Experience and motivation shape leader-follower interactions in fish shoals

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ABSTRACT

Leadership is an important process shaping collective movement in some species. Recent work has demonstrated that experienced or motivated individuals can emerge as leaders, and provides insight into the mechanisms by which this occurs. Ultimately, leadership depends upon the effectiveness with which would-be leaders can entrain followers, and while the properties of leaders have received much attention, less is known about the factors that affect the propensity of their groupmates to follow them. Here the roles of experience and state (hunger) in shaping leader and follower behavior were investigated using shoals of sticklebacks (*Gasterosteus aculeatus*). A first experiment revealed that individuals trained to approach a target could entrain and lead their naïve groupmates out of a refuge towards it, and that they did so more effectively when they (the trained fish) were food-deprived. In the second experiment the hunger level of the trained fish was held constant, while that of the naïve fish was varied. Here, leadership by trained fish was only apparent when the hunger levels of the naïve group members were intermediate. When naïve fish were recently fed they took a long time to visit the target and their arrival times were not affected by the presence of a trained individual. Very hungry groups recruited to the target most rapidly, but again with no evidence of influence by their trained groupmates. These experiments demonstrate that leadership in animal groups depends not only upon the state and experience of the leader but also upon that of the potential followers.

KEY WORDS: Leadership; Self-organization; Social foraging; Social information; Social organization

INTRODUCTION

Leadership, as it occurs within groups of non-human animals, may generally be defined as movement in a particular direction that is initiated by one or more group members that are subsequently joined and followed by others (Krause et al. 2000; Dyer et al. 2009; King & Cowlishaw 2009; Ward & Webster 2016). Research has identified a number of different factors affecting leadership. Leaders may be bolder (Ward et al. 2004; Harcourt et al. 2009; Webster & Ward 2011; Jolles et al. 2015) or socially dominant individuals (Peterson et al. 2002; King et al. 2008; Flack et al. 2013). In other cases they may be more experienced or more motivated group members (Rands et al. 2003; Conradt et al. 2009; Maclure et al. 2011; Dyer et al. 2009; Ioannou et al. 2015).

For many species, particularly those without well-defined dominance hierarchies, leaders may arise as a function of their recent experience, or because they have information that others in the group do not possess. For example, Reebs (2000) showed that a minority of fish (golden shiners, *Notemigonus crysoleucas*) that had been trained to expect food at a particular time and place each day were able to lead the rest of their naïve group mates to that location. Within threespine stickleback (*Gasterosteus aculeatus*) shoals, fish that have found food patches tend to return to them, with uninformed fish locating the food patches by following these individuals (Atton et al. 2012; 2014; Webster et al. 2013). In pigeons (*Columba livia*), individuals that showed greater fidelity to their own learned travel route tended to emerge as leaders when paired with partners that were less faithful to their own route (Freeman et al. 2010).

In other cases, individuals may influence the movements of the rest of the group because they are motivated, for example by hunger, to begin moving or searching, to travel to a particular area, or to move to a position within the group from which they can more strongly affect the movement of others. Nakayama et al. (2012a) found that for pairs of sticklebacks, movements out of cover were typically initiated by the hungrier individual. Krause et al. (1992) and Krause (1993) showed that food-deprived roach (*Rutilus rutilus*) occupied forward-most positions in the shoals more often than did recently fed fish, from which they can exert more influence over group movements than those in rearward positions (Bumann & Krause 1993). The mechanism of leadership through which motivated individuals are able to recruit and lead groupmates by balancing their attraction towards a target or goal and their social attraction towards nearby group members has been termed leading according to need (Conradt et al. 2009). This effect has been demonstrated using simulation models (Rands et al. 2003; Conradt et al. 2009) and validated experimentally (Dyer et al. 2009; Ioannou et al. 2015).

Ultimately, the effectiveness of a would-be-leader depends upon the effectiveness with which it is able to entrain followers (King 2010), and simulation models and empirical research using shoaling fish have shown that feedback between leaders and followers plays a significant role in determining collective movement (Harcourt et al. 2009; Johnstone & Manica 2011; Nakayama et al. 2012b; Jolles et al. 2015). Given that internal state is known to influence the emergence of leaders, it seems likely that it may also influence the likelihood of group members following others. Accordingly, in this study, the role of experience and motivation in determining the emergence of leadership, and motivation alone in driving followership were investigated.

In the first of two experiments, individual threespine sticklebacks were either trained to associate a stimulus, a green light, with a food reward, or sham-trained, so that they were exposed to the stimulus but did not learn to associate it with a reward. These were then embedded within groups of naïve, untrained fish, and placed inside a shelter within a larger arena. At the far end of the arena, in a shallow and exposed area, were a hidden prey patch and above it a green light, the stimulus to which some of the fish had been trained. It was predicted that the trained fish would act as leaders, recruiting their naïve shoal mates towards the food reward more rapidly than the sham trained fish. Moreover, it was predicted that hungry trained fish would be more effective leaders than those that had been recently fed. A second experiment focused upon the following behavior of the naïve group members. Here, trained fish were embedded within groups that had either been recently fed, or which had been deprived of food for some period of time. It was predicted that recently fed fish would be less responsive to leaders than hungrier fish, and that they would prioritize remaining in cover over travelling into open and exposed areas, which may under natural conditions be associated with greater predation risk. The predictions of both experiments were supported.

METHODS

Study animals

Threespine sticklebacks (35-40mm standard length) were collected using dip-nets from the Kinnesburn stream, St Andrews, UK in August 2013 and transported to a laboratory. There they were held in groups of 30 in several 90L aquaria. The temperature was held at 8°C and the light:dark regime at 12:12. Each aquarium contained a sand substrate, artificial plants and was connected to an external filter. The fish were fed daily with frozen bloodworms

(*Chironomus* sp. larvae) unless otherwise stated below. Fish that displayed signs of being in reproductive state were not used in the experiments, since this has been shown to affect social behavior in sticklebacks (Webster and Laland 2011). Within trials, all fish were size matched to within 3mm standard length. One week prior to being tested each fish was fitted with a non-invasive temporary disc tag on its first dorsal spine. These allow individual fish to be identified during trials, and do not affect fish shoaling behavior (Webster & Laland 2009). These were removed after the fish had been tested. No fish was used in more than one trial, and after testing they were retained in the laboratory for use in a different study. Experiments took place between October 2013 and March 2014.

Training and sham-training

Both of the experiments described below considered the behavior of groups of five fish within which one individual had been trained to associate a stimulus, a green light, with a food reward. In order to determine the effectiveness of such training in generating leadership, further groups were tested in which one fish had been sham-trained, that is exposed to the green light and a food reward at separate times, so that it was familiar with both but did not learn an association between the two.

The fish were trained / sham-trained in groups of five. Each group was housed with a 45L aquarium containing 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 during this time. At the beginning of the second week training began. Half of the aquaria were randomly selected and assigned to green light training or to sham-training. A green LED light consisting of a circle of 24 individual LEDs set within a 5cm diameter case (Trimble, Milton Keynes, UK) with a green filter overlay (Neewer, Shenzhen, China) was 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 associate the green lights, food (bloodworms) 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. The naïve fish were exposed to the green light in a similar manner to and at the same time as the sham-trained fish, albeit within the 90L housing tanks (that is the lights were switched on for 15 minutes one hour after they had been fed). This was performed to reduce the chances of any neophobic response to the light by the naïve fish during the trials.

Fish were trained in batches of 6 groups each. For Experiment 1, a total of four batches were trained. These were set up one week apart. Experiment 1 ran between October and December 2013. For Experiment 2, 5 batches of 6 groups were trained. Again, these were set up one week apart, with the experiment running between January and March 2014.

Experiment 1

The aim of this experiment was to determine the extent to which experienced (trained) and hunger-motivated individuals were able to recruit and lead naïve groupmates towards a particular location. The experiment also validated the efficacy of the training described above by testing groups of fish containing trained (and sham-trained) individuals in the presence and in the absence of the green light stimulus. A fully factorial design was used, in which groups of fish containing an individual that was either trained and food-deprived, trained and recently fed, sham-trained and food-deprived or sham-trained and recently fed were tested in the presence or in the absence of the green light stimulus. As such there were eight treatment combinations, with 15 replicate shoals tested within each. Each replicate shoal consisted of one trained / sham-trained individual and four naïve fish. The naïve fish were drawn from separate holding tanks from each other and from the trained / sham-trained fish, since familiarity between individuals is known to affect shoaling and social foraging behavior in this species (Atton et al. 2014). The naïve fish were deprived of food for 24 hours before being tested. The recently-fed implanted fish were fed six hours before being tested, while the food-deprived fish were fed 24 hours before the beginning of the trial. Trial order was randomized with respect to treatment across the four batches.

Experimental arena

Trials took place within opaque green plastic arenas measuring 150cm long by 25cm wide and 25 cm deep (Figure 1). These contained a 1cm deep layer of fine sand. One end of the arena was raised, such that this end was shallower than the other. The water depth at the deep end was 20cm, dropping to 10cm at the shallow end. The deep end contained a starting shelter. Here, a removable colorless Perspex wall was set within runners 20cm from the end of the arena. Within the shelter were four artificial plants. After the fish had been added to this area (see below), a cover made from a diffusion filter (Lee Filters, Andover, UK) set within a plastic frame was placed over the shelter. The shelter acted as a refuge, being deeper and darker than the rest of the tank and containing cover. At the shallow end of the arena a green light of the same type as that used in the training / sham-training procedure was fixed to the wall directly above the water line. Beneath this, 20 cm from the wall at the shallow end of the arena was a barrier protruding 2 cm above the sand substrate. Halfway between the end wall and this barrier was a patch of 10 bloodworms. The 20 x 25cm area behind the barrier was designated the goal zone. Five such arenas were set up, allowing multiple trials to be run simultaneously. These were placed within a larger structure (240cm by 300cm and 190cm tall), the walls and ceiling of which were constructed from sheets of white corrugated plastic. Banks of LED lights were placed along the walls of the structure. Trials were recorded using high definition webcams (Logitech C920, Logitech International SA, Lausanne, Switzerland) mounted above the arenas.

Experimental procedure

In the trials where the green light stimulus was provided (half of the trials in Experiment 1, above and all of the trials in Experiment 2, below), this was switched on immediately before the fish were added. Next, the four naïve fish and the trained / sham-trained fish were netted from their respective holding tanks and carefully placed together in the starting shelter of the arena at the start of the trial. The diffusion filter cover was then placed over the shelter. This was done for all five arenas. The fish were given 30 minutes to settle before the trial began. Following this, the Perspex walls that formed the front of the sheltered areas were carefully raised and removed, with care being taken not to disturb the water too vigorously or to cast shadows over the sheltered areas, so as not to startle the fish. This began the trials. The arenas were filmed for one hour. From the videos, the times at which each fish entered the goal zone areas were recorded. Fish typically emerged in groups of 3-5 individuals. There were few ‘false starts’ where fish emerged but then turned back. For this reason, only data on the first visit to the goal zone by members of each replicate group were used in analyses in both experiments. For each visiting individual the arrival time into the goal zones, along with the identity of the fish (trained / sham-trained or naïve) were recorded. A fish was determined to have entered the goal zone once its head had crossed the barrier, and its entry time was recorded to the nearest second. It was decided in advance to terminate the trial 60 seconds after the arrival of the first fish. As reported in the overview section of the results below, the maximum observed time difference between the arrival of the first and last fish were well below this threshold in both experiments.

Experiment 2

This experiment investigated the effectiveness of trained fish in recruiting followers when the motivation of the naïve followers varied. Here the trained / sham-trained fish that were implanted into the groups were all food deprived for 24 hours. The four naïve fish that made up the rest of each replicate group were either recently fed (1 or 6 hours prior to being tested), or were deprived of food for 24, 48 or 72 hours before the trials began. A factorial design with five different hunger treatments and two trained / sham-trained treatments was used, with 15 replicate groups tested within each treatment combination category. Trial order was randomized across the five batches. As in experiment 1, within each replicate group the fish were all drawn from different holding tanks so as to exclude any effects of familiarity upon social behavior. The experimental arenas and procedure were as described above.

Statistical analysis

In experiment 1, the latencies of the first fish in each group within each of the treatments to enter the goal zone were compared using Cox regressions, an appropriate analysis for time-to-event data. In the models presented below, the training of the implanted fish (trained or sham-trained), their hunger state (recently fed or food-deprived) and the presence or absence of the stimulus (green lights on or off) were included as categorical factors. A three-way interaction between these was also included. Two such analyses were performed, one for the arrival times of the first fish in each group irrespective of whether it was trained or naïve, and one specifically for the first naïve fish.

In order to determine whether trained fish arrived first at the prey patch, as would be expected if they were leading, the arrival times of first and second naïve fish relative to the trained / sham-trained fish were compared. To determine the relative arrival time of the naïve fish, the arrival time of the first and second naïve fish was subtracted from that of the trained / sham trained fish for each trail, with a positive score indicating that the trained / sham trained fish arrived first and negative score that it arrived after the naïve fish. If the trained fish were leading we would expect it to arrive before the naïve fish, but if it had no leadership role and was moving as part of the crowd then it should not tend to arrive first on average. Of course a fish could initiate movement but still not arrive first, so these outputs have to be interpreted alongside the data for the absolute arrival time of the group, in order to make inferences about leadership. The arrival times of the third and fourth naïve fish were not considered due to low sample sizes (due to these fish failing to recruit in some trials). In this analysis MANOVA was used, with the adjusted relative arrival time of the first and second naïve fish included as dependent variables, and the training of the implanted fish, their hunger state, the presence or absence of the green light stimulus and the interactions between these included as fixed factors.

In experiment 2, the arrival times in the goal zone of first fish from each group within each of the treatments were compared using a Cox regression. Food-deprivation duration of the four naïve fish (1, 6, 24, 48 or 72 hours) and training (trained or sham-trained) of the fifth fish were included as categorical covariates. Difference contrasts, in which each category of the hunger treatment was compared to the average effects of the preceding categories were used to make comparisons between the food-deprivation treatments. Two such analyses were performed, one for the arrival times of the first fish in each group irrespective of whether it was trained or naïve, and one specifically for the first naïve fish.

Finally, as in the first experiment, in order to determine whether trained fish arrived first at the prey patch, a MANOVA comparing the arrival times of the trained / sham trained fish minus the arrival times of the first and second naïve fish was performed. Once again, the arrival times of the third and fourth naïve fish were not considered due to low sample sizes caused by fish failing to recruit in some trials. Training, hunger and the interaction between these were included as fixed factors.

RESULTS

Overview

The majority of fish within each replicate group recruited to the goal zones within 60s of the arrival of the first fish in most trials. In Experiment 1, all five fish recruited in 38 out of 120 trials (31.7%) across all treatments, four fish recruited in 81 trials (67.5%) and three fish recruited in only 1 trial (0.8%). In experiment 2, five, four, three and two fish recruited in 76, 29, 40 and 5 trials out of 150 respectively (50.7, 19.3, 26.7 and 3.3%). In the first experiment the mean time span between the arrival of the first and last fish to recruit was 10.3s (minimum 2.3s, maximum 31.5s). In Experiment 2 the mean time span was 14.1s (minimum 2.7s, maximum 39.0s).

Experiment 1.

A Cox regression of the arrival time of the first fish (irrespective of training) within each group revealed that groups containing trained fish arrived sooner than those containing sham-trained fish (Wald X^2=12.54, df=1, P<0.001), while those containing food-deprived implanted fish also arrived sooner than those where the implanted fish was recently fed (Wald X^2=12.63, df=1, P<0.001). There was also an effect of green light stimulus, with groups arriving sooner when this was present (Wald X^2=5.12, df=1, P=0.024). Finally, there was a three-way interaction between these (Wald X^2=7.54, df=1, P<0.006). This interaction suggests that the trained fish were responding to the stimulus and not that they were simply more active than naïve individuals (Figure 2). The same pattern was observed when the analysis was repeated for the arrival time of the first naïve fish only from each group (training: Wald X^2=13.01, df=1, P<0.001; hunger: Wald X^2=11.72, df=1, P<0.001; green light on or off: Wald X^2=4.04, df=1, P=0.036; three-way interaction: Wald X^2=8.62, df=1, P=0.003).

Next, the arrival times of the first and second naïve fish at the goal zone relative to the trained / sham-trained individual were considered. In some trials, the trained / sham-trained individual did not arrive at the goal zone at all. These trials were excluded from this analysis. These excluded trials totaled: sham-trained and food-deprived, lights on, 2 trials; sham-trained and recently fed, lights on, 1 trial; trained and food-deprived, lights off, 2 trials; trained and recently fed, lights off, 3 trials; sham-trained and food-deprived, lights off, 4 trials; sham- trained and recently fed, lights off, 3 trials). For the arrival time of the first naïve fish, effects of implanted fish training, and interactions between training and hunger and training and light stimulus were seen (Table 1 and Figure 3). The first naïve fish arrived after the implanted fish when the implanted was trained (i.e. values were positive), but tended to arrive before it when the implanted fish was sham-trained (values were negative). This implies a leader role for trained, but not for sham-trained fish. The lag between the arrival of the trained fish and the first naïve fish was greater when the trained fish was hungry compared to when it was recently fed, and also when the stimulus lights were present versus absent. The latter interaction further supports the idea that the trained fish were responding to the green light stimulus. The arrival time of the second naïve fish relative to the implanted trained / sham-trained fish did not vary between any of the treatments.

Experiment 2

The arrival time of the first fish from each group into the goal zone was affected by group hunger level, with hungrier fish tending to arrive sooner. While training had no effect by itself, there was an interaction between hunger and training. Here, fish in the 24 and 48h groups arrived sooner if they were accompanied by trained fish than by a sham-trained fish. This was the case both for a model that considered the arrival time of the first fish irrespective of whether it was trained / sham-trained or naïve, and for a model than only considered the arrival times of the first naïve fish in each group (Table 2 and Figure 4).

The arrival times of the first and second naïve fish were affected by the training of the implanted fish, and the hunger level of naïve group members (Table 3 and Figure 5). The arrival time of the first, but not the second naïve fish was affected by an interaction between these variables. The first and second naïve fish arrived later than the trained fish in all hunger treatments except the 72 hour food deprived treatment. In trials with sham-trained individuals, the first and second fish tended to arrive sooner than these, or else did not differ in their arrival times across all hunger level treatments (see mean absolute values and confidence intervals in Figure 5). In the groups with sham-trained individuals, some of the sham-trained fish failed to arrive at the goal zone (6 hours hunger treatment, 3 trials; 24 hours, 2 trials; 48 hours, 1 trial). These trials were excluded from the analysis.

DISCUSSION

This paper presents two experiments that together reveal (1) that both experience, in the form of a trained association between a stimulus and a food reward, and motivation through food deprivation can shape the effectiveness with which leaders can entrain groups of uninformed followers and lead them towards a goal, and (2) that followership is affected by state, with both satiated and very hungry group members being less responsive to would-be leaders than intermediately hungry members.

In experiment 1, groups that contained trained and hungry individuals arrived most rapidly at the prey patch, while groups containing trained but recently fed individuals also arrived faster than those with sham-trained individuals. Recruitment of followers by trained and hunger-motivated leaders may potentially be explained by lead according to need mechanisms. These operate via the interaction between the leader’s attraction towards a target destination and the mutual social attraction between the leader and nearby group mates with no inclination to move in a particular direction, which can result in the leader influencing the movement of the group, entraining and leading them in its preferred destination (Conradt et al. 2009; Dyer et al. 2009; Ioannou et al. 2015).

In the second experiment, groups that had been deprived of food for 72 hours recruited to the prey patches substantially faster than those that were food deprived for shorter periods of time. The latency of fish in this treatment group to visit the prey patch was similar for groups that contained trained and sham-trained individuals, suggesting that the trained fish had less influence in this treatment group. This is further supported by the observation that both trained and sham-trained fish within 72 hour food deprived groups tended not to arrive first at the goal zone, suggesting that they were not leading the group as it entered the prey patch. It is plausible that naïve fish in these groups were already sufficiently motivated by hunger to leave cover and search for food so as to make them less susceptible to the influence of the trained group member. In contrast, the arrival times for 24 and 48 hour food-deprived groups accompanied by trained fish were lower compared to those deprived of food for the same length of time which were accompanied by sham-trained individuals, suggesting that here the trained fish did affect the behavior of their naïve groupmates. While this absolute arrival time effect was not present in the 1 and 6 hour food-deprived groups, it was found that the trained fish -but not the sham-trained fish- tended to arrive at the patch first in all treatments except the 72 hour treatment. This may suggest a recruitment mechanism by the trained fish, though it is not clear what form this might take. Among groups of damselfish (*Dascyllus aruanus*) moving between coral patches, movements are initiated by one individual, with a pronounced pre-departure phase (Ward et al. 2013), and though the experimental design used in the present study precluded observation of the sticklebacks prior to their emergence (a diffusion filter covered the starting shelter), future work could revisit pre-departure behaviour to look for evidence of recruitment. Another explanation might be that while the trained fish was unable to initiate movement by itself, once the group did set off it simply assumed a position at the front from where it was able to influence movement.

The finding that leaders arrived first in the 1 and 6h treatment groups even though their absolute arrival latencies were the longest suggests that unwilling followers can have an inhibitory role upon informed or motivated group members. Where the costs of leaving the group are high, individuals may be prevented from searching for or exploiting resources if the majority of the group is unwilling to travel with them. In groups where social attraction is weaker, or where individuals are sufficiently motivated to trade-away the benefits of remaining with the group, or where enough of a minority is motivated or informed to break away, the group may fragment.

These findings have implications for our understanding of the ways in which experience and state might affect leader-follower dynamics in large groups in heterogeneous environments. Models and experimental studies have demonstrated that a relatively small proportion of group members are able to influence the movement of the whole group, influencing its movement and leading it towards goals or targets such as prey patches (Couzin et al. 2005; Conradt et al. 2009; Dyer et al. 2009; Faria et al. 2010). It would be interesting to conduct further research in this area, incorporating variation in individual internal state. Here, we might predict that within groups in which individual group members are less motivated to travel to a particular location, a greater proportion of leaders may be needed in order to initiate and sustain movement of the group. This may also apply to quorum decision-making (Sumpter et al. 2008; Ward et al. 2008; 2012), where research might investigate whether the number or proportion of group members needed to initiate, for example, movement through potentially dangerous areas of the environment, varies as a function of the state of motivation of the individuals within the group. Variation in state or motivation among members within groups may also have implications for the likelihood of group fragmentation. Differences in hunger levels have been shown to predict the distributions of individuals within groups, with hungry individuals tending to occupy positions towards the front of the group, which may be associated with greater likelihood of encountering food first (Krause et al. 1992; Krause 1993). Such individuals might also be more likely to leave groups altogether, if doing so reduces competition for food, or if their group mates are not motivated to engage in mobile foraging. Heterogeneity in the physical environment may conceivably interact with within-group variation in internal state. Variation in risk and reward associated with different patches of the environment may produce conflicts of interest within groups, with some individuals prioritizing searching for food for example, while others prioritize saving energy and reducing exposure to predators or other hazards by remaining in cover. Differences in internal state and the differing priorities of individual group members may play a role in driving the low group fidelity and high rates of subgroup fission and formation observed in some species (Hoare et al. 2000; Ward et al. 2002; Croft et al. 2003; 2005), and may conceivably lead to groups being sorted to some degree by internal state. These ideas make specific predictions, and there is scope for further research in this area. Integrating multiple factors that account for differences in how individual animals interact with one another could provide a fuller understanding of the processes that together determine leader-follower dynamics in animal groups.

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DATA ACCESSABILITY

Analyses reported in this article can be reproduced using the data provided by Webster (2016).

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FIGURE LEGENDS

Figure 1. The experimental area measured 150cm long by 25cm, and with the water depth decreasing from 20cm to 10 cm along its length. The starting shelter (a) at the deep end contained four artificial plants for cover. Fish were held in place behind a colorless barrier (b) that was removed at the beginning of the trial. A green light (c) provided a cue to the trained fish. The area behind the 2cm high opaque barrier (d) was designated the goal zone, and contained a prey patch (the star, e). See main text for further details.

Figure 2. Survival plots showing the goal zone arrival times of the first fish in each group in Experiment 1. Black lines indicate groups with trained individuals that were food-deprived (solid line) or recently fed (dashed line). Grey lines groups with sham-trained individuals that were food-deprived (solid line) or recently fed (dashed line). Panel (a) shows arrival times for groups tested when the green stimulus lights were switched on and (b) shows the arrival times for groups where they were switched off.

Figure 3. Arrival times of the first-fourth naïve fish in Experiment 1 in each treatment relative to the trained / sham-trained individual (arrival time of trained / sham-trained fish – arrival time of naïve fish, mean +/- 95% CI). A positive score indicates that fish arrived after the trained individual, while a negative score indicates that they arrived before. Treatment codes, T & FD: trained and food-deprived; T & RF: trained and recently fed; S-T & FD: sham-trained and food-deprived; S-T 7 RF: sham trained and recently fed. White bars show data for groups tested when the green stimulus lights were switched on and grey bars show groups where they were switched off. Mean values are not shown for treatments where the fourth fastest naïve fish failed to arrive in five or fewer trials. Instead, data points

corresponding to actual values are shown for each trial where the fourth fish arrived. Statistical analysis of the arrival times of the first and second naïve fish were performed. Details of these are presented in the main text and in Table 1.

Figure 4. Survival plots showing the goal zone arrival times of the first fish in each group in Experiment 2. Treatments where the naïve fish were fed 1, 6, 24, 48 and 72 hours prior to testing are shown by the black solid, black dashed, dark grey solid, dark grey dashed and light grey lines respectively. Panel (a) shows arrival times for groups tested with a trained individual present and (b) shows the arrival times for groups where a sham-trained individual was used.

Figure 5. Arrival times of the first-fourth naïve fish in Experiment 2 in each treatment relative to the trained / sham-trained individual (arrival time of trained / sham-trained fish – arrival time of naïve fish, mean +/- 95% CI). A positive score indicates that fish arrived after the trained individual, while a negative score indicates that they arrived before. Treatment codes refer to the period of time for which the naïve fish had been deprived of food. White bars show data for groups tested with a trained group member and grey bars show groups tested with a sham-trained fish. Mean values are not shown for some treatments where the third and fourth fastest naïve fish failed to arrive in five or fewer trials. Instead, data points corresponding to actual values are shown for each trial where the fourth fish arrived. Statistical analysis of the arrival times of the first and second naïve fish were performed. Details of these are presented in the main text and in Table 3.

Table 1. Results of a MANOVA of arrival times of first and second naïve fish relative to implanted trained / sham-trained individual in Experiment 1.

Source	**df**	**F**	**P**
First naïve fish			
Corrected model	1	5.85	<0.001
Intercept	1	19.20	<0.001
Training	**1**	**19.58**	**<0.001**
Hunger	1	0.51	0.47
Stimulus lights	1	0.09	0.76
Training*Hunger	**1**	**8.08**	**0.01**
Training*Lights	**1**	**5.97**	**0.01**
Hunger*Lights	1	1.75	0.19
Training*Hunger*Lights	**1**	**3.36**	**0.07**
Error	97		
Total	105		
Corrected Total	104		
Second naïve fish			
Corrected model	1	0.85	0.54
Intercept	1	3.07	0.08
Training	1	1.96	0.64
Hunger	1	1.27	0.26
Stimulus lights	1	0.16	0.68
Training*Hunger	1	0.29	0.58
Training*Lights	1	1.80	0.18
Hunger*Lights	1	0.02	0.89
Training*Hunger*Lights	1	0.19	0.67
Error	97		
Total	105		
Corrected Total	104		

Table 2. Results of two Cox regressions for the time taken to arrive at the prey patch by the first fish (a) and first naïve fish (b) in each group.

Source	**Wald X^2**	**df**	**P**
(a) First fish to arrive			
Hunger	**58.87**	**4**	**<0.001**
Difference contrast			
6h	1.58	1	0.20
24h	**8.21**	**1**	**0.01**
48h	2.32	1	0.12
72h	**49.80**	**1**	**<0.001**
Training	2.37	1	0.12
Training*Hunger	**47.74**	**4**	**<0.001**
Difference contrast			
6h	0.59	1	0.44
24h	**28.37**	**1**	**<0.001**
48h	**20.9**	**1**	**<0.001**
72h	1.74	1	0.18
(b) First naive fish to arrive			
Hunger	**56.72**	**4**	**<0.001**
Difference contrast			
6h	1.53	1	0.22
24h	**8.14**	**1**	**0.01**
48h	2.22	1	0.14
72h	**49.77**	**1**	**<0.001**
Training	2.24	1	0.17
Training*Hunger	**42.24**	**4**	**<0.001**
Difference contrast			
6h	0.61	1	0.43

24h	**28.57**	**1**	**<0.001**
48h	**21.4**	**1**	**<0.001**
72h	1.72	1	0.19

Table 3. Results of a MANOVA of arrival times of first and second naïve fish relative to implanted trained / sham-trained individual in Experiment 2

Source	**df**	**F**	**P**
First naïve fish			
Corrected Model	9	8.94	<0.001
Intercept	1	40.74	<0.001
Training	**1**	**41.44**	**<0.001**
Hunger	**4**	**7.00**	**<0.001**
Training*Hunger	**4**	**2.37**	**0.05**
Error	130		
Total	140		
Corrected Total	139		
Second naïve fish			
Corrected Model	9	5.10	<0.001
Intercept	1	1.48	0.22
Training	**1**	**14.04**	**<0.001**
Hunger	**4**	**5.63**	**<0.001**
Training*Hunger	4	2.07	0.08
Error	130		
Total	140		
Corrected Total	139		

Figure 1.

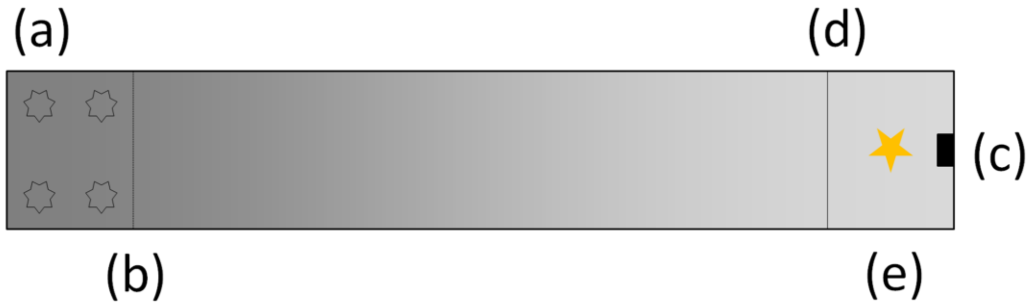


Figure 2.

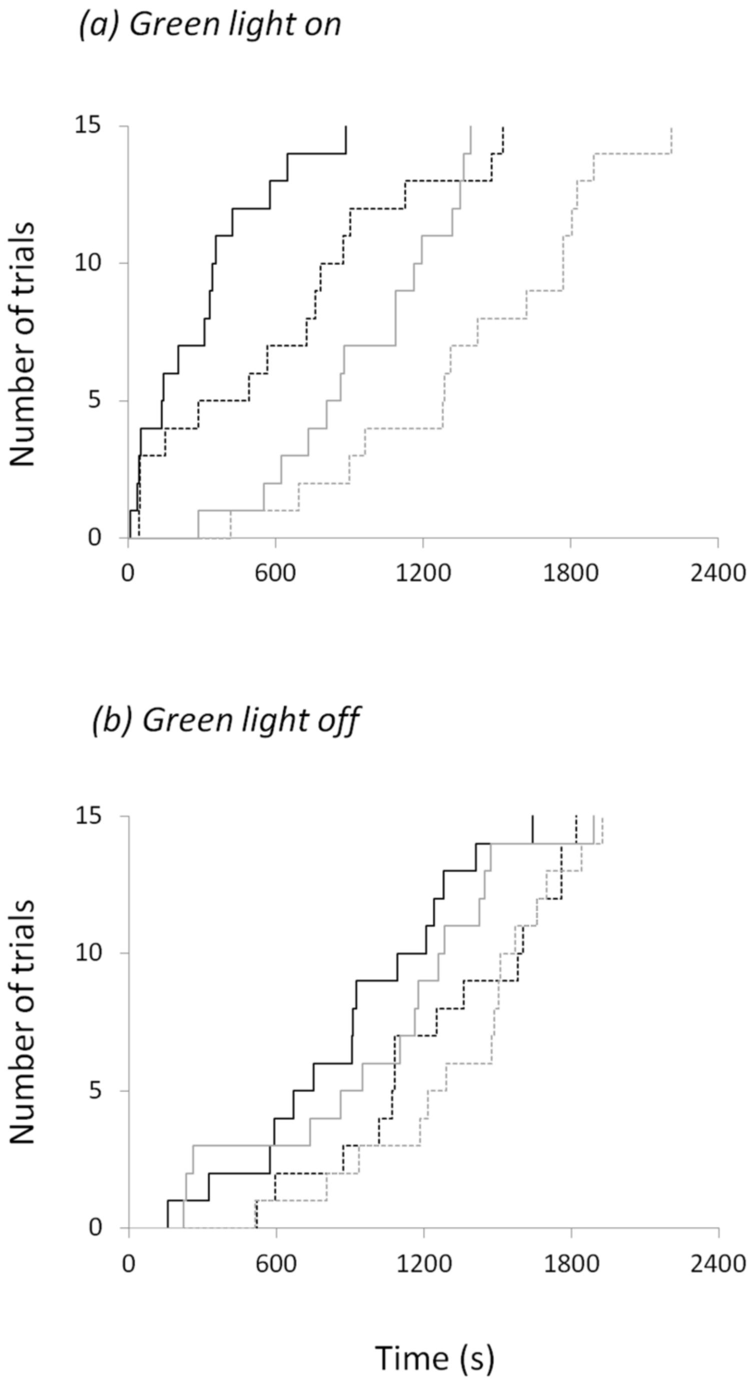
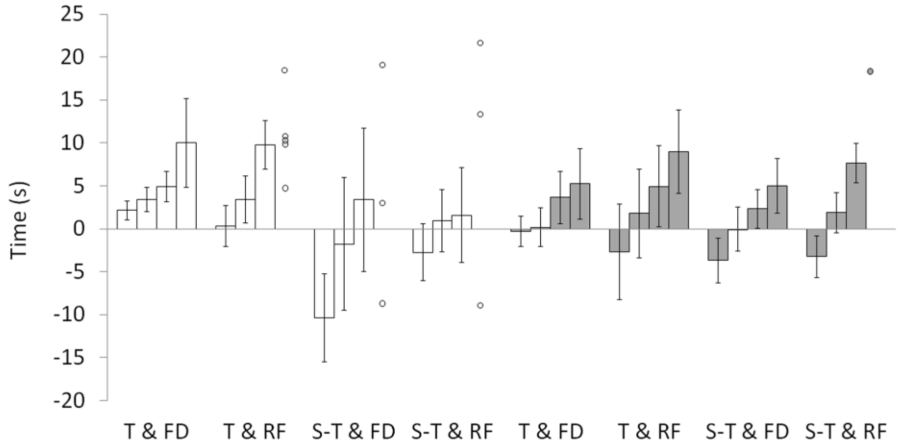

(a) Green light on
15
10
5
0
Number of trials
0
600
1200
1800
2400
(b) Green light off
15
10
5
0
Number of trials
0
600
1200
1800
2400
Time (s)

Figure 3.



Time (s)
25
20
15
10
5
0
-5
-10
-15
-20
T & FD
T & RF
S-T & FD
S-T & RF
T & FD
T & RF
S-T & FD
S-T & RF

Figure 4.

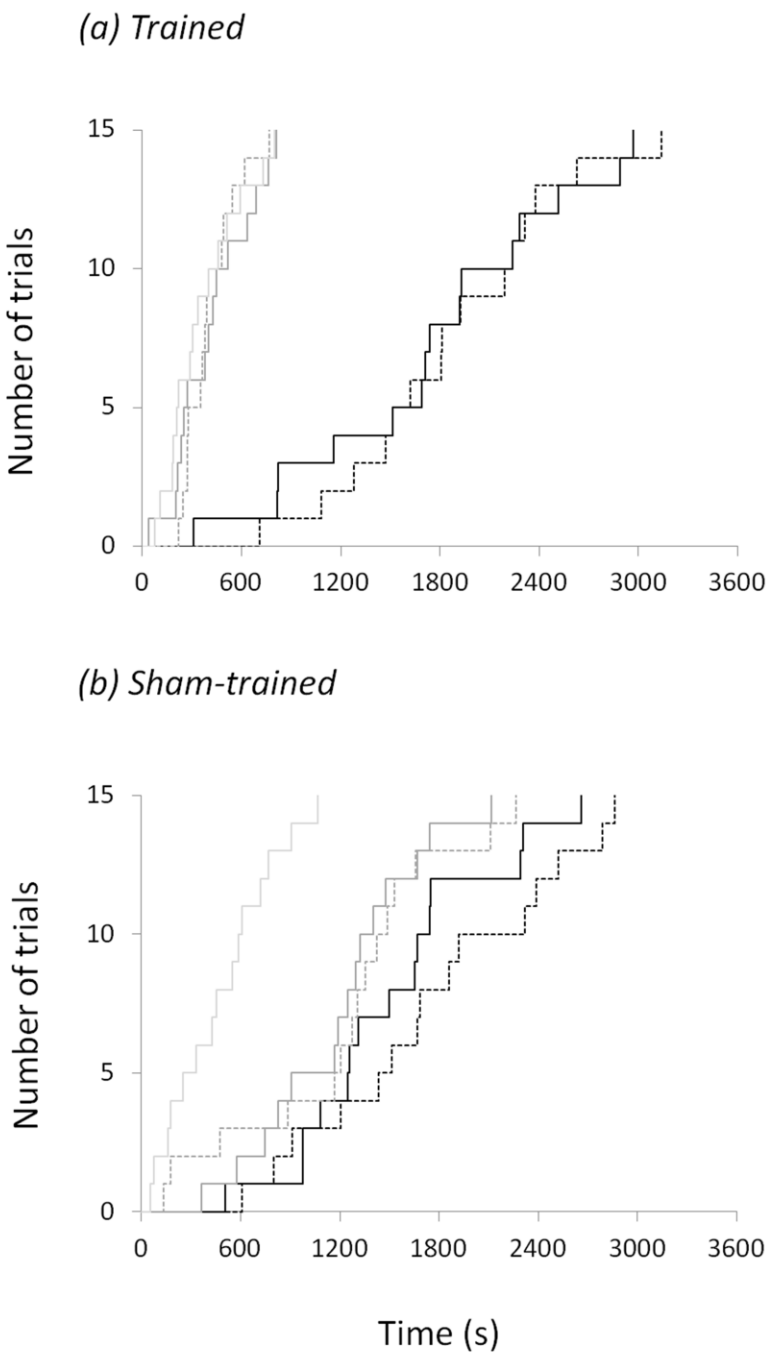

(a) Trained
15
10
5
0
Number of trials
0
600
1200
1800
2400
3000
3600
(b) Sham-trained
15
10
5
0
Number of trials
0
600
1200
1800
2400
3000
3600
Time (s)

Figure 5.