or visual-search properties.

To address this issue, we selected the archerfish as an animal model. The archerfish is an aquatic vertebrate that lacks a fully developed cortex (Karoubi, Segev, & Wullimann, 2016) but exhibits complex visual behaviors and possesses a unique hunting skill based on vision (Ben-Simon, Ben-Shahar, Vasserman, Ben-Tov, & Segev, 2012; Rossel, Corlija, & Schuster, 2002; Schlegel & Schuster, 2008; Schuster, Rossel, Schmidtman, Jäger, & Poralla, 2004; Temple, Hart, Marshall, & Collin, 2010; Tsvilling, Donchin, Shamir, & Segev, 2012). The archerfish mainly lives in mangrove habitats of the South Pacific and Indian Oceans (Allen, 1978). It is primarily carnivorous, gaining nourishment from

insects, small fish, and crustaceans (Simon & Mazlan, 2010). It is mostly known for hunting terrestrial insects found on foliage and low-lying branches by shooting a powerful and accurate water jet at them (Burnette & Ashley-Ross, 2015; Vailati, Zinnato, & Cerbino, 2012) that causes them to fall into the water so the fish can eat them (Lüling, 1963). Its remarkable hunting skill is due to its large eyes which enable binocular vision to targets above it, its good eyesight (Ben-Simon et al., 2012), its color vision (Temple et al., 2010; Vasserman, Shamir, Simon, & Segev, 2010), and its ability to take into consideration the refraction effect of light as it passes through air to water (Dill, 1977). It is possible to train the archerfish to distinguish between artificial objects presented on a computer monitor and shoot at them, thus enabling overt observation of its visual decisions in controlled behavioral experiments in the lab (Ben-Tov, Ben-Shahar, & Segev, 2018; Newport, Wallis, Temple, & Siebeck, 2013).

In addition to its general capacities, the archerfish has other capabilities that make it an excellent animal model for visual-search research. Rischawy and Schuster (2013) have demonstrated that the archerfish can perform serial search on static targets, and a recent study (Ben-Tov, Donchin, Ben-Shahar, & Segev, 2015) has confirmed that the archerfish exhibits both parallel and serial search modes during visual search with moving targets. Specifically, this fish appears to exhibit parallel search to detect moving bars when they differ from the distractors in their speed or direction of motion. However, when the target is defined by a conjunction of speed and width, the archerfish resorts to serial search. A different study has shown that orientation contrast in the archerfish triggers saliency (Mokeychev, Segev, & Ben-Shahar, 2010), enabling visual search through one of the most prominent visual features identified in other species. Newport et al. (2013) reported that the archerfish is capable of serially scanning symbols when given a four-alternative test.

Here we examine the visual-search behavior of the archerfish with a new set of visual-search tasks of the four common visual features known to pop out for humans—color, size, orientation, and motion (see example in Figures 1A)—as well as shape and conjunction search tasks (see examples in Figure 1B and 1C). Finally, we compare the results to what has been found in humans. For the sake of simplicity, in this study we use the terminology of parallel and serial search as the two extreme visual-search modes in the continuum of search efficiencies (Wolfe & Bennett, 1997). Unlike humans, our animal model performed only a small total number of visual-search tasks, leaving open the question of the existence of a similar continuum. At this point, we thus allow ourselves the original bimodal terminology and

discrimination between two search modes (parallel vs. serial) based on the search-time slope. The details now follow.

## Methods

Fourteen archerfish (*Toxotes chatareus*), 6–14 cm in length, were used in this study. The fish were caught in the wild and purchased from a local animal vendor. Each was housed in a separate water tank, 32 × 50 × 28 cm in size, filled with brackish water (2–2.5 g of red sea salt mix per 1 L of water). The water was filtered, oxygenated, and kept at a temperature of 25°–28°C. The room was illuminated with artificial light on a 12:12-hr day–night cycle.

All experiments were approved by the Ben-Gurion University of the Negev Institutional Animal Care and Use Committee and were in accordance with government regulations of the state of Israel. All experiments are also adhered to the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research.

## Fish training

The fish were gradually trained to shoot at a static target presented on a LCD screen (VW2245-T, 21.5 in., BenQ, Taoyuan, Taiwan) placed on top of a transparent tempered-glass plate 32 cm above water level (Figure 2A). First they were trained to shoot at a target shaped as a disc (1 cm in diameter) that appeared at random locations on the screen. The fish were rewarded with a food pellet for each successful hit—that is, only if they shot at the designated object defined as the target. This basic training was considered successful and was terminated when a fish successfully shot the target in less than 5 s from target onset and had a high target-selection rate (above 80%).

The second stage was to train the fish for their designated experimental task (color, size, etc.). First they were trained to shoot at the target alone (red target, big target, etc.), and then they were gradually trained to shoot at the target in the presence of three, six, nine, or 12 (or four, six, 10, or 12) distractors (blue distractors, small distractors, etc.). It was important to gradually introduce the distractors in the training stage, since each fish had its own learning rate and some tasks were more difficult than others. When a fish shot the target in less than 5 s and had a high target-selection rate (above 80%), we began the experiment itself.

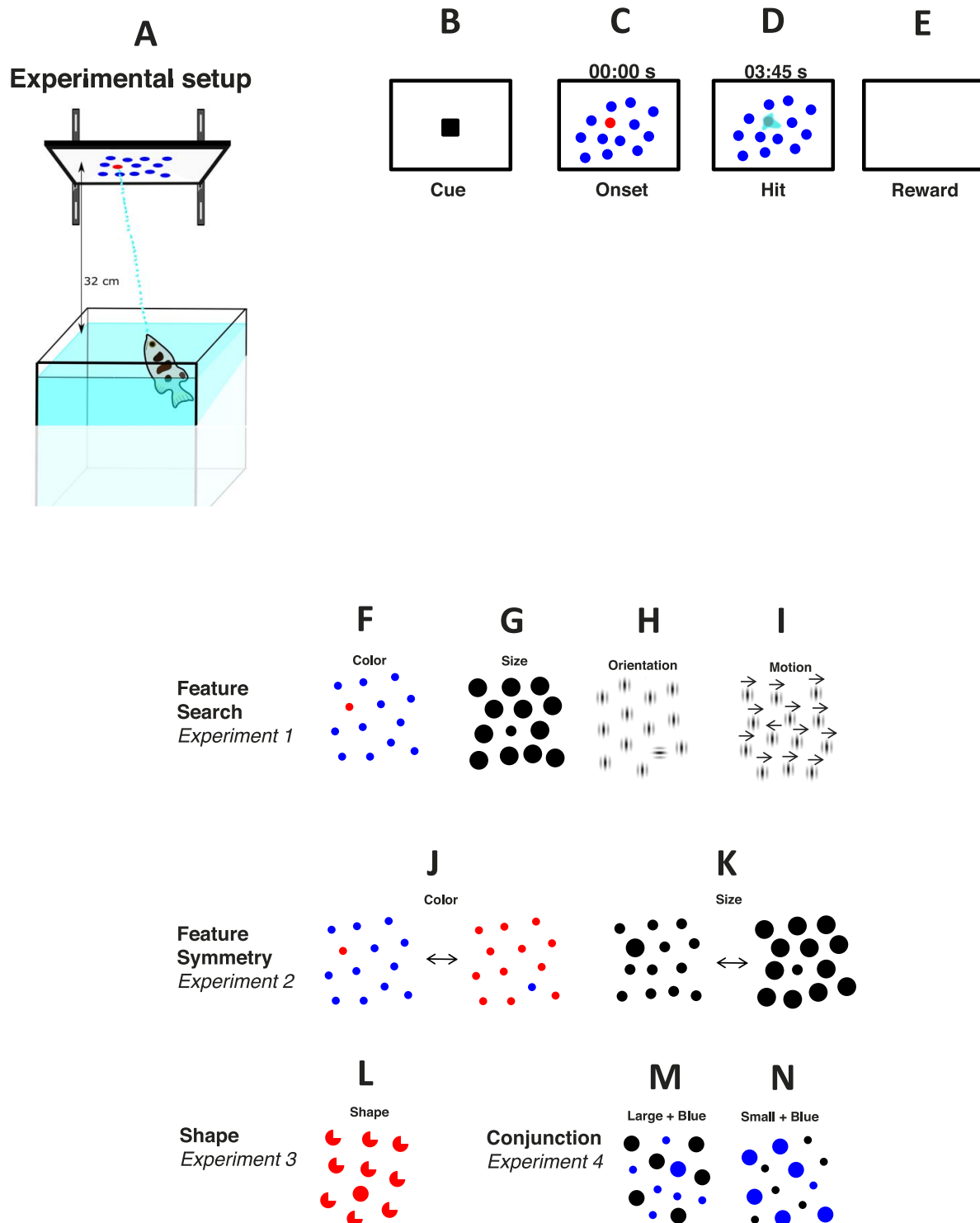


Figure 2. The experimental paradigm. (A) Experiment setup: The fish were trained to shoot at an artificial target presented on a LCD screen. The screen was placed on top of a transparent tempered-glass plate 32 cm above the water level. Experiments were recorded using an HD video camera and stored off-line for further analysis. (B–E) Experiment flow: One trial from an experiment. (B) A blinking square signaled to the fish that the trial was about to begin, enabling it to prepare by gazing up at the center of the screen. (C) The visual-search task appeared and the timer started. (D) As soon as the fish shot, the timer was stopped after the water jet hit the screen. (E) The screen went white and the fish was rewarded if it successfully hit the target. (F–N) Types of visual-search tasks used in the experiment. (F–I) Group 1: Feature-search experiments. In these experiments, we examined four features that make visual search efficient: (F) color, (G), size, (H) orientation, and (I) motion. (J–K) Group 2: Feature-symmetry experiments. The symmetry experiments tested features of (J) color and (K) size. (L) Group 3: Shape experiment. The target was characterized by a single nonefficient shape, which causes the search to be less efficient. (M–N) Group 4: Conjunction of color and size experiments. Two features, color and size, characterized the target. At first, the target was (M) large and blue; in the second set it was (N) small and blue.



## Behavioral experiments

The stimuli were displayed as PowerPoint presentations. The experiments were recorded using an HD camera (Handycam, HDR-CX240, Sony, Tokyo Japan) at 25 frames/s and stored offline for further analysis.

To prevent items in the room from distracting the fish during the experiment, Coroplast boards were placed on the sides of the aquarium before the experiment began. Furthermore, only the experimenter that fed the fish was allowed in the room during the experiment.

An experimental trial started with a blinking square cue located in the middle of the screen, indicating to the fish that the onset stimulus was about to appear (Figure 2B). The fish prepared to shoot by gazing up at the center of the screen. When the cue disappeared, the visual-search stimulus appeared (Figure 2C). Immediately after the water jet hit the screen (Figure 2D), the stimulus was replaced by a white screen and the fish was rewarded if it successfully shot the target (Figure 2E). To keep the fish focused during the experiment, each trial was limited to 5 s maximum. After 5 s the stimulus (target and distractors) disappeared automatically via the slide timeout feature in PowerPoint. Technically, these timeouts are accurate up to the frame rate of the display, an uncertainty well below the scale of stimulation times of interest. The frequencies of timeout events varied across fish but were always excluded from the analysis.

Four groups of experiments were carried out based on this general procedure.

### Experiment 1: Feature-search experiments

Four features that are known to elicit parallel search in humans were tested as follows:

- Experiment 1A: color. The target was a red ([1 0 0] RGB, 52 lx), black ([0 0 0] RGB, 1.1 lx), or blue ([0 0 1] RGB, 11 lx) disc, and the distractors were discs in one of the two remaining colors (Figure 2F). The colors were selected randomly (red vs. blue in three experiments, and blue vs. red, black vs. red, and red vs. black in two experiments each).
- Experiment 1B: size. The target and distractors were black discs differing in size (Figure 2G). In some experiments the target diameter was twice that of the distractors (2 vs. 1 cm), and in others it was half that of the distractors (1 vs. 2 cm). The visual acuity of the archerfish (Ben-Simon et al., 2012; Temple, Manietta, & Collin, 2013) was the factor in choosing the disc radii.
- Experiment 1C: orientation. The target and distractors were static Gabor patches—that is,

patches composed from exponent functions multiplied by a cosine wave. The target and distractor patches were orthogonal in orientation to each other (Figure 2H). Their orientations were constant throughout the experiment and aligned with the cardinal axes of the aquarium and the screen.

- Experiment 1D: motion. The target and distractors were Gabor patches that had moving phases in opposite directions (Figure 2I, where arrows indicate the phase). The speed of all the patches was 1.5 cm/s.

### Experiment 2: Feature-symmetry experiments

To control for a fish's preferences for target color or size, we conducted a symmetrical task (Figure 2J and 2K) where we alternated between the target and the distractors (i.e., the target's feature became the new feature of the distractors and the feature of the distractors became the new feature of the target).

### Experiment 3: Shape experiment

To test whether a certain shape could elicit a serial search mode in the archerfish, we used a red disc as the target with red distractor Pac-Men (Figure 2L). To keep the average intensity of the target and distractors equal, the target diameter was 1.7 cm and the distractors were slightly larger, measuring 1.95 cm in diameter.

### Experiment 4: Conjunction of color and size experiments

In these experiments, the target was defined by a combination of features, specifically color and size. Conjunction tasks are generally more difficult than feature tasks, and in humans usually require serial search. We explored whether this conjunction search task would require serial search in archerfish also. To control for the possibility that, similar to humans, conjunction search in archerfish can elicit an efficient visual search (Eckstein, 1998), we conducted two different conjunction experiments:

- Experiment 4A: The target was a large blue (2 cm in diameter) disc. Half of the distractors were small blue (1 cm) discs, and the other half were large black discs (Figure 2M).
- Experiment 4B: The target was a small blue (1 cm in diameter) disc. Half of the distractors were large blue discs, and the other half were small black discs (Figure 2N).

To verify that a serial search in the conjunction experiment (Experiment 4) was not the result of one of the single features alone (i.e., size or color), each fish

also completed the color (Experiment 1A) and size (Experiment 1B) tasks, thus making a total of three experiments.

## Experimental framework

In the single-feature experiments, the fish were presented with displays that contained a target and three, six, nine, or 12 distractors, so that the independent parameter (i.e., number of distractors) is distributed uniformly in parameter space. In the conjunction experiments, the fish were presented with displays that contained a target and four, six, 10, or 12 distractors. In this case, the number of distractors was set even in each trial to control for the type of distractors and to have the same number of distractors of each type. Since the fish could only be rewarded with a limited amount of food per day, each experiment was run on consecutive days. Therefore, in each experiment each fish was presented with 10 trials per condition, for a total of 40 trials per day. In the full experiment, each fish thus completed 50 trials per condition and 200 trials in total. The position of the target and the distractors on the screen varied randomly between trials to avoid inducing bias toward a specific location.

## Statistical analysis

The recorded videos were analyzed to extract the reaction times and target-selection rates of the archerfish. The reaction time was defined as the time between stimulus onset and initiation of the shot (with an accuracy of 0.04 s).

To verify that the fish could perform the task, the binomial cumulative distribution function for the target-selection rates was estimated and compared to chance values using a binomial test to determine whether the true probability of choosing the target was above chance (25%, 14.5%, 10%, and 7.5% chance values, respectively, for three, six, nine, and 12 distractors).

To determine whether the reaction time increased linearly as a function of the set size we performed a permutation test with 1,000 repetitions in the following manner: First we calculated the data's median reaction time for each condition and fitted a line to these medians using standard linear regression to find the slope of the regression. Then we repeated this process of finding the slope for the reaction times after being permuted 1,000 times. This enabled us to build a slope population ( $N = 1,000$ ) out of the data. Finally we compared the original slope to the slope population to assess its probability. A probability below 0.05 was

considered statistically significant and implied that the reaction time increased as the set size increased.

## Results

To investigate the visual-search mode elicited in the archerfish by different features, we measured the reaction time and target-selection rate in the visual-search tasks already described. Specifically, we examined whether the reaction time increased as a function of the number of distractors. The search conditions indeed resulted in different search modes.

### Color, size, orientation, and motion are efficient features for fish

We measured the behavior of 14 archerfish in the four feature-search (Experiment 1) tasks: color, size, orientation, and motion (Figure 2F–2I; see Methods). Some fish were tested in multiple experiments (Supplementary Table S1).

To verify that the fish could perform the task, we compared the target-selection rate to the probability of selecting the target by chance. In all experiments, the target-selection rates were 58% or above (and as high as 100% in some experiments); hence they were significantly higher than chance ( $p < 0.001$ , binomial test; see Methods).

Next, we explored which visual-search mode was used in the tasks by examining the slope of the reaction time (blue lines in Figure 3; see Methods). The slope of the regression line was not significantly different from zero ( $p > 0.05$ , permutation test; see Methods) in most of the experiments—specifically 8/9 in the color experiment, 8/8 in the size experiment, 3/4 in the orientation experiment, and 3/3 in the motion experiment. This was true also for the pooled data from the entire fish population in all four experiments (Figure 3A–3D, right panel), suggesting that in general reaction time did not increase with the number of distractors for these four features. Hence, the target effectively pops out (for all results and slope values, see Supplementary Figure S1).

Though in all tasks the archerfish used a parallel search mode, there was a significant difference in the overall reaction time per se (one-way analysis of variance),  $F(3, 80) = 5.04$ ,  $p < 0.01$ . Specifically, reaction times for color and size were significantly shorter than for motion ( $p < 0.01$ , Tukey test; Figure 4). Reaction times for orientation were not significantly different from those for color and size ( $p = 0.25$ , Tukey test; Figure 4) or for motion ( $p = 0.18$ , Tukey test; Figure 4).

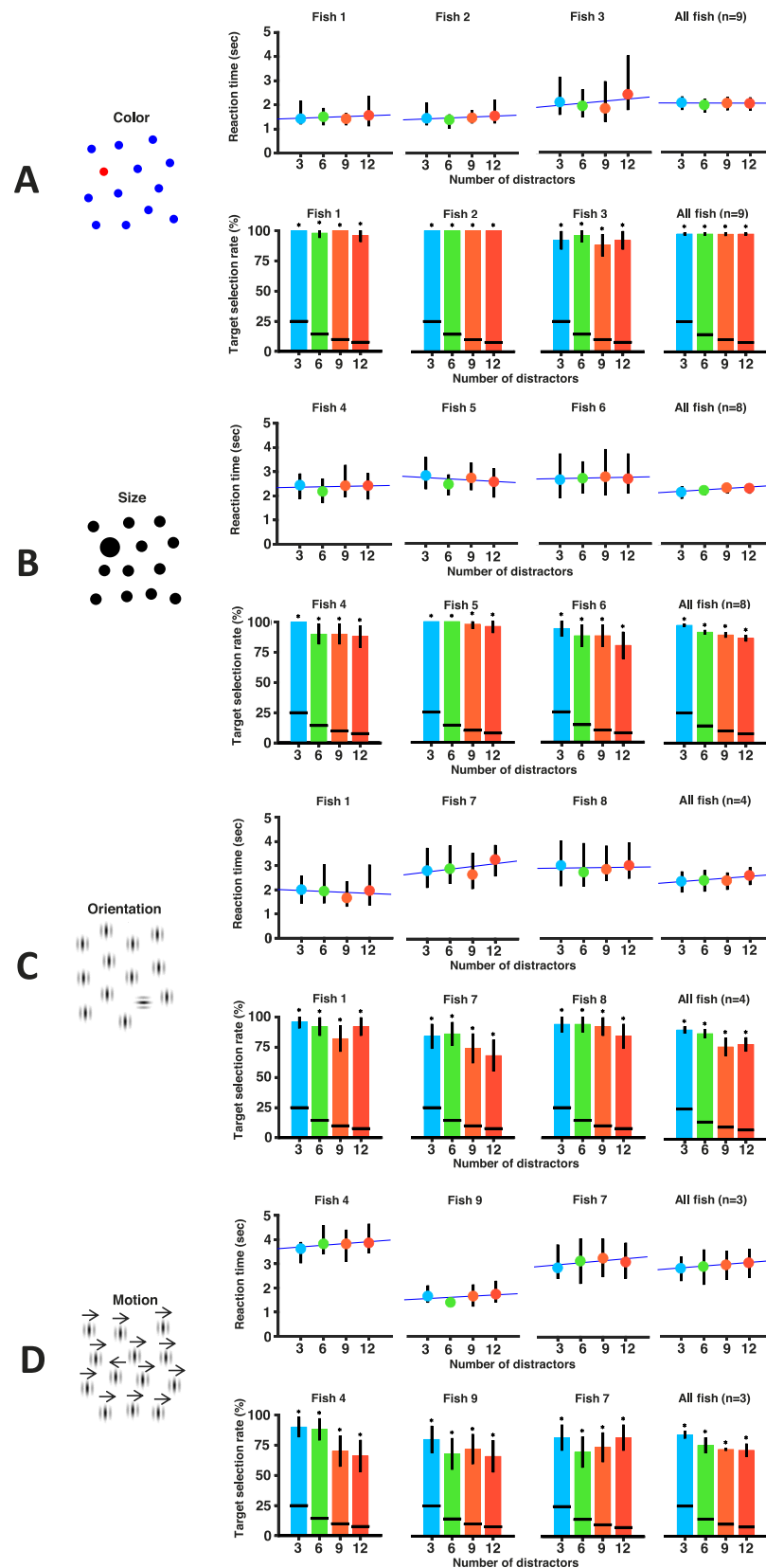


Figure 3. Color, size, orientation, and motion enable pop-out for the archerfish. Feature-search experiment results: (A) color ( $n = 9$ ), (B) size ( $n = 8$ ), (C) orientation ( $n = 4$ ), and (D) motion ( $n = 3$ ). Upper rows are reaction times for three representative fish and the whole sample (median and 25th and 75th percentiles for individual fish, mean of medians and standard error for the total fish population) calculated for three, six, nine, and 12 distractors. Reaction times did not increase as a function of the number of

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distractors (permutation test,  $p > 0.05$ ), implying that the target popped out and the fish used parallel search to detect it on these tasks. Blue line denotes the slope of the standard linear regression. Lower rows are the target-selection rate of each individual fish and all fish as a whole (mean and 95% confidence interval for individual fish, mean and standard error for the total fish population). In all experiments, all fish shot at the target with significantly higher probability than predicted by chance (black lines). \* $p < 0.001$ .

We would like to state that though the target-selection rates seem to decrease as a function of set size, the decrease is not significant for color,  $H(3, 36) = 0.27$ ,  $p = 1$ , for orientation,  $H(3, 16) = 5$ ,  $p = 0.17$ , or for motion,  $H(3, 12) = 4$ ,  $p = 0.26$ . The decrease is significant for size,  $H(3, 32) = 12.27$ ,  $p < 0.01$ , but finer grained research is needed to understand why it appears that this task is harder for the fish. We would like to emphasize that we do not think this decrease indicates the use of a different search strategy. During all experiments, the archerfish was motivated to succeed at hitting the target because it received a reward (a food pellet) only upon success. Furthermore, in different experiments (shape and conjunction) the reaction time increased with set size, and we assume the archerfish did not use a different strategy for those tasks.

Finally, taking into account reaction times and target-selection rates, we assume that color might be the most efficient feature for the archerfish.

### Feature-symmetry task of color and size elicits parallel search

To test whether the visual-search mode used for feature search was symmetric with respect to the

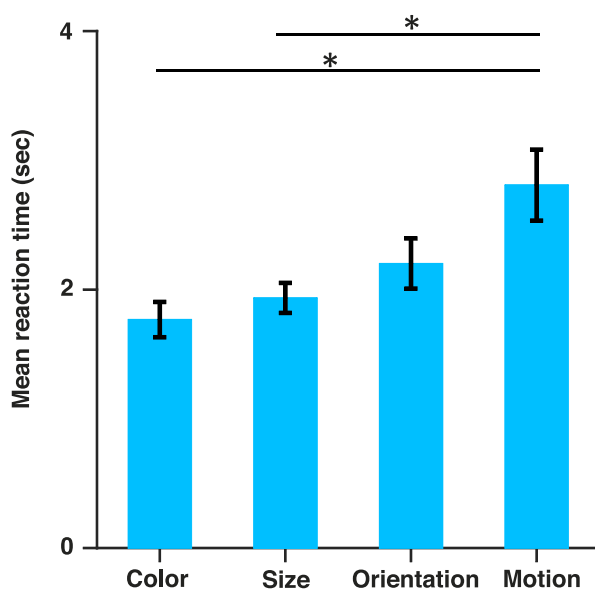


Figure 4. Mean reaction time and standard error of each feature-search experiment. \* $p < 0.01$ .

feature that triggered it, we conducted an additional set of experiments (Experiment 2) where the target and distractor features were reversed. For this purpose, four fish that performed the feature-search task (Experiment 1A or 1B) in parallel search were given the symmetrical task (Experiment 2) where the target and distractor features were alternated (see Methods). Two fish were administered a symmetric color task (Figure 5A), and two others were administered a symmetric size task (Figure 5B).

The results indicated that all the fish used parallel search in the feature-symmetry task as well, and had relatively high target-selection rates (Figure 5). Thus, the features of color and size were symmetric and enabled the target to pop out to the fish regardless of the relationship of the feature value between the target and the distractors.

Though the performance for all fish in the feature-symmetry task resulted in slopes that were not significantly different from zero, the general reaction time did differ on switching to the second task for three out of four fish (paired  $t$  test)—Fish 9:  $t(3) = 4.56$ ,  $p = 0.02$ ; Fish 3:  $t(3) = 1.83$ ,  $p = 0.16$ ; Fish 11:  $t(3) = 4.15$ ,  $p = 0.03$ ; Fish 12:  $t(3) = 4.5$ ,  $p = 0.02$ . However, the differences were small with respect to differences in other fish's reaction times and probably resulted from accumulating experience with the lab experiments, changes in physiological abilities, and mood. We expected these factors to have a general effect on the reaction time but not on the mechanism driving these experiments; thus, these differences should not be assumed to affect the interpretation of the results.

### Searching for a unique shape that elicits serial search

In the shape visual-search task (Experiment 3), the target was a disc and the distractors were Pac-Men (three-quarter discs with adjusted diameters to equal the total intensity; see Figure 2L and Methods).

Three fish were tested in this experiment (Figure 6). The results indicate that this task elicited a serial search mode in the fish: search reaction times of 110 ms/distractor for Fish 3, 50 ms/distractor for Fish 13, and 70 ms/distractor for Fish 14 ( $p < 0.05$  for all fish). The target-selection rates were higher than chance but relatively low, indicating that this task was hard for the fish.



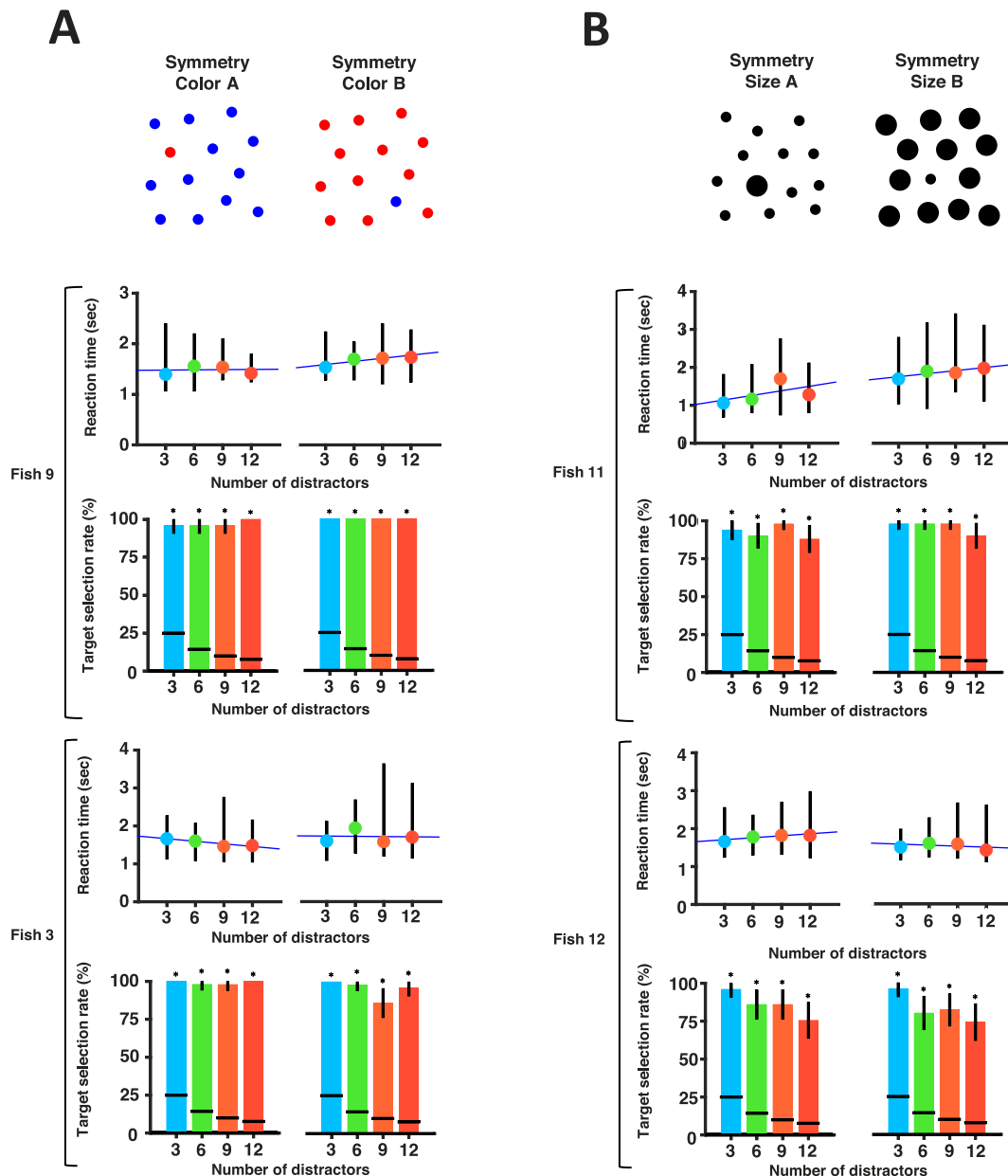


Figure 5. Feature-symmetry results: (A) color and (B) size. In all cases, the slope did not differ significantly from zero—Fish 9: 1 and 20 ms/distractor; Fish 3: –20 and –2 ms/distractor; Fish 11: 40 and 30 ms/distractor; Fish 12: 20 and –9 ms/distractor (all  $p > 0.05$ , permutation test; see Methods)—indicating that the feature itself causes the target to pop out.

## The conjunction task can elicit both parallel and serial search modes

Next we investigated the visual-search mode the archerfish used in a conjunction of color and size search scenarios (Experiments 4A and 4B). Each fish was also tested in feature-search tasks (Experiments 1A and 1B) implementing each of the two features tested in the conjunction task, to verify that effects in the conjunction were not the result of a single feature. In all experiments, the target-selection rates were significantly higher than chance ( $p < 0.001$ , binomial test; see

Methods), indicating that the fish could perform the task.

Four fish were tested in the conjunction task displaying a large blue target (Figure 7A). In this case the fish exhibited parallel search to detect the target: –3 ms/distractor for Fish 3, 8 ms/distractor for Fish 12, and –20 ms/distractor for Fishes 6 and 7 ( $p > 0.05$ , permutation test; see Methods). In the second conjunction task, with a small blue target, three fish were tested (given fish mortality, only two could be tested in both conjunction tasks). This time, all the fish exhibited a serial search mode: 100 ms/distractor for Fish 3, 70

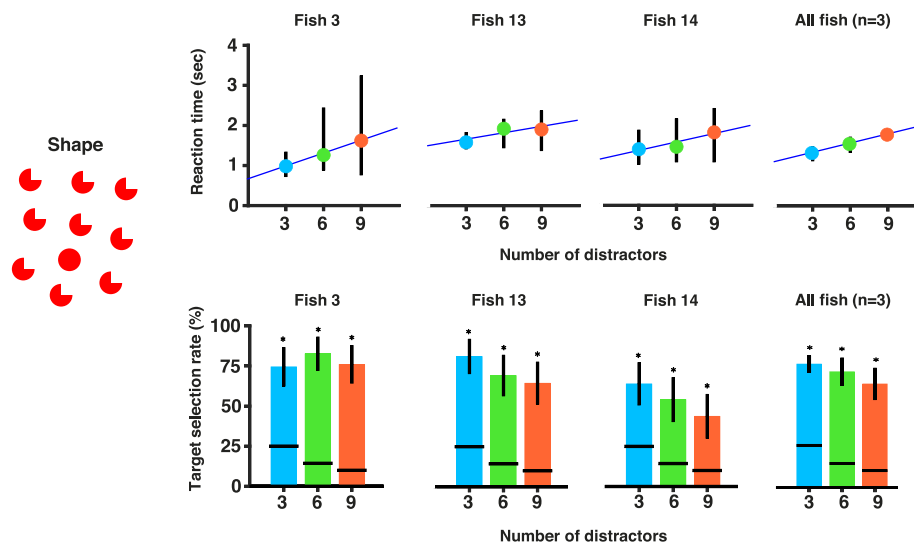


Figure 6. Shape can elicit serial search in the archerfish. In all cases the search was serial—110 ms per distractor for Fish 3, 50 ms per distractor for Fish 13, and 70 ms per distractor for Fish 14, ( $p < 0.05$  for all fish)—and the target-selection rate was low in comparison to the target-selection rate on the feature-search tasks ( $t_{85} = 6.97$ ,  $p < 0.0001$ ,  $\bar{x}_{\text{single}} = 92\%$ ,  $\bar{x}_{\text{shape}} = 68\%$ ).

ms/distractor for Fish 12, and 80 ms/distractor for Fish 11 ( $p < 0.05$  for all fish, permutation test; Figure 7B).

## Discussion

### The four features identified in humans elicit pop-out visual search in the archerfish too

One of the key questions in the field of visual search is which visual features guide attention. There is a general consensus that in humans, the features of color, size, orientation, and motion are fundamental and significant in the context of pop-out (Wolfe & Horowitz, 2004, 2017). The effects of other features such as color change (Theeuwes, 1995; von Mühlenen & Conci, 2016), shape (Bergen & Julesz, 1983; Treisman & Gormican, 1988; Wolfe & Bennett, 1997), or line termination (Julesz & Bergen, 1987; Taylor & Badcock, 1988) are less conclusive. Here we examined whether these four guiding features are specific to humans alone or if they also guide other vertebrates.

We tested archerfish performance in different visual-search tasks in which the target was defined by color, size, orientation, or motion. We found that these four features elicit parallel search in the archerfish in a similar way to how they elicit parallel search in humans. In addition, the search was characterized by high target-selection rates, an indication of the saliency that these features trigger in the archerfish visual system.

Since there is an enormous evolutionary distance between humans and archerfish, and given similar

findings in other vertebrates such as barn owls (Harmening, Orlowski, Ben-Shahar, & Wagner, 2011; Orlowski et al., 2015; Orlowski, Ben-Shahar, & Wagner, 2018), rats (Botly & De Rosa, 2011), and pigeons (P. M. Blough, 1984), we speculate that these four features are processed equally efficiently in vertebrates in general.

### Why do color, size, orientation, and motion guide attention in the archerfish?

Since all animals are constrained by the physics of their environment and by the behavioral needs of survival, food, and reproduction, one fundamental question is how the archerfish can benefit from color, size, orientation, and motion pop-out.

The archerfish needs to navigate daily in a cluttered environment filled with branching mangroves and other fish. In addition, since the archerfish live in the shallows, light absorption is minimal. Therefore, their habitat is characterized by colorful fish, plants, and insects above the water level, some of which they hunt. In such a busy environment, it would be to the animal's advantage to exploit every possible cue available to find and catch its prey.

The four pop-out features explored here could help it do just that easily and quickly. For instance, these features are very useful to detect a red-colored insect standing on a green leaf, a spider moving along its web, or a bug walking on a branch. Hence, while the archerfish is cruising the shallows looking for prey above it, pop-out of these features could help in detecting and identifying an insect that is only a couple

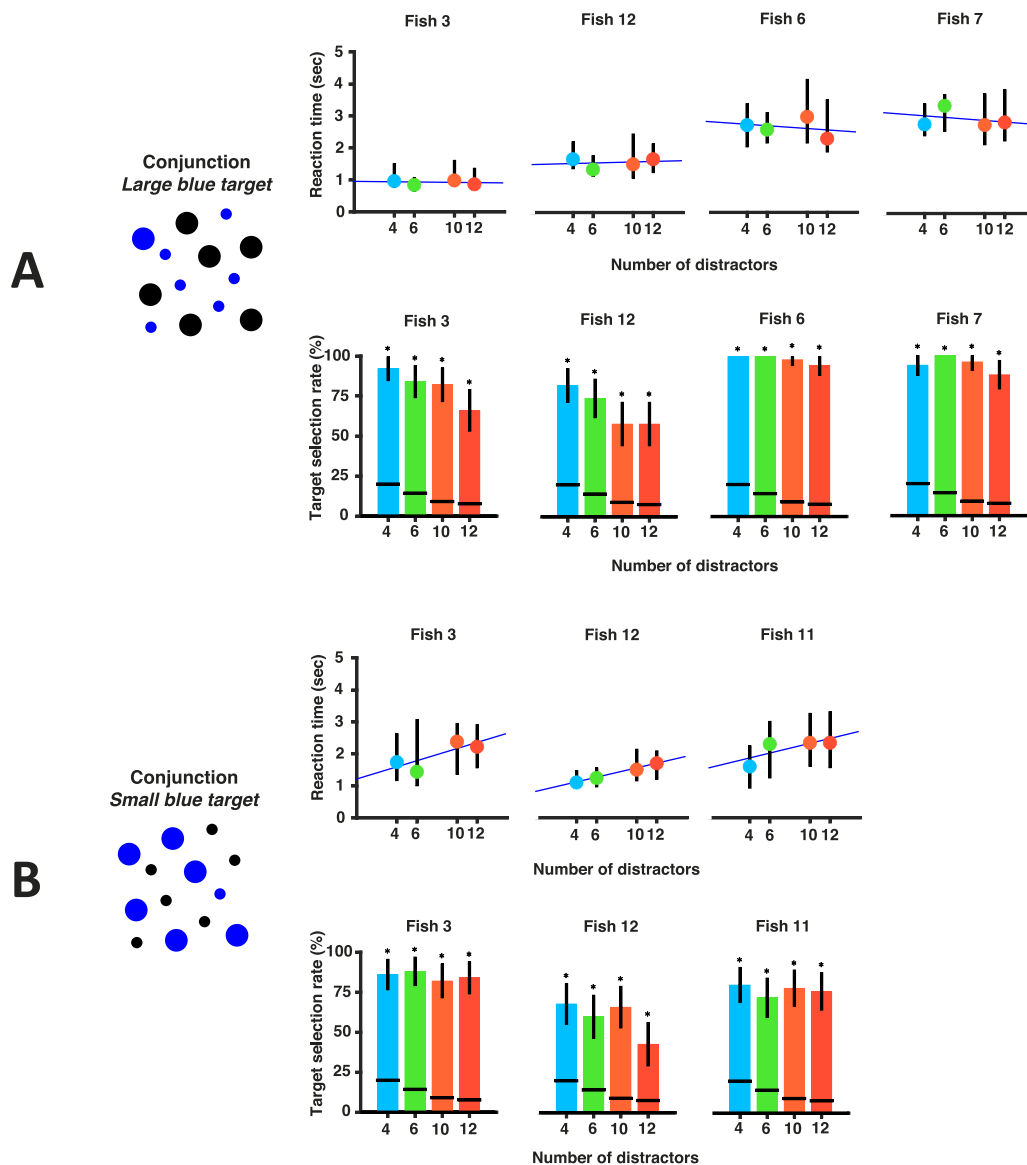


Figure 7. Archerfish can perform conjunction visual search. (A) A large blue disc was the target. Half of the distractors were small blue discs and the other half were large black discs. All fish implemented parallel search on these tasks—Fish 3:  $\sim 3$  ms/distractor; Fish 12: 8 ms/distractor; Fishes 6 and 7:  $\sim 20$  ms/distractor ( $p > 0.05$ , permutation test; see Methods). (B) A small blue disc was the target. Half of the distractors were small black discs and the other half were large blue discs. The fish used serial search to detect this target—Fish 3: 100 ms/distractor; Fish 12: 70 ms/distractor; Fish 11: 80 ms/distractor ( $p < 0.05$  for all fish, permutation test).

of millimeters long at distances of over a meter (Ben-Simon et al., 2012).

Visual pop-out could be also useful for hunting underwater. There is evidence that for visual predator fish, the size, shape, motion, and orientation properties of prey are important for it to be able to decide in advance whether or not an object is worthy of capture (Crowl, 1989; Cunha & Planas, 1999). It also might affect foraging tactics, as they change in some cases with prey visibility (Holmes & Gibson, 1986). Similarly, these features can help the archerfish in hunting small fish or crustaceans underwater.

## Color experiment

From our experience in the lab, it is easy to train the archerfish to shoot discs colored in a variety of colors including blue, black, red, and green. Archerfish do exhibit color preference between these colors, but it is more or less evenly distributed in the population (Karoubi, Leibovich, & Segev, 2017). Ecologically, black and green are useful for the archerfish in finding prey against a background of foliage, while black and blue are useful in detecting prey against a background of bright sky or following the silhouette of an aerial

predator. Red, however, is not among the salient colors, given its spectral sensitivity (Temple et al., 2010). However, some archerfish have a great preference for red (Karoubi et al., 2017). Furthermore, since we wanted to test color as a feature per se, an archerfish had to be able to accomplish the color task with no color dependency (see Experiment 2), no matter what is its color preference and even if the color was not among the salient colors given its spectral sensitivity. In this sense, our results demonstrate the effect of color as a feature in general rather than an innate or learned preference for a particular cone response.

## A single feature that elicits serial search

Next we explored the existence of a single visual feature that does not drive the archerfish's attention and thus elicits serial visual search. We tested the archerfish on a shape task in which the target was a solid disc and the distractors were in the shape of Pac-Man. In this experiment, the target was less salient to the archerfish, as it resulted in relatively low target-selection rates, and it elicited serial search, similar to humans in many cases (Treisman & Gormican, 1988; Wolfe, 2001). Indeed, it is unclear what aspects of shape guide attention in humans. For example, a feature such as a line terminator (Julesz & Bergen, 1987; Taylor & Badcock, 1988) can distinguish between O and Q but will not necessarily guide attention in all other cases. Our findings confirmed that the shape task (which presented the Pac-Man shape) did not trigger the underlying feature search that allows pop-out and parallel search. Given such results, we posit that the line terminator is not a useful feature for archerfish either.

We speculate that, just like in humans, shape search would exhibit asymmetric behavior in the archerfish—for example, that a Pac-Man target among solid-disc distractors will elicit pop-out. That being said, the study of shape search asymmetries in the archerfish warrants research of its own (e.g., Allan & Blough, 1989) and is part of our short-term future research.

## Conjunction search asymmetry

Generally speaking, a target that is characterized by a combination of two or more features is harder for the human visual system to detect (Treisman & Gelade, 1980). Here too, a conjunction of color and size elicited serial search but only when the target was small and blue and the background consisted of large blue and small black distractors. On the other hand, when one of the features is more dominant in a conjunction task, it can guide attention and switch the search to the parallel

mode (Figure 7A; Eckstein, 1998; Kaptein, Theeuwes, & Van der Heijden, 1995). Our experiments show that archerfish may be no different from humans in this aspect too, as the conjunction search task for large blue targets elicited parallel search. This result may imply that this condition made the search much easier, likely because it allowed the archerfish to narrow down the dimensionality of the problem (i.e., Theeuwes & Kooi, 1994). In particular, we speculate that the fish focused relatively easily on the large discs (virtually ignoring the small ones), thus turning the conjunction task into a color task involving large discs only.

## Parallel and serial visual search across vertebrates

Besides humans, studies have explored the performance of more species during behavioral visual-search tasks. Generally, it has been demonstrated that some visual tasks are significantly more difficult than others by comparing reaction time, target-selection rate, or both. In some cases, the slope of the reaction time as a function of set size has been examined to determine whether the search was parallel or serial in a similar way to our study.

One family of species relatively well explored in the context of visual search is birds. For example, studies on barn owls (Harmening et al., 2011; Orłowski et al., 2015) show that orientation and luminance contrast elicit the parallel search mode in these birds. More recently, a low-contrast feature task and two conjunction tasks involving both high- and low-contrast orientation have demonstrated serial search in this species (Orłowski et al., 2018). Studies on pigeons, on the other hand, have demonstrated that shapes (D.S. Blough, 1977) and letters (P.M. Blough, 1984) are both inefficient features resulting in increasing reaction time and decreasing target-selection rates as set size increases. Allan and Blough (1989) showed that in contrast to humans, a line terminator does not help pigeons efficiently distinguish a target from distractors when the basic shape is a circle, square, or triangle. Finally, it has been demonstrated that pigeons are able to group items with a similar feature of color, size, orientation, or shape and discriminate the resulting figure from items with a different property (e.g., for color, red vs. blue; Cook, Cavoto, & Cavoto, 1996). Through comparison of the target-selection rates in each task, it was also shown that the color, size, orientation, and shape features are more efficient than a conjunction search.

In terrestrial primates, behavioral visual-search experiments have been conducted with color and shape features. A covert visual-search task performed by monkeys indicated that color popped out to them and



represented a significantly more efficient search than shape (Lee & McPeck, 2013). Botly and De Rosa (2011) demonstrated that rats used parallel search in color or shape (of triangle and square) feature search and that the target-selection rates were significantly higher in the feature task than in the conjunction task of color and shape. This again indicates that similar to humans, feature search is more efficient than conjunction search.

Finally, a recent study has confirmed that the archerfish exhibits both parallel and serial search modes during visual search with moving targets (Ben-Tov et al., 2015). Specifically, it was shown that the speed and direction of moving bars enable the target to pop out but the size of the moving bar does not. Moreover, previous studies have demonstrated that archerfish use serial search when looking for an image of an insect embedded in a set of differently shaped stationary distractors (Rischawy & Schuster, 2013). Here we followed up on such studies and showed, for the first time, that archerfish use parallel search with static targets, and we extended the visual-search experimental arsenal by testing a variety of different features and their conjunctions.

Generally, other species than humans demonstrate that visual-search tasks on color, size, orientation, and motion are efficient, while visual search on shape and conjunction tends to be less efficient. As the foregoing discussion implies, the efficiency of visual-search performance is similar across humans and other vertebrates, including nonhuman primates, birds, and fish. Since these vertebrates are relatively spread over the phylogenetic tree, we speculate that visual search possessing similar characteristics should exist in many more species.

## Visual search with different brain structures

What might constitute the neural code of detecting these visual features? In mammals, contextually modulated neurons in V1 that encode aspects of saliency have been suggested as neural correlates. Specifically, the responses of these contextually modulated neurons are modulated when there are specific differences between the properties of the visual stimuli inside and outside their classical receptive field, implying a differentiation of what is salient for the visual system. Saliency maps are generated concurrently across the entire visual field and shift attention to salient objects in the visual scene. Pop-out might be achieved by decision-making computation, such as a winner-take-all mechanism that detects the most active—that is, salient—location in the map.

Ben-Tov et al. (2015) recorded single-neuron activities in the optic tectum of the archerfish. The findings indicated that the majority of these neurons possess

contextual modulation properties—that is, their firing rate increased when the moving-bar stimulus inside their receptive field had different motion properties of speed and direction compared to their surround. The researchers hypothesized that as terrestrial mammals' V1 neurons have been found to function as the basis of saliency maps (Allman, Miezin, & McGuinness, 1985; Kastner, Nothdurft, & Pigarev, 1997; Knierim & van Essen, 1992; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995), these neurons could constitute the neural substrate for a saliency map in the archerfish visual system as well. Based on the findings here, we posit that the other three features (color, size, and orientation) may be part of the saliency-map mechanisms in the archerfish. Further studies should aim to explore how they are encoded in the fish brain and the extent to which these coding mechanisms are universal among vertebrates.

Importantly, this could inform on the evolutionary and developmental perspectives of visual search. In the archerfish, the optic tectum is the largest brain region where much of the visual and sensory integration functionalities take place (Northmore, 2011). Since the optic tectum is homologous to the mammalian superior colliculus (Butler & Hodos, 2005) but has common ground in functionality with the primary visual cortex of mammals, it has been suggested that the saliency map migrated over the course of evolution from the superficial layers of the optic tectum to the primary visual cortex (Zhaoping, 2016). Exploring more species of fish could confirm this possibility.

*Keywords: visual search, reaction times, response times, serial search, parallel search, pop-out, conjunction search, visual attention, selective attention, vision, archerfish*

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