Fish pool their experience to solve problems collectively

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ABSTRACT

Access to information is a key advantage of grouping. While experienced animals can lead others to solve problems, less is known about whether partially informed individuals can pool experiences to overcome challenges collectively. Here we provide evidence of such ‘experience-pooling’. We presented shoals of sticklebacks (*Gasterosteus aculeatus*) with a two-stage foraging task requiring them to find and access hidden food. Individual fish were either inexperienced, or had knowledge of just one of the stages. Shoals comprising individuals trained in each of the stages pooled their expertise, allowing more fish to access the food, and to do so more rapidly, compared to other shoal compositions. Strong social effects were identified- the presence of experienced individuals increased the likelihood of untrained fish completing each stage. These findings demonstrate that animal groups can integrate individual experience to solve multi-stage problems, and have significant implications our understanding of social foraging, migration, and social systems.

Group-living provides animals with both ready access to valuable social information and the potential, by processing information through social interactions, to achieve solutions to cognitive problems that might lie beyond the reach of lone individuals[1-11]. Information processing by groups can occur via a number of different mechanisms, and distinguishing between these is a key challenge faced by researchers[10]. Such mechanisms include swarm intelligence, facilitation, and pool-of-competence effects. Swarm intelligence refers to improved cognitive performance that stems from distributed, self-organised decision making, with decisions emerging from repeated local interactions between individuals[12,13]. The many-wrongs principle of collective navigation is an example of swarm intelligence. Here, individuals' motivation to follow their varied and imperfect estimates of the correct travel direction interacts with their drive to remain in close proximity to their neighbours, resulting in a group-level compromise on preferred direction that is more accurate than the separate estimates of most individuals[14,15]. A second mechanism, facilitation, occurs when necessary costs such as vigilance for predators are shared among group members, allowing individuals to allocate more effort to other problems, such as searching for resources[11]. Finally, pool-of competence describes effects arising from group size and diversity, with larger groups being statistically more likely to include more experienced, motivated, persistent or bold individuals that are more likely to solve problems and from which others in the group can acquire information[10,16].

Our study is concerned with one aspect of the pool-of-competence effect, specifically variation in experience amongst group members. It is likely often the case in nature that within a given group, members will hold different information about the environment, with some individuals possessing relevant experience in solving a particular challenge that other members lack. This may be especially so in populations with fission-fusion social structure and in those where group fidelity is low, resulting in high turnover of group membership and frequent disbandment and formation of groups. Research has demonstrated that minorities of experienced individuals can lead their uninformed groupmates[17-20]. Here, leadership may emerge as an outcome of the experienced individuals' attraction to the target and the mutual social attraction between these and their naïve groupmates,[3,17,21] that is without any communication or direct transmission of information about the target from leader to follower occurring. Often, different group members might have partial but complementary information about the component parts of a particular task that can be broken down into a number of 'stages' or elements. They may be familiar with different sections of a navigation route for example, or some may know where to find food while others might know how to access it. Plausibly, groups of animals may be able to overcome such multi-stage problems through social interactions that combines the separately-held information possessed by individuals, allowing them to reach integrative solutions that lie beyond the grasp of single individuals.[5] Here we set out to test whether groups of partially informed individuals could indeed pool their knowledge about the separate components of a task to solve complex problems in this manner.

We presented shoals of sticklebacks (*Gasterosteus aculeatus*) with a two-stage navigation and foraging task that required them first to locate a hidden patch of food within a mesh feeder box by swimming through a structured environment towards a light cue (stage 1), and then to access the box by swimming through a small hole in order to obtain the food (stage 2). Some subjects were given prior experience of solving the navigation component of the task, and others experience of accessing food from the food-box, but no single fish had prior experience of both components of the task. We varied the prior experience possessed by individual fish and arranged these into four different combinations, performing ten replicates per combination. One combination consisted solely of individuals with no prior training (neither knowledge of stage 1, nor stage 2). Two combinations consisted of a majority of untrained fish plus a minority of individuals that had been trained to complete either the navigation part of the task, or to access food from the feeder box (either knowledge of stage 1, or stage 2). Finally, one combination consisted of shoals containing equal numbers of untrained, navigation-trained and feeder-trained fish (both knowledge of stage 1, and of stage 2). We predicted that fish in this latter group would access the food patch most rapidly and that more individuals overall would be successful.

RESULTS

The composition of the group (treatment) strongly influenced the number and rate of entries to both the goal area and the feeder (Supplementary Fig. 1).

Numbers of group members entering goal area and feeder

More fish entered the green light goal area in groups that contained trained fish (light trained, Wald Z=7.37, $p<0.01$; feeder trained, Wald Z=3.6, $p<0.01$; combined Wald Z=6.36, $p<0.01$) than in shoals of untrained fish. As predicted, fish in the combined and light-trained groups entered the goal area more often than those in the feeder-trained groups (light trained compared to feeder trained, Wald Z=-4.63, $p<0.01$; combined compared to feeder trained Wald Z=-4.9, $p<0.01$). More fish entered the feeder unit in groups with training (light trained, Wald Z=3.17, p<0.01; feeder trained, Wald Z=3.31, p<0.01; combined Wald Z=7.2, p<0.01) than in untrained groups. Again as predicted, we observed elevated rates of entry in the combined groups compared to other treatments (light trained, Wald Z=-5.07, p<0.01; feeder trained, Wald Z=-4.94, p<0.01 Figure 1a).

When we focused only upon the proportion of naive fish from each group that entered the goal area and the feeders we see a similar pattern of results. There was an increased number of entries into the goal area for shoals containing fish with any type of training (light trained, Wald Z=6.23, p<0.01; feeder trained, Wald Z=3.07, p<0.01; combined, Wald Z=4.74, p<0.01) compared to untrained groups. We also saw an increased rate of entry into the feeder by naive fish in treatments with training (light trained, Wald Z=3.01, p<0.01; feeder trained, Wald Z=1.96, p<0.05; combined, Wald Z=4.96, p<0.01).

Rate of entry

The time of the first fish in each group to enter the green light goal area was lower in the combined and light-trained groups than it was in the feeder-trained and untrained groups (Cox regression: Wald Z= 4.05, P<0.001 and Wald Z= 4.39, P<0.001). The entry times of the first fish in the combined group did not differ from that of the light-trained treatment groups (Wald Z= 0.93, P=0.35). Regarding entry times into the feeder, as predicted, the first fish in the combined group were faster than all of the other treatment groups (untrained, light-trained and feeder-trained: Wald Z= 5.42, P<0.001; Wald Z= 4.13, P<0.001; and Wald Z= 4.16, P<0.001 respectively, Figure 1b).

An identical pattern was seen when we only considered rates of entries by naïve fish from each group into the goal area and the feeders. For goal area entries there was no difference between the light-trained and combined groups in the rate at which untrained fish first entered the goal area (Wald Z= 0.64, P=0.52). The first fish from the untrained and feeder-trained groups took longer to enter the goal area compared to the combined groups (Wald Z= 2.60, P=0.009 and Wald Z= 2.21, P=0.027). As predicted, the first naïve fish in the combined groups to enter the feeder did so sooner than the first fish from the untrained, light-trained and feeder-trained groups (Wald Z= 3.73, P<0.001; Wald Z= 1.96, P=0.049 and Wald Z= 2.72, P=0.007 respectively).

Hazard models

Following these analyses we also ran two proportional hazard models to understand the factors that contributed to the fish entering each area (Figure 2).

We first ran a set of models that analyzed the rate of entry without explicit consideration of the effect of social information. We found that fish who had prior light-training entered the goal area faster than those without it (Wald Z=4.62, p<0.01), and that fish in the presence of conspecifics with light-training entered the goal area faster than those without (Wald Z=10.37, p<0.01). A similar, but weaker, effect on rate of entering the goal area was observed for feeder-trained fish (Wald Z=2.1, p=0.04), and fish in a group with feeder-trained fish (Wald Z=3.15, p<0.01). We also found that prior feeder-training (Wald Z=3.09, p<0.01), but not prior light-training (Wald Z=1.55, p=0.12) increased the rate at which fish entered the feeder, and that the presence of feeder trained fish in the group significantly increased the rate at which all fish entered the feeder

(Wald Z=2.81, $p<0.01$). Interestingly, the presence of light-trained fish significantly reduced the rate at which other fish entered the feeder (Wald Z=-2.72, $p<0.01$).

Extended models that incorporated social information in more complex ways revealed that previous training to approach the green light (Wald Z=5.67, $p<0.01$), the number of light-trained fish (Wald Z=5.05, $p<0.01$), and the number of feeder-trained fish (Wald Z=3.19, $p<0.01$) all positively increased the rate at which fish entered the goal area. We also found a strong positive effect of having a shoal mate previously enter the goal area in the last 10 seconds (Wald Z=19.25, $p<0.01$), but no effect of having had a shoal mate leave in the previous 10 seconds (Wald Z=0.48, $p=0.63$). Overall, the number of fish in the goal area was associated with a decrease in the rate of entry for other fish to enter the goal area (Wald Z=-2.79, $p<0.01$).

We found a similar pattern of results when analyzing entry of the feeder. Prior feeder training significantly increases the rate that fish enter the feeder (Wald Z=2.84, $p<0.01$), and fish are disproportionately more likely to enter the feeder within 10 seconds of a shoal mate doing so (Wald Z=12.83, $p<0.01$). We did not find a significantly increased rate for fish entering the feeder within 10 seconds of another fish leaving it (Wald Z=1.53, $p=0.13$). Overall the number of fish currently in the feeder was associated with a decrease in the rate at which other fish entered the feeder (Wald Z=-5.39, $p<0.01$). Model coefficients for the goal area and the feeder hazard models can be found in Supplementary Tables 2 and 3.

DISCUSSION

This experiment provides clear evidence of experience-pooling, with groups of partially informed fish integrating their experience to solve a two-stage foraging problem collectively. A greater proportion of group members gained access to the food patch, and did so sooner, in the mixed groups that contained some fish experienced in the navigation part and others in the feeder-access aspect of the task compared to fish in other treatments which contained members experienced in only one or in neither of the two components of the task. Moreover, naïve fish in the mixed groups also benefitted by accessing the food sooner compared to naïve fish in the other groups. Both experience and social information were significant in affecting entries into the goal area, the first stage of the task. We saw that light-trained fish entered the goal area at a greater rate than did untrained fish, as expected, but also that feeder-trained fish did too. This latter effect possibly arose because the fish were able to see the feeder as they came close to the goal area and, having learned an association between the feeder and food, were more motivated to approach it and enter the goal area than were fish untrained in either task. At the group level, fish in the light-, feeder- and combined groups were more likely to enter the goal area compared to those in the untrained treatment group. Fish with prior feeder-training, and those that were grouped with feeder-trained fish entered the feeder at a greater rate, but we also found a negative effect of the presence of light-trained fish upon feeder entries. This may have resulted from the fact that light-trained were given experience of feeding beneath the green lights, but not in the feeder itself- they may therefore have anticipated finding food beneath the lights, causing them to remain in this area, where they attracted other group members, delaying their entry into the feeder. Further analyses that incorporated social transmission in more nuanced ways revealed that a fish entering the feeder or goal area substantially increased the likelihood that other fish did so in the next ten seconds. This is consistent with both past experimental findings analysing the following behavior of fish[22,23] and theory predicting that individuals that are both motivated to move towards a particular location and socially attracted to their groupmates may be able to entrain the group and move them towards the target, a principle termed ‘leading according to need’.[17,18,20,21] We found no evidence that the rate at which fish entered the goal area increased immediately after a fish left either the feeder or the goal area suggesting that this effect is mediated by following rather than attention to cues or locations. Such following effects were also identified in a study of recruitment of naïve fish to prey patches by experienced shoal-mates by,[23] who termed them ‘untransmitted social effects’. Interestingly, in both hazard models we saw that the number of fish in the goal and feeder areas was associated with a decrease in the rate of entry for other fish into those areas. The reason for this effect is unclear. One possibility is that it was due to trained individuals entering the goal or feeder areas sooner, with naïve fish either entering quickly soon after (fish were more likely to enter the goal and feeder areas if a group mate had entered within the last 10 seconds), or else taking much longer to find or access the patch because they had been left behind. Taken together, our analyses when considered alongside the findings other studies[17,18,20,21], suggest that leadership arising from the balance between goal orientedness and social attraction may be sufficient to generate collective problem solving.

Several factors potentially contribute to the ability of groups to process information and solve problems, from facilitation, to pool-of-competence effects to swarm intelligence, with these mechanisms potentially acting concert.[10,16] For example, among flocks of songbirds, Morand-Ferron & Quinn[16] showed that larger groups of naïve birds were more likely to obtain food from novel feeding devices, that the presence in the group of a knowledgeable bird further increased the likelihood of the group accessing food and that larger groups were more likely to contain such individuals than smaller ones. Moreover, birds had more success when they were in larger groups and when the feeding devices were closer to cover, compared to when they further away, suggesting that facilitation through reduced predation risk might also affect problem solving. In our study we directly manipulated the experience of group members whilst holding group size constant, allowing us to show that information held by the group could be pooled. This approach also allowed us to rule out other mechanisms, although it doesn't discount the possibility that multiple effects might operate together under natural conditions, as was observed by Morand-Ferron & Quinn.[16] Our findings suggest that for groups of ecological generalists negotiating variable environments, diversity in experience and a distributed knowledge base across a group may be of critical importance, potentially more-so than the presence of 'omniscient' individuals will full knowledge of the challenges.[24] Experience pooling might be especially important within populations that exhibit fission-fusion social structures, where at any point current group members might be expected to possess a greater range of experience than those of more stable groups that have travelled and experienced the same conditions together. We anticipate that experience-pooling, underpinned by leader-follower interactions similar to those seen in our study, might be found in groups of animals facing challenges ranging from learning how to exploit novel foods and avoid new predators to navigating between ephemeral resources and tracing long migration routes.

METHODS

Subjects

Threespine sticklebacks (N=360) were collected using hand nets from the Kinnessburn steam in St Andrews, UK in July 2012, and housed in the laboratory in groups of 40 in 90l aquaria. Each aquarium contained a layer of sand and artificial plants, and was connected to an external filter. The temperature in the laboratory was held at 8°C, and the lights were on for 12 hours per day. The fish were fed daily with frozen blood worms, unless otherwise stated below. We used fish measuring 30-35mm in length that showed no signs of been in reproductive condition. Fish were not sexed.

Overview

The experiment presented 40 groups of 9 fish with a two-stage navigation task. In order to access a food reward, the fish first had to travel to the far end of a large structured arena, where a feeder box containing the food was hidden behind an opaque screen, and to gain access to the food in the feeder box by entering through one of two small holes. The end of the arena with the feeder box and food reward contained two green lights. We tested groups of fish that contained different combinations of individuals trained to approach green lights, trained to enter the feeder box through the target holes, or not trained in either task. Fish that were not trained to the green lights or to the feeder box were nevertheless exposed to these during training, so as to remove any neophobic responses to the stimuli that may otherwise have confounded their behaviour in the experiment proper. The training procedure and two pilot experiments designed to test the efficacy of the training are described in the supplementary material. All procedures were reviewed and approved by the departmental ethics committee.

Experimental Arena

The arena (Supplementary Figure 2) consisted of a black plastic box measuring 160cm long, 100cm wide and 40cm tall. It contained a 2cm-deep layer of fine sand, and was filled with water to a depth of 25cm. The feeder box was placed 10cm from one end of the arena, 40cm from each long wall. It was suspended 10cm above the sand substrate. The feeder box measured 20cm long by 10cm tall and wide. It consisted of a 2mm-wide plastic frame around which were stretched a fine nylon mesh. A 2cm x 2cm square hole was cut in each end of the feeder box, which enabled fish to swim inside and access the food reward (20 dead bloodworms placed in the centre of the feeder box). The use of a mesh feeder had the advantage that olfactory cues emanating from the food would diffuse through the sides, and would not provide an odor gradient leading to the entrance hole. The food was also visible through the mesh walls and floor of the feeder box, leaving the fish highly motivated to solve the task. However, the fish could not find food simply by swimming towards the sight or smell of it, and previous experiments have shown that this arrangement leaves finding the entrance a challenging task.[25]

A white plastic screen measuring 40cm x 40cm was placed 10cm in front of the feeder box, and 30cm from each of the long walls of the arena. This prevented the group of fish, which began the experiment at the other end of the arena, from being able to see the feeder box. In order to reach it, they had to swim either side of this barrier. Either side of the feeder box we placed a green LED unit (Trimble, Milton Keynes, UK). These consisted of a circle of 24 individual LEDs set within a case with a diameter of 5cm. A green filter was taped over each LED unit. Each unit was suspended 10cm above the surface of the water, 20cm either side of the feeder box, and 20 cm from each longwall of the arena. The light produced by the LED units was visible to the fish at the far end of the arena at the beginning of the experiment. A high definition webcam (Logitech C920, Logitech International SA, Lausanne, Switzerland) was mounted 80cm above the feeder box. This was used to film the end the arena immediately behind the barrier, which was designated the ‘green light goal area’.

At the other end of the arena we placed a holding unit constructed from colourless, perforated plastic. This measured 20cm x 20cm, and 40cm tall. The bottom and top of the holding unit were open. It was placed directly upon the sand substrate, 5cm from the back wall, and 40cm from each long side wall of the arena. This was used to house the fish at the beginning of the experiment.

In the middle section of the arena we placed four artificial plants. These measured approximately 10cm tall and 10cm in diameter. One pair of plants were placed 20cm apart, 30cm from each longwall of the arena, and 40cm from the end of the arena where the fish holding unit was placed. The second pair of plants were placed 20cm from these, and 50cm from the white plastic barrier. The plants provided cover for the fish once they were released into the main arena at the beginning of the trial, and facilitated movement throughout the centre of the arena.

Experimental groups

Fish were allocated using a random number algorithm to replicate groups in four treatments that differed in the experience (i.e. prior training) possessed by constituent members. Each group contained nine fish, and we ran 10 replicates in each of the four treatments. The first treatment consisted of groups of nine naïve (i.e. non-trained) fish. In the second, each group contained three fish that had been trained to approach the green light and six naïve fish. The third treatment comprised shoals that contained three fish that had been trained to enter the feeder box and six naïve fish, and the fourth contained shoals with three fish from each training regime plus three naïve fish. Hereafter, these treatment groups respectively are referred to as *untrained*, *light-trained*, *feeder-trained* and *combined*. For clarity, individual fish that had not been trained are referred to as naïve, while the treatment consisting entirely of naïve fish is referred to as untrained. Because familiarity has been shown to affect social foraging interactions in this species,[26] within each group each fish was drawn from a separate holding tank, ensuring that all were equally unfamiliar to one another. Within each group, every fish was fitted with a non-invasive, colour-coded circular tag on its first dorsal spine.[27] These were fitted on the last day of training, and the day before the experiments were performed. This allowed us to recognise each individual fish in the videos. Sample sizes were informed by an earlier social foraging experiment conducted in our laboratory.[26]

Experimental procedure

For each trial, the experimental arena was established as above, and food items (20 dead bloodworms) added to the feeder box. The experimental group was added to the holding unit and allowed to acclimate for 15 minutes, before the holding unit was raised 15cm using a pulley, releasing the fish and beginning the trial. The trial ran for a further 45 minutes. From the webcam footage we recorded the identity of each fish as it entered the green light goal area. For every second of the trial we recorded whether each fish was inside or outside the goal area and inside or outside of the feeder box. We performed five such trials each day (see Supplementary Table 1 for schedule). Following each trial we replaced the water and sand substrate and feeder box prey in the arena.   The experimenter was not blind with respect to treatment group.

Data availability

The datasets analysed during the current study are available from the corresponding author on request.

Statistical analysis

We analyzed the total proportion of fish and the proportion of untrained fish that entered the green light goal area and the feeder box during the trial using a binomial model. We examined the time at which the first fish entered each area for different groups using Cox regressions, focusing upon the entry times of the first fish (irrespective of training) and the first naive fish from each group. We then used Cox proportional hazard models to model all entries in the group and gain a finer temporal resolution of the factors that predict whether and when fish enter either the goal area or the feeder, and the frequency at which they enter the areas. We examined the rate at which fish entered the feeder and goal area predicted by their previous training, previous time spent in the goal area during the trial, the number of light trained fish, the number of feeder trained fish, and three social cues: the number of fish that had entered the goal/feeder area in the last 10s, the number of fish that had exited the goal/feeder area in the last 10s, and the total number of fish in the goal/feeder area. Our data met the assumption of proportional hazards expected by these tests. All proportional hazard models were run in R[28] using the “survival” package.[29]

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AUTHOR CONTRIBUTIONS

MMW designed and performed the experiments, MMW, AW & KNL analysed the data and co-authored the paper.

COMPETING FINANCIAL INTERESTS

We declare no competing financial interests.

MATERIALS & CORRESPONDENCE

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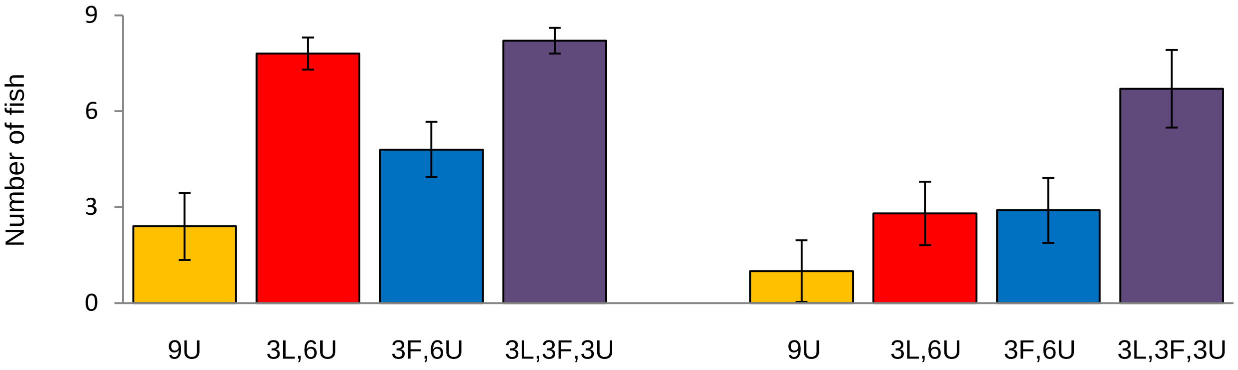
FIGURES

Figure 1. (a) The number of fish in each group to enter the green light goal area and the feeder (mean +/- 95% CI). (b) Survival plots showing the time for the first fish in each group to enter the goal area and feeder. 9U: 9 untrained fish; 3L,6U: 3 light-trained and 6 untrained fish; 3F,6U: 3 feeder-trained and 6 untrained fish; 3L,3F,3U, 3 feeder-trained, 3 light-trained and 3 untrained fish.

Figure 2. (a) The proportion of fish for each level of training to enter the green light goal area broken down by treatment group. (b) The proportion of fish for each level of training to enter the feeder area broken down by treatment group (c) The proportion of fish for each level of training who entered the goal area and then entered the feeder area broken down by treatment group. In each case, mean +/- 95% CI is shown. 9U: 9 untrained fish; 3L,6U: 3 light-trained and 6 untrained fish; 3F,6U: 3 feeder-trained and 6 untrained fish; 3L,3F,3U, 3 feeder-trained, 3 light-trained and 3 untrained fish.

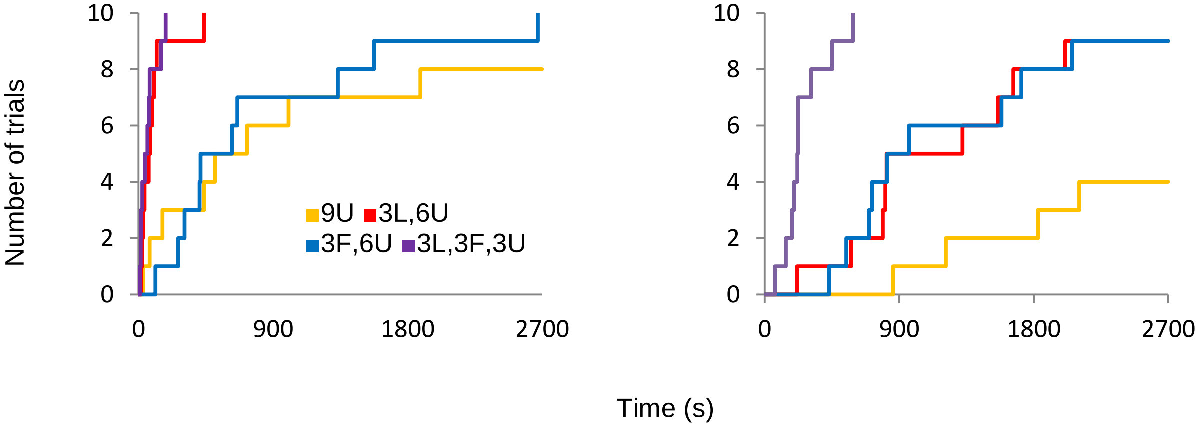
Figure 1. Number and rate of goal zone and feeder entries

(a) Proportion of fish entering zone


(*i*) Goal zone

(*ii*) Feeder

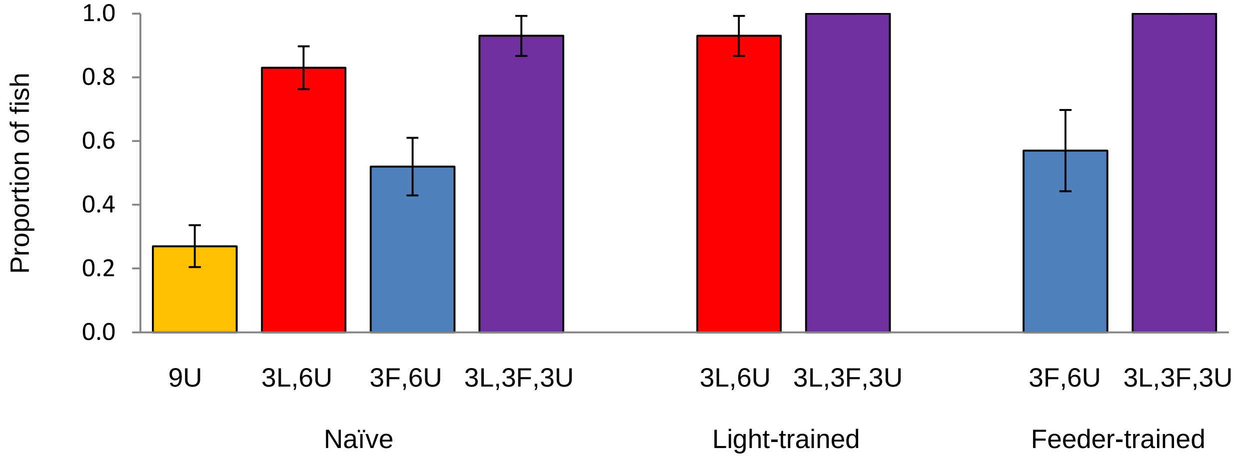
(b) Time for first fish to enter zone


(*i*) Goal zone

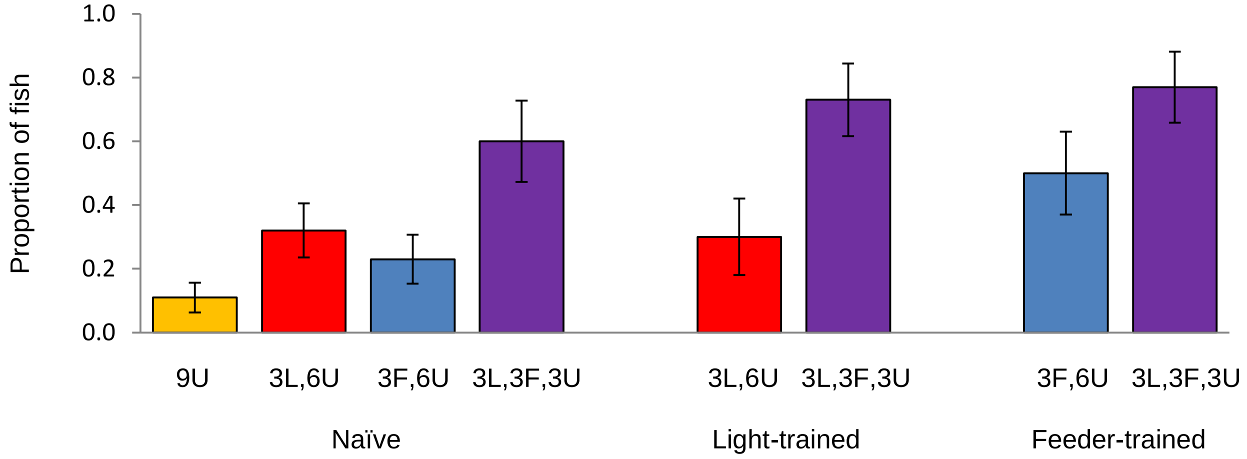
(*ii*) Feeder

Figure 2. Proportion of naïve fish entering the goal and feeder areas

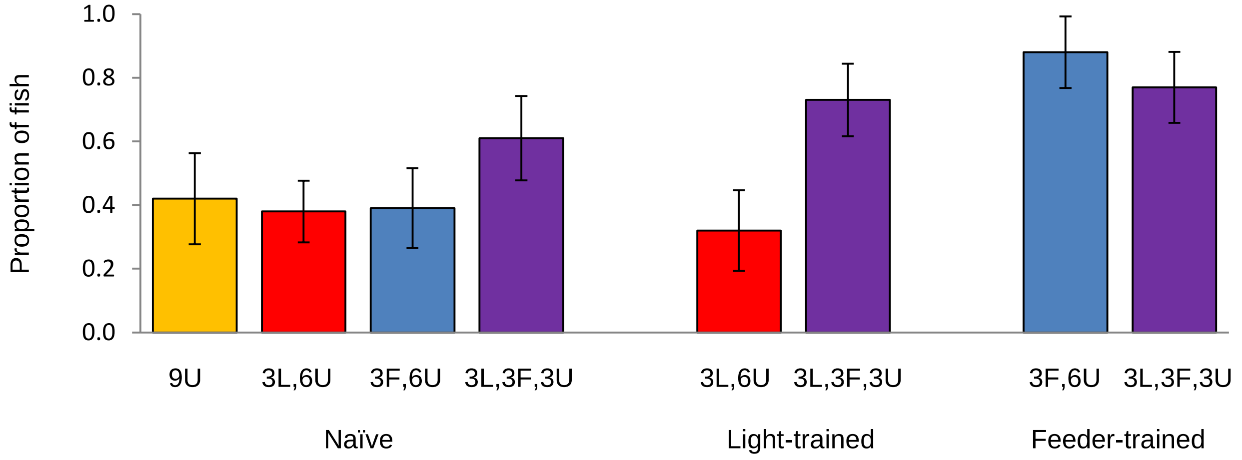
(a) Goal area



(b) Feeder area



(c) Feeder area given goal area



Supplementary information for:

Fish pool their experience to solve problems collectively

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Contents

Supplementary Methods

Training fish to approach the green lights and to access the feeder box

Prior to beginning the experiments it was necessary to first train the fish. Some fish were trained to approach the green light, some were trained how to enter the feeder box and other fish were not trained to either task. The fish were trained in six batches (Supplementary Table 1). The fish from batches one and two were used in pilot experiments designed to assess the efficacy of the training, with the fish from the third to sixth batches being used in the experiment proper.

In batch one and two we set up nine aquaria. Batches three to six contained 18 aquaria. These were sub-divided into two sets of nine aquaria each (referred to as a and b in Supplementary Table 1), with the training and testing regimes in the first set running one day ahead of those in the second. This allowed us to split the experimental trials over two days. Each aquarium contained 10 fish. Only five fish from each aquarium were randomly selected for use in the experiments. We trained additional fish because we anticipated that we would lose some to mortality over the course of training. In fact, none of the trained fish died, but we did not have time to test them all. Untested fish were retained in the laboratory for use in a separate experiment.

Each aquarium had a volume of 45l and contained a 2 cm deep layer of fine sand, and was equipped with an external filter. The aquaria were visually and chemically isolated from one another. The training procedure lasted for four weeks. During the first week the fish were allowed to acclimate. They were fed daily with frozen bloodworms and were not exposed to the green lights or to the feeder box during this time. At the beginning of the second week training began.

In batches one and two, three aquaria were randomly selected and assigned to green light training, three to feeder box training, and three were not trained in either task. In batches three to six, which contain 18 aquaria overall, each subset of nine aquaria was randomly assigned to one of the four experimental treatments (described in main text), such that all nine aquaria received no training, three were trained to the green light while six received no training, three were trained to the feeder while six received no training or three were trained to the feeder, three to the light and three received no training. See Supplementary Table 1 for an overview of the training order and schedule. Fish that were not trained to the green lights or to the feeder box were nevertheless exposed to these, so as to remove any neophobic responses to the stimuli that may otherwise have confounded their behaviour in the experiment proper.

A pair of green lights identical to those used in the experimental arena described above were fitted to the end of each aquarium. These were switched on for 15 minutes twice per day at 10am and 4pm. In the aquaria where fish were trained to approach the green lights, food was provided directly beneath the lights at the same time they were switched on. The food was always consumed within the 15 minute period during which the lights were on. In the aquaria where the fish were not trained to associate the lights with food, the lights were kept off during the two daily feeding periods, and were only switched on for 15 minutes one hour after the fish had been fed, and after they had consumed all of the food. Training was repeated daily for three weeks.

In each aquarium we also placed a feeder box, as described above. This was suspended 10cm above the bottom of the tank. In the aquaria where fish were trained to access the feeder box, training was structured as follows. During the first week they were presented with a feeder box in which both ends had been removed. Food was placed within the feeder box twice per day at 10am and 4pm. The fish were easily able to access the food by swimming into the feeder box through the open ends. During the second week, the feeder box was replaced with one with 5cm square holes in either end, with food placed inside as before. During the third week the feeder box was replaced with one with 2cm square holes, identical to the one used in the experiment itself. In both the second and third weeks fish were seen to readily enter the feeder box and eat the food. In the aquaria where the fish were not trained to this task, we used feeder boxes with completely closed ends. For these groups food was provided directly on the sand substrate beneath the feeder box. The fish in these groups had no experience of entering the feeder boxes and no experience of detecting food within them.

Training: pilot experiments

Fish were tested individually in an experimental arena measuring 45cm long by 30cm tall and wide. The arena was screened in black plastic and contained a 2cm deep layer of fine sand, and was filled with water to a depth of 25 cm. At one end of the arena we placed a holding unit measuring 5x5cm wide, and 35cm tall. This was constructed from colourless perforated plastic. It was open at the top and bottom, and was placed directly upon the sand substrate. A high-definition WebCam was fixed directly above the experimental arena. This was used to record the trials. Five such arenas were established, allowing five trials to be run simultaneously.

We performed two pilot experiments, one in which fish were given the opportunity to approach two green lights located at one end of the tank, and one in which they were presented with a feeder box containing 20 dead blood worms. The lights and the feeder box were as described for the experiment proper, above. We tested the fish from batch one in the green light pilot experiment and those from batch two in the feeder box pilot experiment. Of the 10 fish in each training aquarium, we randomly selected five to be tested. For each pilot experiment we tested three treatment groups (the fish trained to the green light, fish trained to the feeder box and fish that were trained to neither), with 15 replicates in each treatment group. They were tested on the day immediately following the end of the training period.

In the green light pilot experiment, two green lights were suspended 10cm above the surface of the water at the end of a tank directly opposite the holding unit (Supplementary Figure 3a). No prey were present in the tank in this experiment. The holding unit was used to contain the test subject at the start of the trial. A fish was randomly selected, and carefully transferred from its training aquarium to the holding unit in the experimental arena. It was allowed to acclimate for 10 minutes. During this period the green lights were switched off. The lights were then switched on and the fish was allowed to settle for another 10 minutes. Following this, the holding unit was carefully raised and removed, releasing the fish and beginning the trial. The trial lasted for a further 10 minutes. From the videos of the trials, we recorded the latency of each fish to enter a 10cm wide goal zone beneath the lights.

In the feeder box pilot experiment, we suspended a feeder box 10cm above the substrate and 10cm from the back wall of the arena (Supplementary Figure 3b). The feeder box was accessible via two 2x2cm holes, identical to the one described above, and as used in the experiment proper. The feeder box contained 20 dead bloodworms. These were added to the feeder box immediately before the fish was added to the holding unit. The fish was allowed to acclimate for 20 minutes before the holding unit was carefully raised and removed, beginning the trial. The trial lasted for 10 minutes. We recorded the latency of the fish to enter the feeder box.

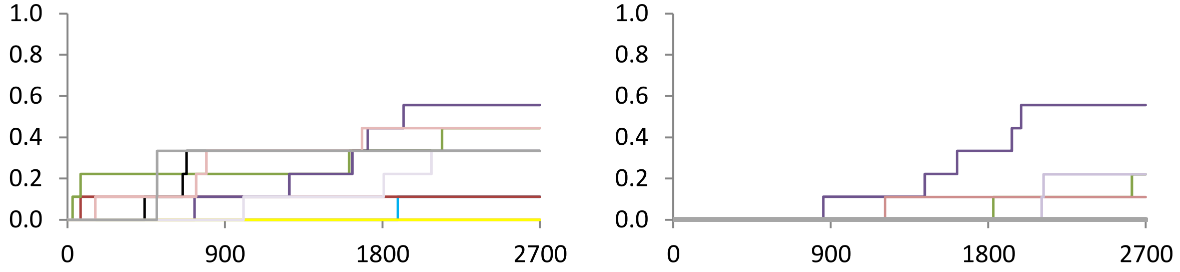
Statistical analyses

In the green light and feeder box pilot experiments respectively we compared the latency of the fish to enter goal zone beneath the lights or to enter the feeder box. We used Cox regressions to compare the performance of the fish trained to the green light, to the feeder box and fish that were trained to neither, using the untrained fish as a reference category for an indicator contrast.

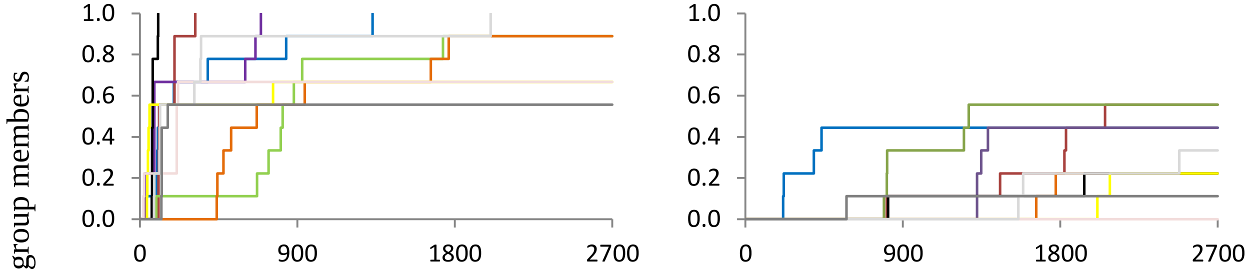
Pilot experiment results

In the green light pilot experiment fish that had been trained to associate the green light with food approached it sooner than did the untrained fish (Wald X^2= 21.24, df=1, P<0.001), while the feeder-trained fish were no faster than the untrained fish (X^2= 0.91, df=1, P=0.34 Supplementary Figure 4a). In the feeder box pilot experiment it was the feeder box-trained that entered it sooner than the untrained fish (Wald X^2= 18.06, df=2, P<0.001), while the light-trained fish and the untrained fish did not differ (X^2= 0.81, df=1, P=0.37 Supplementary Figure 4b). In this experiment, while all of the feeder box-trained fish entered the feeder during the trial, only four of the green light-trained and two of the untrained fish (out of fifteen) entered feeder box. Based on these findings we determined that the two training protocols had been effective.

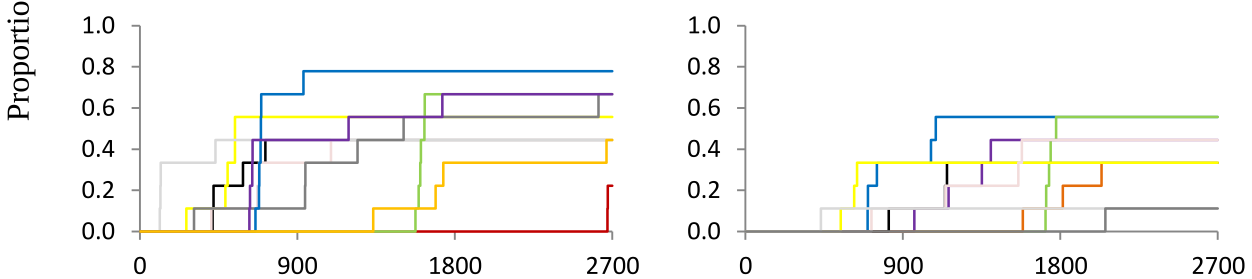
(a) 9 untrained



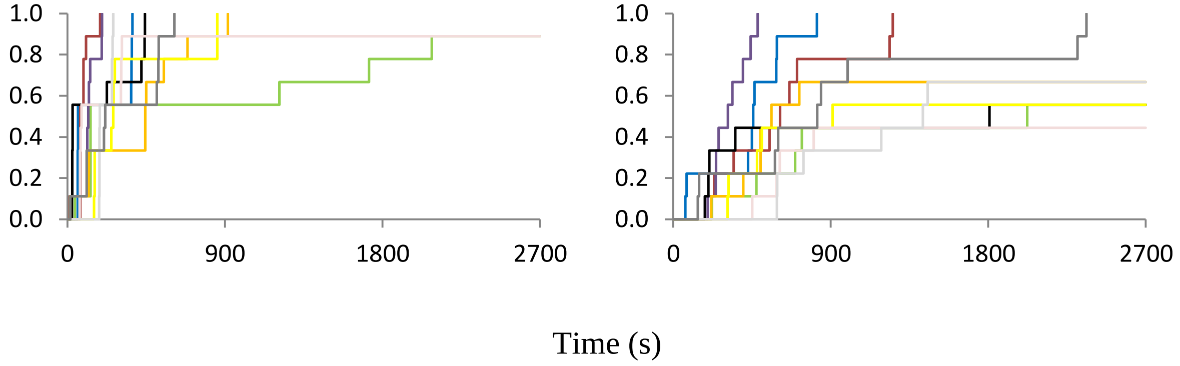
(b) 3 green light trained, 6 untrained



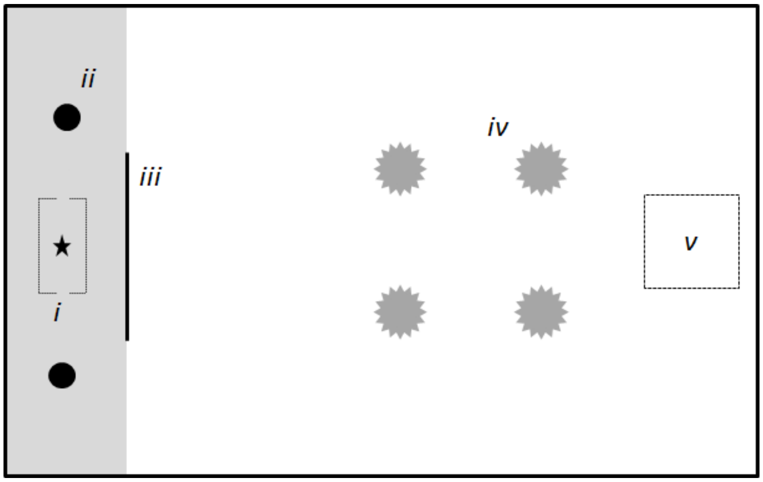
(c) 3 feeder trained, 6 untrained



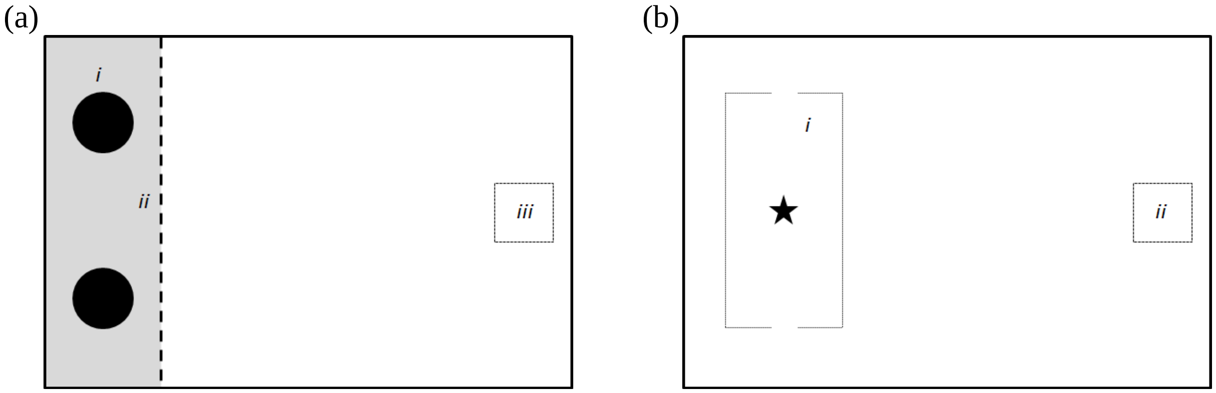
(d) 3 green light trained, 3 feeder trained, 3 untrained



Supplementary Figure 1. Survival plots showing the time (s) that each fish first entered the green light goal zone (left panels) and the feeder (right panels). Each line represents a single replicate, with the same coloured line referring to the same replicate between the left and right panels. (a) - (d) present results for the four different treatments.

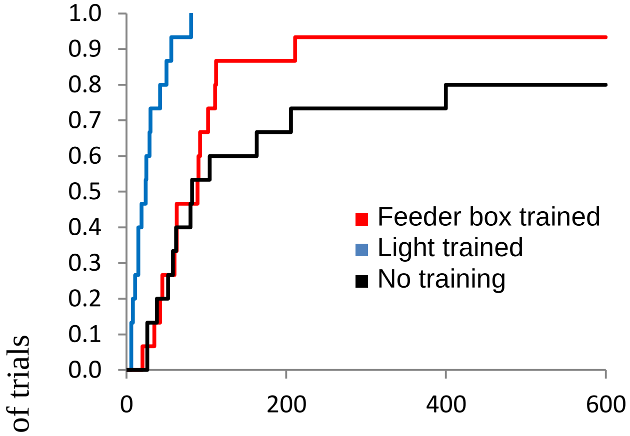


Supplementary Figure 2: The experimental arena, consisting of a feeder box (*i*) containing a prey patch, two green lights (*ii*), which fish in some trials had been trained to approach, an opaque screen (*iii*), artificial plants (*iv*) and a holding unit (*v*), within which were housed before the start of the trial. See main text for further details and experimental procedure.

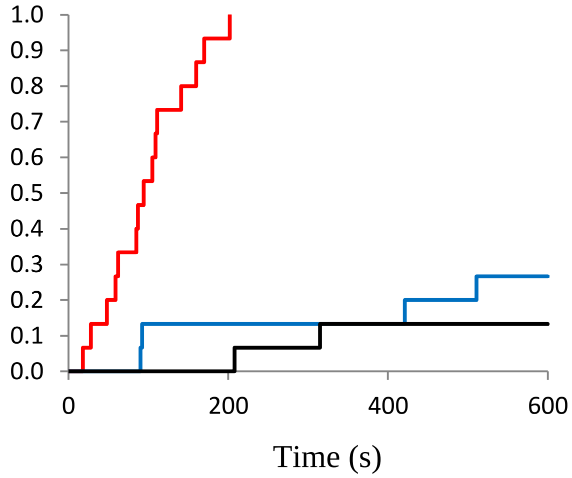


Supplementary Figure 3. The experimental areas used in the pilot experiments. (a), the light-training pilot, indicating the location of the green lights (*i*), the goal zone (*ii*) and the holding unit (*iii*) used to house the fish at the start of the trial. (b), the feeder-training pilot, with the feeder unit (*i*) and the holding unit (*ii*). See text for further details and procedure.

(a) Green light training pilot experiment



(b) Feeder box training pilot experiment



Supplementary Figure 4: The latencies of fish to enter the goal zone in the green-light training pilot (a) and the feeder box in the feeder-training pilot (b).The light- and feeder-trained fish were faster in each respective experiment.

Supplementary Table 1. Training batches and testing schedule. U refers to untrained fish, F to feeder-trained and L to light-trained, with the number of fish in each referring to the group composition of the experimental treatment. See main text for further details.

Batch	**Experiment**	**When tested**	**Replicates per treatment per batch**			
			9U	3F, 6U	3L, 6U	3L, 3F, 3U
1	Pilot (Light)	Sept 2012	-	-	-	-
2	Pilot (Feeder)	Oct 2012	-	-	-	-
3a	Main	Nov 2012	5			
3b	Main	Nov 2012		5		
4a	Main	Jan 2013				5
4b	Main	Jan 2013			5	
5a	Main	Feb 2013				5
5b	Main	Feb 2013	5			
6a	Main	Mar 2013			5	
6b	Main	Mar 2013		5		

Supplementary Table 2. Model coefficients for predicting the rate at which fish enter the goal zone. The social cues are linear predictors based on the number of fish that fit a criteria (e.g. number of fish in the goal area).

Variable	**Coefficient**	**SE**	***z***	***p***
Experience	-0.01	0.01	-1.25	0.21
Social Cues, Number of...				
… fish in the goal area	-0.14	0.05	-2.79	<0.01
… entrances within 10s	2.13	0.11	19.25	<0.01
… exists within 10s	0.29	0.60	0.48	0.63
… green trained light fish	0.43	0.09	5.05	<0.01
… feeder trained fish	0.19	0.06	3.19	<0.01
Training				
Light	1.01	0.18	5.67	<0.01
Feeder	0.31	0.19	1.64	0.10

Supplementary Table 3. Model coefficients for predicting the rate at which fish enter the feeder. The rates for Naïve fish are fixed to zero. The social cues are linear predictors based the number of fish that fit a criteria (e.g. number of fish in the goal area).

Variable	**Coefficient**	**SE**	***z***	***p***
Experience	-0.01	0.01	-2.14	0.03
Social Cues, Number of...				
… fish in the goal area	-1.48	0.27	-5.39	<0.01
… entrances within 10s	6.95	0.54	12.83	<0.01
… exists within 10s	0.76	0.50	1.53	0.13
… green trained light fish	-0.23	0.14	-1.68	0.09
… feeder trained fish	0.01	0.15	0.05	0.96
Training				
Light	0.18	0.23	0.79	0.43
Feeder	0.63	0.22	2.84	<0.01