



An educated guess: how coral reef fish make decisions under uncertainty

Cait Newport ^{a,*}, Adelaide Sibeaux ^a, Guy Wallis ^b, Lucas Wilkins ^a,
Theresa Burt de Perera ^a

^a Department of Biology, University of Oxford, Oxford, U.K.

^b Centre for Sensorimotor Performance, School of Human Movement and Nutrition Sciences, University of Queensland, Brisbane, Australia

ARTICLE INFO

Article history:

Received 22 May 2023

Initial acceptance 3 August 2023

Final acceptance 11 January 2024

Available online 7 March 2024

MS. number: 23-00257R

Keywords:

adaptive decision making
alternative forced-choice test
cognition
fish
learning
vision

For many animals, making informed decisions is crucial to survival. A critical problem is how to make optimal decisions in the face of incomplete, unreliable or conflicting information. In many aquatic environments, fish use visual information to guide key behaviours, but the environment itself can alter or mask the very signals they rely on. Here, we asked how a highly visual species, *Rhinecanthus aculeatus*, responds to a learned discrimination task as signal reliability decreases, and whether probabilistic information gained during previous experience can be incorporated into their decision strategy. Fish were first trained to select a target (dark grey circle) from three distractors (light grey circles). In the first experiment, the target was more likely to appear in one of four possible stimulus positions. In the second experiment, the target appeared in all positions equally. In a series of trials, the difference in brightness between the target and distractors was reduced until all four stimuli were identical. We found that target selection accuracy decreased with decreasing target and distractor disparity. In experiment 1 where the target was more likely to be in one position, fish increasingly selected stimuli in the biased position as target selection accuracy decreased, but not in experiment 2. These results demonstrate (1) that fish learned more than a simple select/avoid rule based on stimulus brightness; they also integrated information (stimulus position), which could be considered ancillary to the primary task. (2) Fish can learn probability distributions and apply this knowledge as uncertainty increases, ultimately increasing the overall frequency of correct choices. Our results reveal that probabilistic decision rules can be used by fish when visual information is unreliable, indicating a possible mechanism for decision making given the inherent noise in incoming sensory information.

© 2024 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Vision is an important sensory system guiding a wide range of behaviours in many fish (e.g. predation, signalling, spatial learning, etc). Errors in signal processing can lead to nonadaptive behaviour, and ultimately impact the survival and fitness of individuals. Nevertheless, aquatic visual environments can be extremely noisy, and sensory pollution can create distraction and misleading information, or it can lead to signals being masked (Dominoni et al., 2020). For example, decreases in water clarity cause scattering and attenuation of light, reducing detection distances and scene contrast. In particular, underwater caustics, caused by the refraction of downwelling light, produce moving bands of light that can interfere with visual signal detection including prey detection

(Attwell et al., 2021; Matchette et al., 2019, 2020). While there is some evidence that aquatic species can evolve visual mechanisms to reduce or eliminate sources of noise (e.g. crabs, *Carcinus maenas*, and cuttlefish, *Sepia officinalis*, by using polarized light; Venables et al., 2022), we know very little about how the vast majority of aquatic species cope with visual noise. Many species must make decisions in situations where the signal to noise ratio is low and where errors in signal detection or interpretation are expected to be high. Given the importance of accurate signal interpretation in governing behavioural output, it makes sense that animals in dynamic and noisy environments have adaptations that allow them to cope with reduced signal fidelity.

The mechanisms that underpin associative learning and the decision strategies animals use (particularly when there is uncertainty about the signal or response) have been the focus of theoretical and experimental studies for decades. This field is at the

* Corresponding author.

E-mail address: caitlin.newport@biology.ox.ac.uk (C. Newport).

intersection of biology, cognition, psychology, ecology, robotics and neurobiology and, consequently, many theoretical models attempt to describe the decisions of animals and identify how information guides their choices. Despite this long history, much of the work on this topic has focused on the behaviour of a few model species (e.g. rats, nonhuman and human primates) or behaviours (e.g. invertebrate scanning behaviours) and we do not know whether current theoretical models explain the behaviour of the vast majority of species. While some theories are stimulus-centric and assume decisions are based entirely on how the animal learns and perceives sensory signals (e.g. diffusion model: Ratcliff & Rouder, 1998; signal detection theory: Green & Swets, 1966), other theories integrate potentially idiosyncratic information such as past choices, choice bias, individual motivation, and hormonal and physiological state (Budaev et al., 2019; Roy et al., 2021). Bayesian inference is a powerful model for describing decision making that combines probabilistic knowledge accrued through previous experience with a measure of the degree of uncertainty about the current sense data into a unified decision-making process (Gershman, 2015; Ma, 2019). Specifically, Bayesian inference is an application of Bayes' theorem which describes the integration of prior probability knowledge of a specific outcome with current incoming information, allowing the assessment of probability to be updated as more information becomes available (McNamara et al., 2006; McNamara & Houston, 1980; Ramírez & Marshall, 2017; Trimmer et al., 2011). It provides a framework for optimal decision making in the face of uncertainty but requires that the decision-maker can learn and remember probabilistic information and alter their expectations based on their current situation. In nonhuman animals, studies evaluating taxonomically diverse species (e.g. bees, crabs, fish, birds, mammals) have demonstrated selection behaviour consistent with Bayesian inference during a range of behaviours including foraging (Alonso et al., 1995; Biernaskie & Gegeer, 2007; Biernaskie et al., 2009; Foley & Marjoram, 2017; Lima, 1984, 1985; Marshall et al., 2013; Milinski, 1994; Olsson & Noël, 1999; Olsson et al., 1999; Valone, 1991, 1992; Valone & Brown, 1989; Valone & Giraldeau, 1993; van Gils et al., 2003), mate searching (Hunte et al., 1985; Luttbeg & Warner, 1999), collective behaviour (Gunji et al., 2018) and natal dispersal (Selonen & Hanski, 2010).

Here we tested whether a similar probabilistic approach underpins the sensory decision-making strategies of one species of fish, and whether their reliance on probabilistic information is related to signal uncertainty. Using an operant learning assay to investigate visual discrimination, we tested whether Picasso triggerfish, *Rhinecanthus aculeatus*, a coral reef species, would integrate previous experience of reward location to optimally weight their choices in the face of variations in the signal strength of their reward stimulus. This harem and territorial species (Kuwamura, 1997) typically lives among coral rubble in the subtidal zone, and has an omnivorous diet (e.g. algae, crustaceans, molluscs). The subtidal zone is often characterized by dynamic lighting conditions which can affect visual signal detection thresholds and distances. For example, turbidity, caustics and the angle of the sun, can influence brightness, contrast and spectral characteristics of visual cues. Picasso triggerfish have been previously used as a model for aquatic sensory ecology (e.g. Cheney et al., 2013; Cheney et al., 2019; Green et al., 2022; Newport et al., 2017; Santiago et al., 2020) and their visual system has been well described (Cheney et al., 2022). Experiments show that noise caused by changes in lighting can impact their visual behaviour: caustics can negatively affect their ability to detect moving prey items (Matchette et al., 2020), and relative illumination alters how they perceive colour (Simpson et al., 2016; Van Der Berg et al., 2020). Here, we investigated the sensory decision-making strategies of this species and whether a cognitive solution, such as Bayesian integration, may

help it cope with sensory noise. Using an experiment in which stimuli become increasingly difficult to discriminate, we asked whether subjects would select stimuli based on acquired knowledge of their most likely position, when visual signals are unreliable.

METHODS

Experimental Overview

In two experiments, individual Picasso triggerfish were presented with a four-alternative forced-choice task in which there was one rewarded (S+) dark grey circular stimulus, and three unrewarded (S-) light grey circular distractors (Fig. 1). Grey stimuli were chosen because a straightforward change in brightness could be used to alter the discrimination difficulty. Stimuli were presented in four possible positions: top right (TR), top left (TL), bottom right (BR) and bottom left (BL). The two experiments differed in terms of the target position distribution. In experiment 1, there was a bias in the target position distribution allowing subjects to learn probability information (biased position: 60%; other positions: 13%). In experiment 2, the target was equally likely to appear in any of the four positions (25% in all positions). In experiment 1, our hypothesis was that fish would fall back on their expectations linked to target location when exposed to conditions of increasing stimulus uncertainty. However, in experiment 2, in which there was no prior position bias, we did not expect the fish to have a preference for any particular position.

Experimental Procedure

At the beginning of an experimental session, a white opaque Perspex trap door was placed in the front third of the home tank (18 cm from the front of the tank) and was used to separate the fish from the remainder of the tank. Once the door was in place, a white stimulus presentation board (40 × 20 cm) was inserted into the final quarter of the tank. There were four possible stimulus positions on the presentation board: TR (17 cm from bottom, 5.5 cm from right edge), TL (17 cm from bottom, 5.5 cm from left edge), BR (7 cm from bottom, 5.5 cm from right edge) and BL (7 cm from bottom, 5.5 cm from left edge).

A trial began with the fish behind the trap door. Once the door was raised, the fish swam into the open area and up to the presentation board and was required to select one of four stimuli. If the fish chose the correct stimulus by biting it, they received either a food pellet (Formula One Marine Pellet, Ocean Nutrition, Newark, CA, U.S.A.) or a piece of fish (Gamma Slice, Tropical Marine Centre Ltd, Chorleywood, U.K.), depending on the experimental trial type. If the fish chose incorrectly, they were not rewarded, the presentation board was removed from the aquarium, and the trial was terminated. After each trial, the fish swam back through the trap door and the door was closed in preparation for the next trial. One session consisting of 10 trials was run each weekday during the experimental period. See [Supplementary Fig. 1](#) for a video example of the testing procedure.

Experiment 1

The experiment was divided into two Training stages followed by a Testing stage. The first Training stage taught fish to discriminate stimuli based on brightness and in the second stage fish were introduced to the target position distribution. In Training stage 1, fish were deemed to have learned the task once they achieved >75% accuracy in three consecutive sessions (10 trials/session). Each fish was given as many sessions as required to learn this task. In

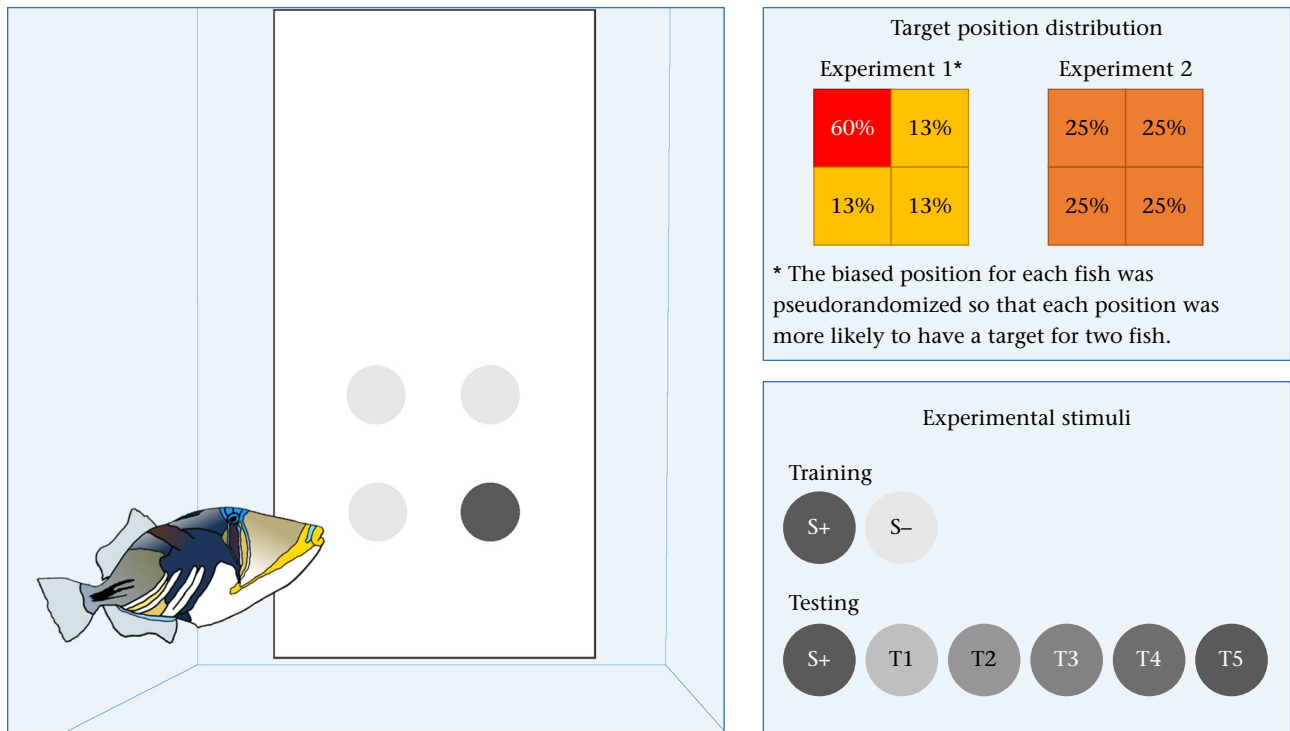


Figure 1. Summary of the experimental protocol. Selection of the target stimulus (S+) was rewarded with food, while the distractor stimuli (S-) were not. The figure is illustrative only and not rendered to scale.

experiment 1, all fish ($N = 8$) completed this stage within 4–11 sessions.

In the second Training stage, the distribution of target positions was altered such that the likelihood of the target appearing at one location increased relative to the other three. All fish were given 12 sessions (10 trials each) in Training stage 2, regardless of target selection accuracy. Of the 120 trials, in 72 trials (60%) the target was presented in the 'biased' position. In the remaining trials, the target appeared 16 times in each of the other three positions. Two fish were trained to each of the four possible positions (TR, TL, BR, BL).

A two-tiered reward system was used with the intention of directing the attention of the fish to the secondary rule. When fish correctly selected S+ in the nonbiased position, they were given a standard food pellet, but when the fish correctly selected the S+ and it was in the biased position, they were given a larger piece of cut-up bait fish. This reward procedure was used throughout Training stage 2 and for Reinforcement trials in the Testing stage. S+ selection accuracy remained high during Training stage 2 (combined mean frequency for all sessions, confidence interval (CI): $95\% \pm 1.8$) and all fish progressed to the Testing stage.

In the Testing stage, S- was replaced with distractors that became increasingly difficult to distinguish from the target stimulus. Testing sessions included five Reinforcement trials (R) and five probe trials (T1–T5). The Reinforcement trials followed the same procedures as those of Training stage 2 (S+ and S-) and were used as a reminder of the original task. Correct selections were rewarded, and the two-tiered reward system was maintained in these trials; therefore, three of the five Reinforcement trials were in the predetermined position. The remaining five trials were probe trials in which the difference in stimulus brightness became increasingly similar and eventually identical. In each Testing session, one of each of the five treatments was presented. Probe trials were unrewarded, and the biased position was not maintained. The order of Reinforcement and Testing trials was pseudorandom so that a

particular trial type (R or T) would not appear in more than two consecutive trials. A total of 24 Testing sessions were run.

Experiment 2

In experiment 2, the methods used in Training and Testing were similar to those of experiment 1, except that fish were not biased to a particular stimulus position in Training stage 2. All fish ($N = 4$) reached the learning criterion for Training stage 1 within 3–11 sessions.

Unlike in experiment 1, there was a difference in reward value and frequency for some fish. For Fish 18K and 17R, the two-tiered reward system was maintained; in 60% of trials (selected pseudorandomly), one of four positions was preassigned a higher reward value if chosen, with an equal frequency for all four positions. For the other two fish, the reward schedule was simplified so that all correct responses resulted in a single pellet. As in experiment 1, the probe trials were not rewarded during Testing for Fish 18K and 17R. However, Fish 24O and 25P were rewarded. Fish maintained an S+ selection accuracy of $97\% \pm 1.5$ CI in Training stage 2.

Subjects

A total of 12 fish were used in this experiment; eight individuals were tested in experiment 1 and another four were tested in experiment 2. Individuals were purchased from local suppliers. The fish were housed in individual aquaria (35.5×60 cm and 31.5 cm high) in a flow-through marine aquarium system and fed a daily mixed diet of pellets and fish pieces as part of experiments. All fish had a rock and a PVC pipe (length: 15 cm; diameter: 10.5 cm) to serve as shelter and enrichment, which were moved during experiments to ensure an unobstructed view of the experimental stimuli. Three fish had previously participated in similar experiments using different training techniques, but the remaining fish

were naïve (Table A1). Prior to this experiment, all fish were at least pretrained to swim through a trap door and to select white discs from a presentation board.

Ethical Note

All fish were cared for according to the code of practice for the care and use of animals for scientific purposes (Local Ethical Review Committee of Oxford University's Department of Zoology). Fish were held individually to minimize stress associated with territoriality. Experiments were conducted within the home tank of each fish to reduce handling and they were provided with enrichment in the form of shelters, rocks and gravel. Fish were offered live coral prior to experiments; however, because the fish destroyed all soft material within an hour, which impacted water quality, these were removed and replaced with standard aquarium rocks.

Stimuli

Stimuli were grey circular discs (2.5 cm diameter) that were printed on photographic paper (Canon matte photo paper), cut out using a hole-punch and laminated. Six stimulus types were made (Fig. 1). The darkest (S+) and brightest (S−) were used in Training and Reinforcement trials (RGB values: S+: 90 90 90; S−: 230 230 230). The remaining four stimuli were used as Testing stimuli with RGB values: T1: 190 190 190; T2: 150 150 150; T3: 130 130 130; T4: 110 110 110). A fifth Testing condition (T5) used S+ stimuli for all four options.

Statistical Analysis

For experiment 1 probe T5, all stimuli presented were identical and therefore it was impossible to state whether the fish had made a correct or incorrect decision based on the visual cue. For the analysis, before testing began, one stimulus was randomly assigned as S+ for each trial. As these trials were unrewarded, the designation had no effect on the fish; however, selection of this S+ was used to calculate the accuracy of those trials.

The selected stimulus (S+ or S−) and position were recorded for all trials. The results were tallied for each probe type and analysed using a generalized linear mixed model (GLMM) with a binomial distribution (logit-link function) to test whether the selection frequencies of each stimulus type (S+ or position) changed along with probes (using the glmer function in the lme4 package; Bates et al., 2015). Selection frequencies of either S+ (test performed for experiments 1 and 2) or the biased position (test performed for experiment 1 only) were included as response variables. Probe was included as a fixed effect and Fish ID as a random effect. Finally, we tested whether the selection frequency at each position changed along with probes (tests performed for experiments 1 and 2). For each position, selection frequency was included as the response variable. Probe and Fish ID were added as fixed and random effect, respectively.

To determine whether the stimulus selection on the nonbiased position was significantly different from selection on the biased position (experiment 1 only) we used a GLMM. For each probe we ran a GLMM and included the selection frequencies as the response variable. Position was added as fixed effect and fish ID as a random effect.

The linear relationship between the selection frequency of S+ and the selection of stimuli in either the biased position (experiment 1) or each of the four possible positions (experiment 2) was analysed using a linear mixed model (LMM, using the lmer function in the lme4 package; Bates et al., 2015). Fish ID was included as a random effect. Pseudo-R² was calculated using the Efron pseudo-R

square formula where the model residuals are squared, summed and divided by the total variability in the dependent variable.

For each model (GLMM or LMM), we assessed the fit between the model and the data, the residuals normality and the residuals dispersion using simulateResiduals and testDispersion functions (DHARMA package in R; Hartig, 2022).

RESULTS

Experiment 1

In the Training stage, selecting stimuli based on their visual characteristics (i.e. the darkest stimulus) would lead to the highest reward rate (100%). In the Testing stage, as the stimuli become harder to discriminate, the likely reward rate decreases, with the level of discrimination difficulty, to chance (25%). However, by changing the decision strategy to include position in their selection criteria, subjects in experiment 1 could increase their chances of receiving a reward (60%). In this paradigm, two questions emerge. (1) Will the fish use position as a cue, and (2) if they do, will they change their decision strategy in such a way as to maximize their food rewards across all probe types, or will they only rely on position when visual cues are completely unusable?

Fish selected S+ at a frequency higher than chance (null frequency: 25%) for R (CI: 95.3–97.8%), T1 (CI: 82.4–92.4%), T2 (CI: 56.4–72.3%), T3 (CI: 38.4–55.3%) but not T4 (CI: 24.3–39.6%) or T5 (CI: 18.3–32.4%). See Tables A1 and A2 for individual fish results for experiments 1 and 2. Moreover, the selection of S+ decreased significantly with decreasing brightness contrast between S+ and the distractor stimuli (all $P < 0.005$; see Table 1), except for T4 and T5 trials ($P = 0.14$) where fish selected S+ at the same frequency. While fish selected stimuli in the biased position at a frequency consistent with chance for R (CI: 56.9–64.3%; note that S+ appeared in the biased position in 60% of R trials) and T1 (CI: 22.5–35.6%), as stimuli became more similar, selection of stimuli in the biased position increased for T2 (CI: 39.1–53.7%), T3 (CI: 46.8–61.4%), T4 (CI: 48.4–62.9%) and T5 (CI: 61.6–75.2%; see Table 2 for P values). Selection of stimuli in all other positions was significantly different from the biased position except for T1 (Fig. 2a; see Supplementary File 2: RS3–RS8; following model assumption test, probe R did not meet model residuals normality

Table 1
Differences in frequency of choice based on probe brightness for experiment 1

Fixed effects	β coefficient	SE	z	P
Intercept	3.40	0.20	16.62	<0.001
T1-R	−1.38	0.29	−4.81	<0.001
T2-R	−2.79	0.24	−11.82	<0.001
T3-R	−3.53	0.23	−15.17	<0.001
T4-R	−4.18	0.24	−17.43	<0.001
T5-R	−4.52	0.25	−18.23	<0.001
T2-T1	−1.41	0.27	−5.22	<0.001
T3-T1	−2.15	0.27	−8.05	<0.001
T4-T1	−2.80	0.27	−10.24	<0.001
T5-T1	−3.14	0.28	−11.20	<0.001
T3-T2	−0.74	0.21	−3.50	0.001
T4-T2	−1.39	0.22	−6.36	<0.001
T5-T2	−1.73	0.23	−7.61	<0.001
T4-T3	−0.65	0.21	−3.04	0.005
T5-T3	−0.99	0.22	−4.45	<0.001
T5-T4	−0.34	0.23	−1.48	0.139
Random effects	Variance	SD		
Individual (intercept)	0.07	0.27		

Results from the generalized linear mixed model with fish ID as random intercept (Supplementary File 2: RS1). P values are given after post hoc analysis to control for multiple comparisons using Holm – Bonferroni adjustment. Significant results are in bold.

Table 2

Differences in frequency of choice for the biased position between pairs of probe trials

Fixed effects	β coefficient	SE	z	P
Intercept	0.43	0.08	5.53	<0.001
T1-R	-1.35	0.17	-7.79	<0.001
T2-R	-0.58	0.16	-3.64	0.003
T3-R	-0.27	0.16	-1.66	0.384
T4-R	-0.20	0.16	-1.26	0.412
T5-R	0.36	0.17	2.11	0.207
T2-T1	0.77	0.22	3.56	0.003
T3-T1	1.08	0.22	5.02	<0.001
T4-T1	1.15	0.22	5.30	<0.001
T5-T1	1.71	0.22	7.64	<0.001
T3-T2	0.31	0.21	1.53	0.384
T4-T2	0.38	0.21	1.84	0.330
T5-T2	0.94	0.21	4.40	<0.001
T4-T3	0.06	0.21	0.31	0.758
T5-T3	0.62	0.21	2.93	0.027
T5-T4	0.56	0.21	2.63	0.061
Random effects	Variance	SD		
Individual (intercept)	0.01	0.12		

Results from the generalized linear mixed model with fish ID as random intercept (Supplementary File 2: RS2). P values are given after post hoc analysis to control for multiple comparisons using Holm – Bonferroni adjustment. Significant results are in bold.

assumption and probe T2 and T4 did not meet model dispersion assumption). In addition, there was a significant negative relationship between selection frequency of S+ and selection of stimuli in the biased position (Fig. 2b; coefficient of regression $\beta = -0.54$, pseudo- $R^2 = 0.76$, $P < 0.001$; Supplementary File 2: RS9). Although the fish were unrewarded in the Testing conditions, had the Training reward schedule held true as the fish likely expected, they would have received a food reward at a rate of at least 50% across probe types, which is much higher than what is predicted by chance (25%).

Experiment 2

When the target was equally likely to appear in any of the four positions throughout Training (null frequency: 25%), selection accuracy of the target S+ decreased similarly to what was observed in experiment 1 and was higher than chance for R (CI: 96.2–98.9%), T1 (CI: 81.7–94.3%), T2 (CI: 60.9–79.4%), T3 (CI: 51.4–70.3%), T4 (CI: 32.3–51.7%) but not T5 (CI: 20.0–37.9%; see Table 3 for significance of S+ selection frequency between the different probes). The selection frequency of stimuli in either of the four positions was not generally above chance levels across treatments (null frequency: 25%), except in the case of the bottom right position (Position BR) which was significantly higher than chance for T4 (CI: 38.4–59.6%) and T5 (CI: 33.5–54.5%). See Fig. 2c for further confidence intervals and Supplementary File 2: RS11–RS16 for tests on difference in position selection frequencies at each probe. There was a significant relationship between the selection frequency of S+ and stimuli in positions BR ($\beta = -0.418$, pseudo- $R^2 = 0.690$, $P < 0.001$) and TL ($\beta = 0.203$, pseudo- $R^2 = 0.587$, $P = 0.006$), but not positions BL ($\beta = 0.056$, pseudo- $R^2 = 0.647$, $P = 0.428$) or TR ($\beta = 0.153$, pseudo- $R^2 = 0.370$, $P = 0.073$; Fig. 2d; Supplementary File 2: RS17).

DISCUSSION

The experiments in this study demonstrate two important findings: (1) Picasso triggerfish can learn probability distribution information, and (2) they can apply this knowledge in a visual discrimination decision-making task in a manner commensurate with increasing visual uncertainty defining the correct choice. When the fish were presented with stimuli they had learned to a

high degree of accuracy, they chose the correct stimulus in almost all trials. However, as their S+ selection error rate increased, the fish appeared to rely more on their previous knowledge of the correct response distribution, and increasingly make selections based on position. The observed responses are consistent with Bayesian inference, but there are other possible explanations or mechanisms for this behaviour. For example, fish could have learned that there were at least two separate tasks: one task with identical stimuli and where choices should be made based on stimulus position and another task that has one stimulus that appears different to all others, and that is always the target. Further experiments are needed to disentangle alternative possibilities, but our results show that the decision strategy used by the fish increased their potential for receiving food rewards (experiment 1). These experiments have thus revealed a powerful mechanism for adaptive decision making when fish are faced with uncertainty about incoming sensory cues.

In this study we have shown that fish can incorporate the statistics of their past experience and their degree of certainty in incoming sensory information, when making decisions. Using this strategy may afford several benefits: (1) fish can use previous experiences to inform current decisions, (2) they can respond flexibly and dynamically to changing situations, and (3) they can make optimized decisions in uncertain conditions. However, as has been observed in the foraging strategies of other species, the behaviour of the fish was not optimized to receive the most rewards possible. To maximize potential food rewards, subjects should have selected stimuli in the biased position in all trials. Instead, fish appeared to apply ‘probability matching’ whereby the stimulus selection rate matched the learned probability distribution. Probability matching has been previously observed in some, but not all (e.g. Herbranson & Schroeder, 2010; Parducci & Polt, 1958; Wilson & Rollin, 1959) animals including fish (Behrend & Bitterman, 1961, 1966; Bullock & Bitterman, 1962; Perez-Escudero & de Polavieja, 2011; Woodard & Bitterman, 1973) and humans (e.g. Gaissmaier & Schooler, 2008; Herbranson & Schroeder, 2010; Rubinstein, 2002). Why it occurs and its evolutionary significance is still debated. One possibility is that it is the result of a cognitive shortcut (Vulkan, 2000), while another possibility is that the randomness of a sequence is not internalized leading to the use of alternative optimizing strategies (e.g. ‘win-stay, lose-shift’; Gaissmaier & Schooler, 2008). However, these explanations are typically considered in the context of human decision making and may not be relevant to all animals, including fish, if such divergent species do not share the same cognitive biases. Both explanations imply that probability matching is an artefact of a cognitive weakness, but it may also provide some benefit to an individual as it allows for sampling of the environment and therefore an opportunity to update priors where conditions may be fluctuating (Pisupati et al., 2021).

Whatever the cause, there is experimental evidence that the application of probability matching may be context dependent, and contingent on incentives, motivation, reinforcement or understanding of the problem (Bitterman, 1971; Börgers & Sarin, 2000; Erev & Barron, 2005; Rivas, 2013; Shanks et al., 2002; Vulkan, 2000; Wolford et al., 2004). In our experiment 1, three of the eight fish chose the biased position in T5 at a higher rate than probability matching predicts (fish: 8M = 96%, 9N = 71%, 21P = 79%). Individual differences such as these have been observed in other studies even with very different experimental protocols (e.g. Bitterman, 1971), suggesting that individual variation is a common occurrence. Although the cause or function of probability matching is outside the scope of this study, for the purposes of our results, this behaviour provides clear evidence that fish in experiment 1 learned the specific probability distributions of the positive stimulus.

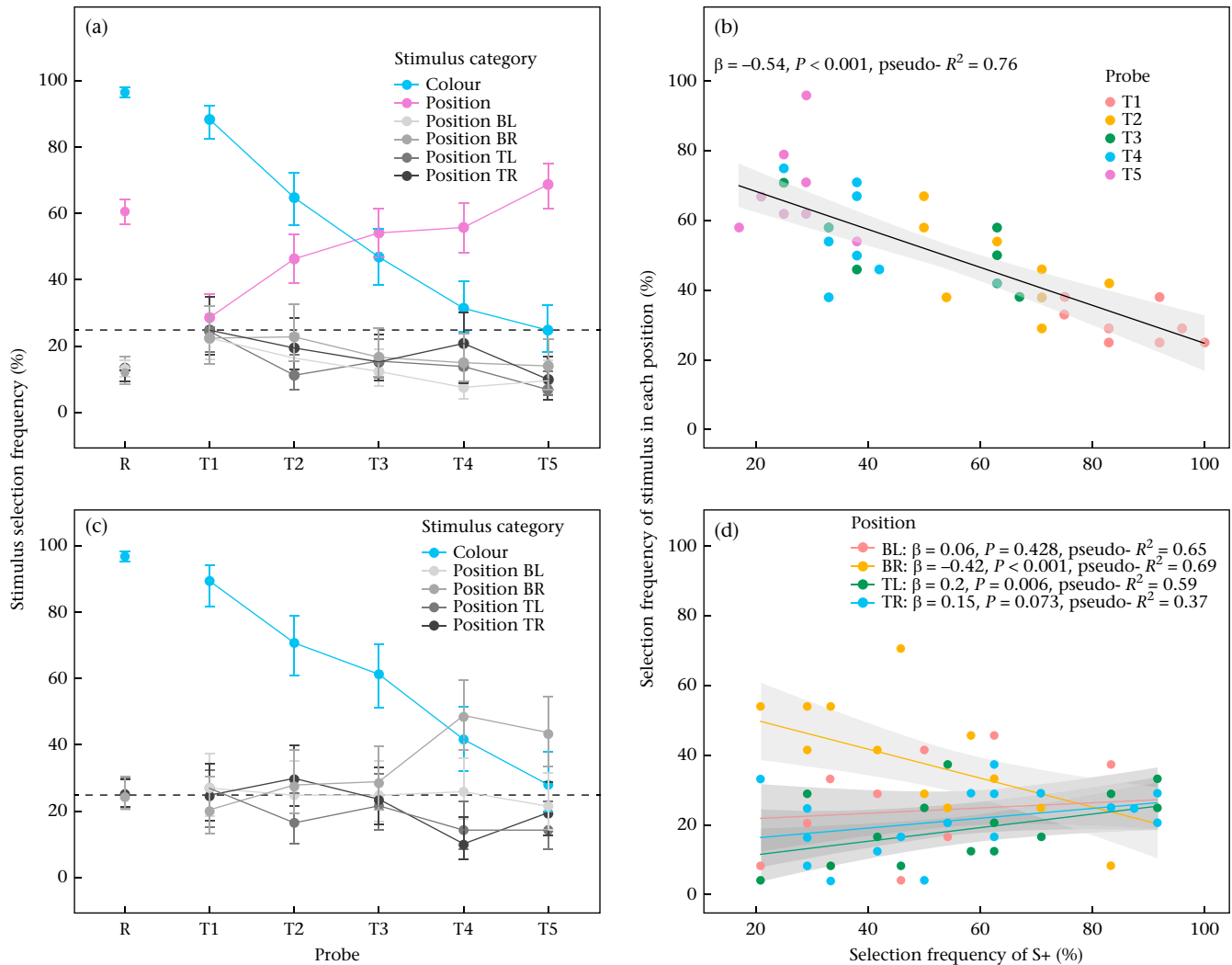


Figure 2. Stimulus selection frequency results of experiments 1 and 2. (a, b) In experiment 1, the target stimulus was 4.5 times more likely to be in one of the four positions when the original conditioned stimuli were presented (S+ and S−). The four possible positions are top right (TR), top left (TL), bottom right (BR) and bottom left (BL). (c, d) In experiment 2, the target stimulus was presented in all positions equally. (a) The mean selection frequency of S+ and all stimuli positions for eight fish. The dashed line at 25% indicates a selection frequency consistent with chance. Error bars represent 95% confidence intervals based on a generalized linear mixed model. Stimuli used in Testing are shown below the figure where the top circles are S+ (not to scale). (b) A linear regression analysis of S+ selection frequency versus selection of stimuli in the biased position. The shaded grey area indicates 95% confidence intervals. (c) The mean stimulus selection frequency for four fish, given no position bias. Symbols are the same as those in (a). (d) Linear regression analyses of S+ selection frequency versus each of four possible stimuli positions.

In experiments 1 and 2, the selection frequency of stimuli in unbiased positions was generally consistent with chance, except in experiment 2, probes T4 and T5. In these cases, stimuli in position BR were chosen at a statistically higher frequency than chance, and position TL at a lower frequency. It is not surprising that as the discriminability of the visual stimulus decreased, and with a dearth of alternative information, fish adopted a strategy of choosing one of four positions. Whether this is because fish believe there is a potential difference in the value of each position or just have a preference cannot be determined from our experiments. However, we do not interpret the results as an indication that BR or TL are particularly important as even individual fish changed their 'preferred' position depending on probe type. For example, the most frequently selected position by Fish 25-O was TL in T3 (38%), but it changed to BR in T4 (42%) and back to TL in T5 (29%). Instead, it is possible that fish may have been sampling the same position repeatedly to gather more information about the likelihood of receiving a reward for that choice.

Our use of a two-tier reward system in experiment 1 served the purpose of directing the attention of fish to the biased position, but it also conflated increased reward probability with increased reward magnitude. We also simplified the reward schedule for two fish in experiment 2, so that all correct choices resulted in the same reward. To our knowledge, there are no experiments specifically testing whether fish incorporate reward magnitude into their decisions. However, cleaner wrasse, *Labroides dimidiatus*, are well known for their ability to assess the value of a client and refrain from biting high-value clients (e.g. large frequent visitors) to ensure those clients return in the future (Wismer et al., 2019). Given the importance of reward magnitude to a wide range of animals, including bees, *Apis mellifera* (Gil & De Marco, 2009), pigeons, *Columba livia* (Rose et al., 2009) and rats, *Rattus norvegicus* (Zoratto et al., 2016), it is likely that reward magnitude also influences fish learning and decision making. Experiments with pigeons have shown that they learn a colour discrimination task faster when given a larger reward (Rose et al., 2009). Rats are more likely to

Table 3
Differences in frequency of choice based on probe brightness for experiment 2

Fixed effects	β coefficient	SE	z	P
Intercept	3.85	0.32	12.05	<0.001
T1-R	−1.70	0.46	−3.67	0.001
T2-R	−2.96	0.39	−7.59	<0.001
T3-R	−3.38	0.38	−8.85	<0.001
T4-R	−4.19	0.38	−11.00	<0.001
T5-R	−4.79	0.39	−12.22	<0.001
T2-T1	−1.26	0.40	−3.14	0.006
T3-T1	−1.69	0.39	−4.27	<0.001
T4-T1	−2.49	0.39	−6.33	<0.001
T5-T1	−3.09	0.40	−7.65	<0.001
T3-T2	−0.42	0.31	−1.37	0.171
T4-T2	−1.22	0.31	−4.01	<0.001
T5-T2	−1.83	0.32	−5.72	<0.001
T4-T3	−0.80	0.29	−2.73	0.019
T5-T3	−1.40	0.31	−4.55	<0.001
T5-T4	−0.60	0.31	−1.96	0.100
Random effects	Variance	SD		
Individual (intercept)	<0.001	<0.001		

Results from the generalized linear mixed model with fish ID as random intercept (Supplementary File 2: RS10). *P* values are given after post hoc analysis to control for multiple comparisons using Holm – Bonferroni adjustment. Significant results are in bold.

choose an option with an uncertain outcome if the eventual reward value is significantly higher than the more reliable choice (Zoratto et al., 2016). In our experiment, we do not know whether the bait fish was perceived as a more attractive reward for the fish than the pellet, or whether there was a novelty effect. Nevertheless, the probability of getting a reward or the probability of getting a higher reward would ultimately predict the same decision outcome. In addition to differences in reward type, two of the fish in experiment 2 were rewarded during probe trials and two were not. Despite these differences in protocol, our statistical analysis shows that the fish all behaved similarly and that these differences had no discernible impact on the choices of the fish (Table 3: random effect (i.e. individuals) variance and standard deviation <0.001).

The specific causes of individual variation observed in this and many other studies of fish behaviour are impossible to determine from our experiments, particularly given our individual fish sample size, but we can speculate. For example, individual variation may be the result of individual differences in signal perception, introducing signal noise at various stages of the information processing systems (Faisal et al., 2008). It may also be due to the differences in reward protocol given to some individuals which could, for example, alter motivational states. Alternatively, it may be a product of a Bayesian decision strategy. Probability-based choices can lead to more of a gradient of choices than other context-specific decision rules such as ‘if-then’ or ‘win-stay, lose-shift’, although this depends on the specifics of the rules learned. A probability-based decision rule may explain not only the range of behavioural outcomes observed in animals, but also the variability in their decisions even when faced with what appears to be identical choices (Beck et al., 2012), such as in a controlled laboratory environment. This is because an individual's priors, their level of uncertainty in a given trial and whether they will make a choice that favours their expectation of a positive outcome or not may differ. Our results also show that individual experience, and by extension memory, plays an important role in fish decision making. Hard-wired rules presumably have less demand on long-term memory, while the application of probability distributions would require some, and possibly a significant, capacity for individual memory. How long these types of memories last and whether or how quickly they can be overwritten by a period of acclimation to new circumstances are interesting questions for future studies and would be valuable to our understanding

of how fish adapt to persistent and stochastic changes in their environment.

Our experiments have tested whether fish can integrate probabilistic information into their decision-making process when faced with uncertain visual signals. Our results show that a Bayesian inference approach may underpin sensory decision strategies, and therefore results are particularly important to our understanding of sensory signal processing in fish. Our results, combined with those of previous studies, provide increasing evidence that Bayesian inference may be generally applicable across taxa and tasks.

Author Contributions

Cait Newport: Conceptualization, Methodology, Software, Investigation, Formal analysis, Resources, Writing – original draft, Visualization, Funding acquisition. **Adelaide Sibeaux:** Formal analysis, Writing – review & editing, visualization. **Guy Wallis:** Conceptualization, Writing – review & editing. **Lucas Wilkins:** Formal analysis. **Theresa Burt de Perera:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Data Availability

All data are provided in the Supplementary Material.

Declaration of Interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

Acknowledgments

We thank Hannah Smithson and Brian Rogers for advice on relative reflectance measurements and John McNamara, Alasdair Houston and Alex Kacelnik for comments on the manuscript. This work was supported by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement [659684], and a Leverhulme Trust Early Career Fellowship (CN). The contents of the article reflect the authors' views and not those of the European Commission.

Supplementary Material

Supplementary material associated with this article is available in the online version at <https://doi.org/10.1016/j.anbehav.2024.02.016>.

References

- Alonso, J. C., Alonso, J. A., Bautista, L. M., & Muñoz-Pulido, R. (1995). Patch use in cranes: A field test of optimal foraging predictions. *Animal Behaviour*, 49(5), 1367–1379. <https://doi.org/10.1006/anbe.1995.0167>
- Attwell, J. R., Ioannou, C. C., Reid, C. R., & Herbert-Read, J. E. (2021). Fish avoid visually noisy environments where prey targeting is reduced. *American Naturalist*, 198(3), 421–432. <https://doi.org/10.1086/715434>
- Börsers, T., & Sarin, R. (2000). Naive reinforcement learning with endogenous aspirations. *International Economic Review*, 41(4), 921–950. <https://doi.org/10.1111/1468-2354.00090>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4 [sparse matrix methods; linear mixed models; penalized least squares; Cholesky decomposition]. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beck, J. M., Ma, W. J., Pitkow, X., Latham, P. E., & Pouget, A. (2012). Not noisy, just wrong: The role of suboptimal inference in behavioral variability. *Neuron*, 74(1), 30–39. <https://doi.org/10.1016/j.neuron.2012.03.016>
- Behrend, E. R., & Bitterman, M. E. (1961). Probability-matching in the fish. *American Journal of Psychology*, 74, 542–551. <https://doi.org/10.2307/1419664>

- Behrend, E. R., & Bitterman, M. E. (1966). Probability-matching in the goldfish. *Psychonomic Science*, 6, 327–328. <https://doi.org/10.3758/BF03330918>
- Biernaskie, J. M., & Gegeer, R. J. (2007). Habitat assessment ability of bumblebees implies frequency-dependent selection on floral rewards and display size. *Proceedings of the Royal Society B: Biological Sciences*, 274(1625), 2595–2601.
- Biernaskie, J. M., Walker, S. C., & Gegeer, R. J. (2009). Bumblebees learn to forage like Bayesians. *American Naturalist*, 174(3), 413–423. <https://doi.org/10.1086/603629>
- Bitterman, M. E. (1971). Visual probability learning in the rat. *Psychonomic Science*, 22(3), 191–192. <https://doi.org/10.3758/BF03332563>
- Budaev, S., Jørgensen, C., Mangel, M., Eliassen, S., & Giske, J. (2019). Decision-making from the animal perspective: Bridging ecology and subjective cognition. *Frontiers in Ecology and Evolution*, 7, 164. <https://doi.org/10.3389/fevo.2019.00164>
- Bullock, D. H., & Bitterman, M. E. (1962). Probability-matching in the pigeon. *American Journal of Psychology*, 75(4), 634–639. <https://doi.org/10.2307/1420288>
- Cheney, K. L., Green, N. F., Vibert, A. P., Vorobyev, M., Marshall, N. J., Osorio, D. C., & Endler, J. A. (2019). An Ishihara-style test of animal colour vision. *Journal of Experimental Biology*, 222(1), jeb189787. <https://doi.org/10.1242/jeb.189787>
- Cheney, K. L., Hudson, J., De Busslerolles, F., Luehrmann, M., Shaughnessy, A., Van Den Berg, C., & Cortesi, F. (2022). Seeing Picasso: An investigation into the visual system of the triggerfish *Rhinecanthus aculeatus*. *Journal of Experimental Biology*, 225(7). <https://doi.org/10.1242/jeb.243907>
- Cheney, K. L., Newport, C., McClure, E. C., & Marshall, N. J. (2013). Colour vision and response bias in a coral reef fish. *Journal of Experimental Biology*, 216(15), 2967–2973. <https://doi.org/10.1242/jeb.087932>
- Dominoni, D. M., Halfwerk, W., Baird, E., Buxton, R. T., Fernández-Juricic, E., Fristrup, K. M., & Barber, J. R. (2020). Why conservation biology can benefit from sensory ecology. *Nature Ecology & Evolution*, 4(4), 502–511. <https://doi.org/10.1038/s41559-020-1135-4>
- Erev, I., & Barron, G. (2005). On adaptation, maximization, and reinforcement learning among cognitive strategies. *Psychological Review*, 112(4), 912–931. <https://doi.org/10.1037/0033-295X.112.4.912>
- Faisal, A. A., Selen, L. P. J., & Wolpert, D. M. (2008). Noise in the nervous system. *Nature Reviews Neuroscience*, 9(4), 292–303. <https://doi.org/10.1038/nrn2258>
- Foley, B. R., & Marjoram, P. (2017). Sure enough: Efficient Bayesian learning and choice. *Animal Cognition*, 20(5), 867–880. <https://doi.org/10.1007/s10071-017-1107-5>
- Gaissmaier, W., & Schooler, L. J. (2008). The smart potential behind probability matching. *Cognition*, 109(3), 416–422. <https://doi.org/10.1016/j.cognition.2008.09.007>
- Gershman, S. J. (2015). A unifying probabilistic view of associative learning. *PLoS Computational Biology*, 11(11), Article e1004567. <https://doi.org/10.1371/journal.pcbi.1004567>
- Gil, M., & De Marco, R. J. (2009). Honeybees learn the sign and magnitude of reward variations. *Journal of Experimental Biology*, 212(17), 2830–2834. <https://doi.org/10.1242/jeb.032623>
- Green, N. F., Guevara, E., Osorio, D. C., Endler, J. A., Marshall, N. J., Vorobyev, M., & Cheney, K. L. (2022). Colour discrimination thresholds vary throughout colour space in a reef fish (*Rhinecanthus aculeatus*). *Journal of Experimental Biology*, 225(7). <https://doi.org/10.1242/jeb.243533>
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. J. Wiley.
- Gunji, Y.-P., Murakami, H., Tomaru, T., & Basios, V. (2018). Inverse Bayesian inference in swarming behaviour of soldier crabs. *Philosophical Transactions of the Royal Society A: Mathematical, Physical & Engineering Sciences*, 376(2135), Article 20170370. <https://doi.org/10.1098/rsta.2017.0370>
- Hartig, F. (2022). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. <https://CRAN.R-project.org/package=DHARMA>.
- Herbranson, W. T., & Schroeder, J. (2010). Are birds smarter than mathematicians? Pigeons (*Columba livia*) perform optimally on a version of the Monty Hall Dilemma. *Journal of Comparative Psychology*, 124(1), 1–13. <https://doi.org/10.1037/a0017703>
- Hunte, W., Myers, R. A., & Doyle, R. W. (1985). Bayesian mating decisions in an amphipod, *Gammarus lawrencianus* Bousfield. *Animal Behaviour*, 33(2), 366–372. [https://doi.org/10.1016/S0003-3472\(85\)80060-9](https://doi.org/10.1016/S0003-3472(85)80060-9)
- Kuwamura, T. (1997). Evolution of female egg care in Harem Triggerfish, *Rhinecanthus aculeatus*. *Ethology*, 103(12), 1015–1023. <https://doi.org/10.1111/j.1439-0310.1997.tb00143.x>
- Lima, S. L. (1984). Downy woodpecker foraging behavior: Efficient sampling in simple stochastic environments. *Ecology*, 65(1), 166–174. <https://doi.org/10.2307/1939468>
- Lima, S. L. (1985). Sampling behavior of starlings foraging in simple patchy environments. *Behavioral Ecology and Sociobiology*, 16(2), 135–142. <https://doi.org/10.1007/BF00295147>
- Luttbeg, B., & Warner, R. R. (1999). Reproductive decision-making by female peacock wrasses: Flexible versus fixed behavioral rules in variable environments. *Behavioral Ecology*, 10(6), 666–674. <https://doi.org/10.1093/beheco/10.6.666>
- Ma, W. J. (2019). Bayesian decision models: A primer. *Neuron*, 104(1), 164–175. <https://doi.org/10.1016/j.neuron.2019.09.037>
- Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., Cowlshaw, G., & Boots, M. (2013). How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions. *Journal of Animal Ecology*, 82(4), 894–902. <https://doi.org/10.1111/1365-2656.12089>
- Matchette, S. R., Cuthill, I. C., Cheney, K. L., Marshall, N. J., & Scott-Samuel, N. E. (2020). Underwater caustics disrupt prey detection by a reef fish. *Proceedings of the Royal Society B: Biological Sciences*, 287(1924), Article 20192453. <https://doi.org/10.1098/rspb.2019.2453>
- Matchette, S. R., Cuthill, I. C., & Scott-Samuel, N. E. (2019). Dappled light disrupts prey detection by masking movement. *Animal Behaviour*, 155, 89–95. <https://doi.org/10.1016/j.anbehav.2019.07.006>
- McNamara, J. M., Green, R. F., & Olsson, O. (2006). Bayes' theorem and its applications in animal behaviour. *Oikos*, 112(2), 243–251. <https://doi.org/10.1111/j.0030-1299.2006.14228.x>
- McNamara, J., & Houston, A. (1980). The application of statistical decision theory to animal behaviour. *Journal of Theoretical Biology*, 85(4), 673–690. [https://doi.org/10.1016/0022-5193\(80\)90265-9](https://doi.org/10.1016/0022-5193(80)90265-9)
- Milinski, M. (1994). Long-term memory for food patches and implications for ideal free distributions in sticklebacks. *Ecology*, 75(4), 1150–1156. <https://doi.org/10.2307/1939438>
- Newport, C., Green, N., McClure, E., Osorio, D., Vorobyev, M., & Cheney, K. L. (2017). Fish use colour to learn compound visual signals. *Animal Behaviour*, 125, 93–100. <https://doi.org/10.1016/j.anbehav.2017.01.003>
- Olsson, O., & Noël, M. A. H. (1999). Gaining ecological information about Bayesian foragers through their behaviour. I. Models with predictions. *Oikos*, 87(2), 251–263. <https://doi.org/10.2307/3546740>
- Olsson, O., Wiktander, U., Holmgren, N. M., & Nilsson, S. G. (1999). Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. *Oikos*, 264–276.
- Parducci, A., & Polt, J. (1958). Correction vs. noncorrection with changing reinforcement schedules. *Journal of Comparative & Physiological Psychology*, 51(4), 492–495. <https://doi.org/10.1037/h0040097>
- Perez-Escudero, A., & de Polavieja, G. (2011). Collective animal behavior from Bayesian estimation and probability matching. *PLoS Computational Biology*, 7(11), Article e1002282. <https://doi.org/10.1371/journal.pcbi.1002282>
- Pisupati, S., Chartarisky-Lynn, L., Khanal, A., & Churchland, A. K. (2021). Lapses in perceptual decisions reflect exploration. *Elife*, 10, Article e55490. <https://doi.org/10.7554/eLife.55490>
- Ramírez, J. C., & Marshall, J. A. R. (2017). Can natural selection encode Bayesian priors? *Journal of Theoretical Biology*, 426, 57–66. <https://doi.org/10.1016/j.jtbi.2017.05.017>
- Ratcliff, R., & Rouder, J. N. (1998). Modeling response times for two-choice decisions. *Psychological Science*, 9, 347–356. <https://doi.org/10.1111/1467-9280.00067>
- Rivas, J. (2013). Probability matching and reinforcement learning. *Journal of Mathematical Economics*, 49(1), 17–21. <https://doi.org/10.1016/j.jmateco.2012.09.004>
- Rose, J., Schmidt, R., Grabemann, M., & Güntürkün, O. (2009). Theory meets pigeons: The influence of reward-magnitude on discrimination-learning. *Behavioural Brain Research*, 198(1), 125–129. <https://doi.org/10.1016/j.bbr.2008.10.038>
- Roy, N. A., Bak, J. H., Akrami, A., Brody, C. D., & Pillow, J. W. (2021). Extracting the dynamics of behavior in sensory decision-making experiments. *Neuron*, 109(4), 597–610. <https://doi.org/10.1016/j.neuron.2020.12.004>
- Rubinstein, A. (2002). Irrational diversification in multiple decision problems. *European Economic Review*, 46(8), 1369–1378. [https://doi.org/10.1016/S0014-2921\(01\)00186-6](https://doi.org/10.1016/S0014-2921(01)00186-6)
- Santiago, C., Green, N. F., Hamilton, N., Endler, J. A., Osorio, D. C., Marshall, N. J., & Cheney, K. L. (2020). Does conspicuousness scale linearly with colour distance? A test using reef fish. *Proceedings of the Royal Society B: Biological Sciences*, 287(1935), Article 20201456. <https://doi.org/10.1098/rspb.2020.1456>
- Selonen, V., & Hanski, I. K. (2010). Decision making in dispersing Siberian flying squirrels. *Behavioral Ecology*, 21(2), 219–225. <https://doi.org/10.1093/beheco/arp179>
- Shanks, D. R., Tunney, R. J., & McCarthy, J. D. (2002). A re-examination of probability matching and rational choice. *Journal of Behavioral Decision Making*, 15(3), 233–250. <https://doi.org/10.1002/bdm.413>
- Simpson, E. E., Marshall, N. J., & Cheney, K. L. (2016). Coral reef fish perceive lightness illusions. *Scientific Reports*, 6(1), Article 35335. <https://doi.org/10.1038/srep35335>
- Trimmer, P. C., Houston, A. I., Marshall, J. A. R., Mendl, M. T., Paul, E. S., & McNamara, J. M. (2011). Decision-making under uncertainty: Biases and Bayesians. *Animal Cognition*, 14(4), 465–476. <https://doi.org/10.1007/s10071-011-0387-4>
- Valone, T. J. (1991). Bayesian and prescient assessment: Foraging with pre-harvest information. *Animal Behaviour*, 41(4), 569–577. [https://doi.org/10.1016/S0003-3472\(05\)80897-8](https://doi.org/10.1016/S0003-3472(05)80897-8)
- Valone, T. J. (1992). Information for patch assessment: A field investigation with black-chinned hummingbirds. *Behavioral Ecology*, 3(3), 211–222. <https://doi.org/10.1093/beheco/3.3.211>
- Valone, T. J., & Brown, J. S. (1989). Measuring patch assessment abilities of desert Granivores. *Ecology*, 70(6), 1800–1810. <https://doi.org/10.2307/1938113>
- Valone, T. J., & Giraldeau, L.-A. (1993). Patch estimation by group foragers: What information is used? *Animal Behaviour*, 45(4), 721–728. <https://doi.org/10.1006/anbe.1993.1086>
- Van Den Berg, C. P., Hollenkamp, M., Mitchell, L. J., Watson, E. J., Green, N. F., Marshall, N. J., & Cheney, K. L. (2020). More than noise: Context-dependant luminance contrast discrimination in a coral reef fish (*Rhinecanthus aculeatus*). *Journal of Experimental Biology*, 223(21), jeb232090. <https://doi.org/10.1242/jeb.232090>
- van Gils, Jan, A., Schenk, I. W., Bos, O., & Piersma, T. (2003). Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *American Naturalist*, 161(5), 777–793. <https://doi.org/10.1086/374205>

- Venables, S. V., Drerup, C., Powell, S. B., Marshall, N. J., Herbert-Read, J. E., & How, M. J. (2022). Polarization vision mitigates visual noise from flickering light underwater. *Science Advances*, 8(36), Article eabq2770. <https://doi.org/10.1126/sciadv.abq2770>
- Vulkan, N. (2000). An economist's perspective on probability matching. *Journal of Economic Surveys*, 14(1), 101–118. <https://doi.org/10.1111/1467-6419.00106>
- Wilson, W. A., Jr., & Rollin, A. R. (1959). Two-choice behavior of rhesus monkeys in a noncontingent situation. *Journal of Experimental Psychology*, 58, 174–180. <https://doi.org/10.1037/h0043061>
- Wismer, S., Pinto, A. I., Triki, Z., Grutter, A. S., Roche, D. G., & Bshary, R. (2019). Cue-based decision rules of cleaner fish in a biological market task. *Animal Behaviour*, 158, 249–260. <https://doi.org/10.1016/j.anbehav.2019.09.013>
- Wolford, G., Newman, S. E., Miller, M. B., & Wig, G. S. (2004). Searching for patterns in random sequences. *Canadian Journal of Experimental Psychology*, 58(4), 221–228.
- Woodard, W. T., & Bitterman, M. E. (1973). Further experiments on probability learning in goldfish. *Animal Learning & Behavior*, 1(1), 25–28. <https://doi.org/10.3758/BF03198993>
- Zoratto, F., Laviola, G., & Adriani, W. (2016). The subjective value of probabilistic outcomes: Impact of reward magnitude on choice with uncertain rewards in rats. *Neuroscience Letters*, 617, 225–231. <https://doi.org/10.1016/j.neulet.2016.02.026>

Appendix

Table A1
Individual fish stimulus selection frequency

Fish ID	S+ selection frequency (%)						Previous experimental experience
	R (N=120)	T1 (N=24)	T2 (N=24)	T3 (N=24)	T4 (N=24)	T5 (N=24)	
Experiment 1							
2-B	100	100	83	67	33	21	Yes
8-M	98	83	63	63	38	29	Yes
9-N	96	75	46	38	38	29	Yes
11-D	98	100	71	58	38	17	No
12-L	94	75	58	33	25	33	No
14-M	95	92	71	33	29	29	No
20-Q	95	88	75	58	38	17	No
21-P	98	92	50	25	25	25	No
Experiment 2							
17-R	98	92	63	58	46	21	No
18-K	98	83	71	63	50	29	No
24-O	100	92	88	71	29	33	No
25-P	97	92	63	54	42	29	No

Table A2
Individual fish position selection frequency

Fish ID	Position	Position selection frequency (%)					
		R (N=120)	T1 (N=24)	T2 (N=24)	T3 (N=24)	T4 (N=24)	T5 (N=24)
Experiment 1							
2-B	TL	13	25	17	17	0	8
	BL	13	25	21	21	0	8
	TR	13	25	21	25	46	17
	BR (BP)	60	25	42	38	54	67
8-M	TL	14	25	8	21	8	0
	BL	12	29	29	12	21	4
	TR	12	21	8	8	0	0
	BR (BP)	62	25	54	58	71	96
9-N	TL (BP)	60	33	58	67	67	71
	BL	15	21	4	4	17	12
	TR	13	29	29	25	17	17
	BR	12	17	8	4	0	0
11-D	TL	15	25	13	8	21	4
	BL	12	25	12	17	0	8
	TR (BP)	59	25	42	46	50	58
	BR	13	25	33	29	29	29
12-L	TL (BP)	62	38	38	46	33	58
	BL	14	17	17	17	8	17
	TR	12	33	38	17	58	21
	BR	12	12	8	21	0	4
14-M	TL	12	25	8	8	8	0
	BL (BP)	59	25	42	58	42	58
	TR	13	25	21	17	8	8
	BR	15	25	29	17	42	33
20-Q	TL	12	25	17	21	29	13
	BL	13	17	17	4	0	8
	TR (BP)	63	33	29	50	50	63
	BR	13	25	38	25	21	17
21-P	TL	14	21	4	17	17	17
	BL (BP)	60	25	67	71	79	79

(continued on next page)

Table A2 (continued)

Fish ID	Position	Position selection frequency (%)					
		R (N=120)	T1 (N=24)	T2 (N=24)	T3 (N=24)	T4 (N=24)	T5 (N=24)
Experiment 2 17-R 18-K 24-O 25-P	TR	14	21	4	4	0	0
	BR	12	33	25	8	4	4
	TL	24	25	13	13	8	4
	BL	25	25	17	13	4	8
	TR	25	29	38	29	17	33
	BR	26	21	33	46	71	54
	TL	25	29	17	21	25	17
	BL	24	38	29	46	42	25
	TR	26	25	29	17	4	17
	BR	24	8	25	17	29	42
	TL	25	21	25	17	8	8
	BL	25	25	25	25	29	33
	TR	26	21	25	29	8	4
	BR	24	33	25	29	54	54
	TL	23	33	13	38	17	29
	BL	25	21	29	17	29	21
	TR	27	21	29	21	13	25
	BR	26	25	29	25	42	25

BP = biased position.