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Grey squirrels (*Sciurus carolinensis*) show a feature-negative effect specific to social learning

Lucy J. Hopewell · Lisa A. Leaver · Stephen E. G. Lea · Andy J. Wills

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Abstract Previous laboratory studies on social learning suggest that some animals can learn more readily if they first observe a conspecific demonstrator perform the task unsuccessfully and so fail to obtain a food reward than if they observe a successful demonstrator that obtains the food. This effect may indicate a difference in how easily animals are able to associate different outcomes with the conspecific or could simply be the result of having food present in only some of the demonstrations. To investigate we tested a scatter-hoarding mammal, the eastern grey squirrel, on its ability to learn to choose between two pots of food after watching a conspecific remove a nut from one of them on every trial. Squirrels that were rewarded for choosing the opposite pot to the conspecific chose correctly more frequently than squirrels rewarded for choosing the same pot (a feature-negative effect). Another group of squirrels was tested on their ability to choose between the two pots when the rewarded option was indicated by a piece of card. This time, squirrels showed no significant difference in their ability to learn to choose the same or the opposite pot. The results add to anecdotal reports that grey squirrels can learn by observing a conspecific and suggest that even when all subjects are provided with demonstrations with the same content, not all learning occurs equally. Prior experience or expectations of the association between a cue (a conspecific) and food influences what can be learned through observation whilst previously unfamiliar cues (the card) can be associated more readily with any outcome.

Keywords Feature-negative effect · Grey squirrels · Social learning · Caching

L. J. Hopewell (✉) · L. A. Leaver · S. E. G. Lea · A. J. Wills
School of Psychology, University of Exeter, Exeter, UK
e-mail: l.j.hopewell@exeter.ac.uk

Introduction

Many animals can observe conspecifics and learn from them in foraging situations (review by Galef and Giraldeau 2001) and, by making their own decisions based on the information generated by conspecifics, rather than simply copying them, they can avoid copying mistakes (Giraldeau et al. 2002). For example, sticklebacks selected foraging sites according to where the rate of feeding was highest rather than simply where the greatest number of conspecifics had congregated (Coolen et al. 2005). In a group of baboons, subordinate animals copied dominant members of the group when choosing which zone of an arena to search for food but one dominant animal learned to choose between the different zones correctly, even when the position of the rewarded zone was moved, by watching the outcome of conspecifics' searches first (Pallaud and Lepoivre 1985). Some scatter-hoarders have also been found to be able to use information obtained by watching conspecifics make caches to pilfer the food (mainly corvids, review by Dally et al. 2006; but also anecdotally, kangaroo rats, Daly et al. 1992 and grey squirrels, Steele et al. 2008). Previous work by some of the authors of the current study found that caching squirrels alter their behaviour to be more secretive when other squirrels are present which is also consistent with the idea that observers are associated with a high risk of pilferage (Leaver et al. 2007; Hopewell and Leaver 2008). To some extent, corvids have been shown to remember which caches have already been recovered as, in a laboratory study, they tended to avoid cache sites they had watched being emptied by another bird 24 h previously (Clark's nutcrackers and Mexican jays, Bednekoff and Balda 1996).

Animals may respond more effectively to some types of behaviour they observe than to others. Two social learning

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studies with rhesus macaques(Darby and Riopelle 1959) and starlings (Templeton 1998) found that when these animals learned to choose between two containers for a food reward after observing a conspecific make a choice, they learned to select the opposite container to the one chosen by the conspecific more readily than to select the same one. In these studies, a conspecific demonstrator opened one of the two containers and found either that it was empty or that it contained a piece of food which could be removed and eaten. The test subjects then had to select the same container if the demonstrator had found food and the opposite one if they had been unsuccessful. The results cannot be explained by a tendency of the test subjects to simply avoid where the conspecific had been, because animals that had to choose the same container performed at chance levels rather than consistently choosing incorrectly. Instead, the results suggest that animals were able to use negative information (no food is present) more readily than they used positive information (food is present).

However, the presence of food in different trials created a confound because the animals may have interpreted the sight of a conspecific removing food to mean either that food could be found in a particular location or that food was no longer available ('the depletion effect', Templeton 1998). An unsuccessful conspecific, on the other hand, unambiguously indicates an empty container. One aim of the current study was to establish whether the results of the previous social learning experiments were dependent on the demonstrator providing different information to the test subjects (i.e. container empty vs. container does/did contain food) or if the tendency to choose the opposite container to a conspecific would persist if the same information is provided to all test subjects.

The results of these social learning studies are of interest because they suggest the presence of a feature-negative effect (FNE). That is, the animals learned that the presence of a conspecific (the feature) at one of the two containers predicted the absence of food more readily than they learned that the conspecific predicted the presence of food. Studies of discrimination learning with non-social features have sometimes found FNEs (with lights as the feature, Haggbloom 1983; Haggbloom and Sheppard 1986; food as the feature, Haggbloom 1983; a tone as the feature, Looney and Griffin 1978) but more commonly, feature-positive effects (FPE), in which the presence of a feature is associated with a reward more readily than with the absence of reward. For example, the FPE was demonstrated in studies with abstract shapes as the feature (Jenkins and Sainsbury 1970) and with motion as the feature (Dittrich and Lea 1993).

Haggbloom and Sheppard (1986) suggest that the FNE will occur whenever the feature (social or non-social) acts as a strong signal to avoid making an error. For example, the FNE in the social learning experiments (Darby and Riopelle 1959; Templeton 1998) could be explained if, through previous experience, a conspecific that fails to find food has become a strong signal to the test subject to avoid making the same error whilst a conspecific that finds food is a weaker signal to make the same choice because, in the past, it has sometimes indicated that food is available and sometimes that it has all been eaten.

The FPE should develop if the subjects have previously experienced the feature as a good predictor of the presence of food because the feature will act as a strong signal to make the choice associated with it. If the feature is unfamiliar to the subject, no learning bias is expected, although a FPE may develop in some cases. Sainsbury (1971a, b, 1973) tested children (aged 4–5 and 8–9 years) on their ability to choose between two computer monitors when they had to select either the one showing an abstract shape (FP discrimination) or the one without the shape (FN discrimination). All of the children readily learned to choose the monitor with the shape but the younger ones were unable to withhold their response to the shape for long enough to choose the other monitor, leading to a FPE.

In the present experiments, we tested grey squirrels on a discrimination between two artificial caches (two food pots with lids) with either a social feature (a conspecific, experiment 1) or an unfamiliar, non-social feature (a cardboard flag, experiment 2). Half the squirrels were tested on a FP discrimination and half on a FN discrimination but, in both cases, food was removed from one of the pots on every trial so that all squirrels observed the same demonstration. If squirrels see a conspecific remove food from a hidden location (a 'cache') they are provided with unambiguous information that the cache is then empty, because in their natural caching behaviour they are accustomed to storing single pieces of food in each cache. This leads to the prediction that, with a social cue, squirrels should show a FNE when learning the discrimination because choosing the opposite 'cache' when the conspecific finds food is consistent with their caching behaviour. The non-social feature had not previously been encountered by the squirrels and so they were not expected to have any bias in their responses to it. They should therefore be able to learn both the FP and FN discriminations, although a FPE may develop if the squirrels are unable to withhold a response to the cache associated with the card.

Methods

Squirrels and housing

Thirteen eastern grey squirrels were housed in four large indoor cages that had metal mesh and concrete walls (three cages of size 1.9 × 1.8 × 2.5 m in one room and one cage of size 3 × 1.8 × 2.5 m in a separate room, Fig. 1). The cages were furnished with shelves, nest boxes, cardboard tubes, trays of compost and wood shavings and ropes. The floors were covered with hemp bedding. Lighting was on a 16:8-hour light:dark cycle. The squirrels were held as two separate groups. The first group consisted of two captive-raised adults (1 male, referred to as BY and 1 female, CD) obtained from a sanctuary in July 2005 and five wild-caught adults (4 females referred to as LF, DR, SM and SH and 1 male, BB) obtained from parkland in Devon using Tomahawk™ traps between November 2003 and June 2005. The captive-raised pair was housed in the single cage room (see Fig. 1) and the wild-caught squirrels were housed in the other room as a male–female pair (BB and SM) in one cage, two females (DR and LF) in one cage and a solitary female (SH) in the remaining cage.

The second group of squirrels consisted of six captive-raised juveniles, aged approximately 10 months at the start of testing (4 males and 2 females) obtained from the sanctuary in July 2007. One male–female pair was housed in the single cage room (MO and DE) and the others were housed in the other room as a male–female pair (SC and IT) in one cage and a male–male pair (RK and NV) in another cage.

The squirrels were fed in their cages on a selection of fruit, vegetables, seeds and various nuts. During testing, their preferred nuts (pecans, walnuts and pistachios) were only available as the reward during testing in the test room and they were fed their maintenance diet when they had completed the daily test session. Water supplemented with 'Vetzyme', a vitamin and mineral supplement, was available ad libitum in the home cages and in the test room.

Test room

The test room was between the two home cage rooms (see Fig. 1). It contained a large cage (3 × 1.8 × 2.5 m) with a metal mesh front and ceiling and solid concrete walls on two sides and at the back. The cage was divided in half by a metal mesh wall. Each half of the cage had a door in the front wall and there was a small squirrel door (20 cm × 20 cm) in the central mesh wall, approximately 5 cm from the ground, which could be opened to allow squirrels to move between the two halves of the cage. Each half of the cage was accessible to the squirrels from one of the home cage rooms via a hole in the wall, approximately 2 m from the ground. The half of the cage adjacent to the single cage home room was the demonstrator's cage (D-cage) and the other half was the observers' cage (O-cage). In the room with three home cages, a metal mesh tunnel connected each of the cages to the test room. The squirrels could enter the tunnel through a hole (20 cm × 20 cm) above their home cage door. All the holes could be covered by metal plate doors. The arrangement of doors was such that at any one time, only squirrels from one cage had access to the test room. The cage in the room containing a single home cage was directly connected to the test room by the hole in the wall which could also be covered by a metal plate door. This set up removed the need to use traps or handling when testing and so minimized stress for the squirrels.

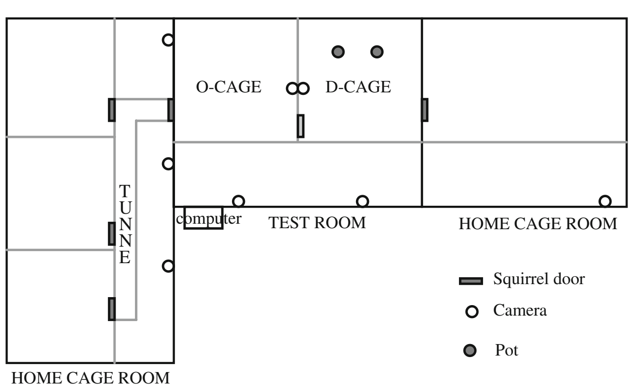

Fig. 1 Plan of the squirrels' housing and test room. All cages were floor-to-ceiling in height with a door in the front wall to allow the experimenter to enter. Thin *grey lines* represent metal mesh walls and *thick black lines* indicate solid walls

A panel containing a video screen and automatic pellet dispenser for use in other experiments was positioned above the front wall doors in each half of the test cage and a shelf was positioned next to each screen. Cameras were attached to the wall opposite each half of the test cage and inside two metal boxes on the central mesh wall. All the cameras were connected to a computer outside the room so that the experimenter could watch the tests on a monitor and record them.

To train the squirrels to enter the test room nuts were placed on the floor of the test cages and the tunnel and wall doors were left open so that squirrels from one cage could enter the test room whenever they chose. The wild squirrels usually entered the test room during their most active periods only, between 10:00 and 12:00 or 15:00 and 19:00 but the captive-raised squirrels entered at any time of day, whenever the door was opened.

Individual squirrels were isolated for testing by closing the cage tunnel door when one squirrel had entered the test room. The door covering the hole in the wall was also closed during testing but was left open if the experimenter needed to enter the test room so that the squirrel could move away into the tunnel.

Apparatus

Two cylindrical white plastic pots (7 cm diam. × 5 cm) were placed on the floor of the D-cage, towards the back wall so that they were both 120 cm from the centre of the door in the dividing mesh wall. Later, to discourage the demonstrator's side bias, the pots were placed 185 cm from the front of the cage and 33 cm apart, one 66 cm and one 99 cm from the central mesh wall. The pots were stuck to the floor with 'Blu-Tak™' to ensure that the squirrels could not tip them over. The reward was a piece of walnut, pecan, or pistachio inside a pistachio shell stuck together with a water-based glue to resemble an intact nut. Providing a variety of nuts ensured that squirrels would participate throughout a session. A nut was placed in one or both of the pots (see 'procedures' for details) and a square piece of brown plastic was placed on top of each pot. The squirrels had to remove these plastic lids to get access to the contents of the pots. A black curtain was hung diagonally from the roof of the D-cage and could be pulled across the cage with a piece of string from outside the room in order to block visual access between the two cages. The curtain had to be hung diagonally to avoid the camera on the central mesh wall.

Social condition

Seven squirrels (the first group described under 'Squirrels and housing') were tested in the social condition between January and September 2006.

Procedure

Demonstrator's training

The captive-raised female (squirrel CD) was used as the demonstrator. She was trained on a visual discrimination to allow the experimenter to control which pot the observer would see being emptied. One pot contained a nut and the other was empty. The location of the nut was determined on each trial from a table of random numbers (odd = right; even = left). A piece of red card was stuck to the pot containing the nut, on the side farthest away from the central mesh wall. At the start of training, to attract the demonstrator squirrel's attention, a large red card was used (5 cm × 5 cm). This was gradually reduced in size over the course of training to a final size of 0.75 cm × 1 cm, positioned so that the label touched the floor but not the rim of the pot. Geometric calculations showed that 0.76 cm was the maximum width of the label that could be used to ensure that it would not be visible from the O-cage. The floor, pots and label were marked with a pen so that they were set up in the same place on each trial.

The demonstrator squirrel entered the test cage from her home cage through the hole in the wall. The door was closed behind her to prevent the other squirrel in her home cage from entering the room. The demonstrator squirrel climbed down one of the mesh walls to the floor and as soon as she had removed the lid of one of the pots, by pushing it aside with her nose, and picked up the food with her mouth, the curtain was drawn across the cage from outside the room. The squirrel was then allowed to look in the other pot if she chose to before the door to her home cage was opened again and she left the test cage. When the door was open, the experimenter distracted the other squirrel in the home cage with a stick toy and/or nuts to prevent him from entering the test room.

The demonstrator was given five to ten trials per day; after this she was satiated and either would not enter the test room, or did so but then did not look in the pots. Training continued 5 days a week until the demonstrator reliably went to the labelled pot first (at least 8 out of 10 trials correct over no more than two consecutive sessions) and was not distracted by the movement of the curtain. The demonstrator had a total of 220 training trials over 28 days. From the eighty-second trial the pots were in the position used during testing and the label was at its final size and position. The demonstrator reached the criterion after a further 90 trials but was trained over 48 extra trials to habituate her to the movement of the curtain.

Observers' pre-training

The remaining six squirrels (BB, DR, LF, SM, SH and BY) were trained as observers. The tunnel door into the test room and one home cage tunnel door were opened to allow one squirrel to enter the left half of the test cage (the O-cage). The doors were then closed so that the squirrel could not return to its home cage. The observer squirrel that was housed in the separate room with the demonstrator (squirrel BY) entered the test room through the hole in the wall into the D-cage. The door in the central mesh wall was then opened to allow him to enter the O-cage. A nut was provided on the floor of the O-cage to encourage the squirrels to enter and to distract them so that the experimenter had time to close the doors. Training began when the squirrel had eaten the nut. The squirrel waited in the tunnel or the O-cage whilst the experimenter placed a nut in each of the two pots in the D-cage; the curtain was drawn across the cage to prevent the observers seeing the setting up process but was pulled open immediately afterwards.

The door in the central mesh wall was then opened and the observer squirrel entered the D-cage to gain access to the pots and the nuts. After 30 trials, the training trials were extended to allow the squirrels to get used to the movement of the curtain. When the squirrel had entered the O-cage and the tunnel door had been closed, the curtain was pulled across the cage from outside the room after approximately one and a half minutes. The tunnel door was then opened and the experimenter entered the room to draw the curtain back and open the door in the central wall. The observer then returned to enter the D-cage and look in the pots. Each observer squirrel received five trials a day and training continued until they did not react to the movement of the curtain and they entered the D-cage and ate the nuts within 5 min of the experimenter leaving the test room.

The observers each had between 50 and 68 training trials. The number differed because some squirrels habituated to the curtain more quickly than others. The percentage of trials in which the left pot was opened first was calculated for each squirrel during the last 50 trials and the observers were assigned to groups so that the side biases were evenly distributed between the conditions (FP group: BL 36%, LF 80%, BB 56%, FN group: SM 16%, DR 70%; SH 50%).

Observers' trials

The labelled pot contained a nut. The position of the rewarded pot was assigned on each trial from a table of random numbers with the limitation that the correct pot was on the same side for no more than four trials in a row. The label was positioned as during training so that it was not visible from the O-cage but could be seen by the demonstrator. The other pot contained an empty pistachio shell, glued together to resemble an intact nut. The purpose of the fake nut was to ensure that even if the demonstrator chose incorrectly, the observer would see a nut being removed from one of the pots.

An observer squirrel was encouraged to enter the O-cage as described in training and the tunnel door was then closed. After at least 1 min, the demonstrator entered the D-cage from her home cage. As soon as she had removed the lid from one pot and picked up the nut, the curtain was pulled across the cage from outside the room. Squirrels pick food up with their mouths before handling it in their front paws which allowed time for the curtain to be closed before the demonstrator could look in the second pot. The demonstrator returned to her home cage and the tunnel door was opened so that the observer could wait in the tunnel. The experimenter entered the D-cage, removed the red label and set the pots up according to the treatment group of the observer. For half the observers (BY, LF, BB), a nut was placed in the same pot that the demonstrator was seen to take a nut from (FP discrimination); for the others (SM, DR, SH), the nut was placed in the other pot (FN discrimination). The second pot was always empty. The pots were set up according to the demonstrator's actual choice, even if she had chosen incorrectly. The curtain was then pulled back, the door in the central mesh wall was opened and the experimenter left the room. The observer entered the D-cage and the first pot it touched with its nose, mouth or front paws was recorded as a correct choice if it contained the nut and incorrect if it was the empty pot. Squirrels had five trials a day and were tested four or 5 days a week for a total of 100 trials. Only two squirrels could be tested each day because the demonstrator squirrel would not do more than ten trials in a day.

Non-social condition

Six captive-raised squirrels (the second group described in 'Squirrels and Housing') were tested in the non-social condition, between December 2007 and January 2008.

Procedure

Observers' pre-training

Pre-training was the same as that given to the observer squirrels in the social condition. The captive-raised squirrels were much bolder than the wild-caught ones and so were each given just 50 pre-training trials.

The percentage of trials (out of 50) in which the left pot was opened first was calculated and squirrels were assigned to groups so that the side biases were as evenly distributed as possible [FP group: IT (46%), DE (50%), NV (44%); FN group: MO (40%), SC (60%), RK (50%)].

Trials

The procedure was the same as that used in the social condition but instead of a conspecific demonstrator, the location of the nut was indicated by a square of brightly coloured red and black checked card (30 cm × 30 cm) standing behind one of the pots during the observation phase and a nut was placed in only one pot. This nut was attached to a length of transparent thread. A nut-sized lump of Blu-Tak™, also attached to a piece of thread, was placed in the other pot. The threads were stretched across the floor from the pots so that the ends stuck out under the cage door. The threads were not visible to the human eye.

For three of the squirrels the card was behind the pot containing Blu-Tak™ (MO, SC, RK; FN group) and for the others the card was behind the pot containing the nut (DE, IT, NV; FP group). The position of the nut-containing pot was randomly assigned for each trial from a table of random numbers with the constraint that the nut was in the same position for no more than four trials in a row. An observer squirrel entered the O-cage and could see the pots and the card. The experimenter stood outside the cages, opposite the door of the D-cage, holding the ends of the threads and looked at a stop watch on the floor. After one and a half minutes (the approximate time it took the demonstrator to open a pot in the social condition), the experimenter pulled on the piece of thread attached to the nut from outside the cage, so that the lid was knocked off the pot and the nut was visible on the floor outside the pot. The other thread was not moved. The curtain was pulled across the dividing wall, the transparent threads with the nut and Blu-Tak™ were removed from the pots, the card was removed, a nut was placed in one pot and the trial continued as described for the social condition.

Analysis

Binomial tests were used to compare the number of correct trials in total and in the first and last 25 trial blocks to chance ($P = 0.5$; $\alpha = 0.05$). The percentage of correct trials per 25 trial block (square root arcsine transformed) was then analysed with a repeated-measure ANOVA for each condition, with trial block as a repeated measure and group (FN/FP) as a between-subject factor.

Results

Trials

Demonstrator in the social condition

The demonstrator chose the correct pot a mean (± SE) of 4.37 ± 0.91 times per five-trial session. The number of correct trials increased over the course of the experiment (Fig. 2) so that the last observer squirrels tested (BB and SH) saw slightly more 'correctly' performed demonstrations than those tested at the start of the study (BY and SM).This should not have made any difference to the observers because the demonstrator always removed a nut (real or fake) from the chosen pot; observers did not show any obvious differences in their behaviour following correct and incorrect demonstrations.

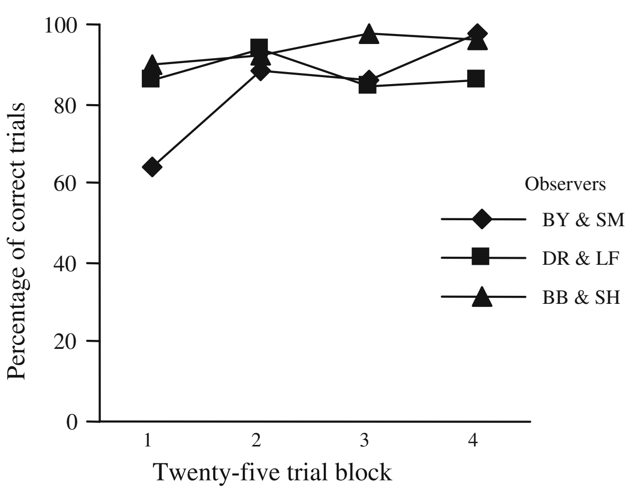

Fig. 2 The percentage of trials performed correctly by the demonstrator in the social condition during each block of trials for each pair of observers

Observers in the social condition

Overall, the three squirrels in the FN group chose correctly more frequently than expected by chance (SM: 59 correct trials, $P = 0.04$; DR: 62 correct trials, $P = 0.01$; SH: 63 correct trials, $P = 0.006$) but squirrels in the FP group did not differ significantly from chance (BY: 49 correct trials, $P = 0.46$; LF: 48 correct trials, $P = 0.38$; BB: 47 correct trials, $P = 0.31$). No squirrels differed significantly from chance in the first block of trials (all chose correctly between 9 and 12 times; all $P > 0.12$) whilst in the last block of trials squirrels in the FN group chose correctly more often than expected by chance (between 18 and 21 correct trials; all $P < 0.023$) but squirrels in FP group did not (between 11 and 13 correct trials, all $P > 0.35$).

Two squirrels, one in each group chose correctly more frequently when the nut was in the pot on the right (SM in FN group chose correctly on 41% of the trials when the nut in the left pot but 88% of trials when it was in the right pot; BY in FP group chose correctly on 22% of left trials and 86% of right trials; all other squirrels chose correctly 53–71% of left trials and 41–62% right trials).

There was a significant effect of group ($F_{1,4} = 123.58$, $P < 0.0001$) with squirrels in the FN group choosing correctly more often than squirrels in the FP group (mean ± SE: FN group = 61.33 ± 1.02; FP group = 48 ± 0.58). There was a significant effect of trial block ($F_{3,12} = 5.92$, $P = 0.01$) showing that squirrels improved over trials. There was also a significant group by trial block interaction ($F_{3,12} = 4.205$, $P = 0.03$), showing that the FN group improved to a greater extent over trials than the FP group (Fig. 3a).

Observers in the non-social condition

Two of the squirrels in the FP group chose correctly over all trials more frequently than expected by chance (IT: 65 correct trials, $P = 0.002$; NV: 60 correct trials, $P = 0.03$); one did not differ significantly from chance (DE: 52 correct trials, $P = 0.38$). All squirrels in the FN group chose as expected by chance (MO: 43 correct trials, $P = 0.097$; SC: 57 correct trials, $P = 0.097$; RK: 57 correct trials, $P = 0.097$). In the first block of trials, five of the squirrels did not differ significantly from chance (between 10 and 16 trials, all $P > 0.21$). The other squirrel, MO, was below chance (7 correct trials, $P = 0.02$). In the last block of trials four squirrels, two in each group, chose correctly more frequently than expected by chance (IT, NV, SC and RK between 18 and 21 correct trials, all $P < 0.02$); the others did not differ significantly from chance (DE and MO, 13 and 16 correct trials, all $P > 0.12$).

One squirrel (DE in FP group) choose correctly more often when the nut was in the pot on the right (she chose

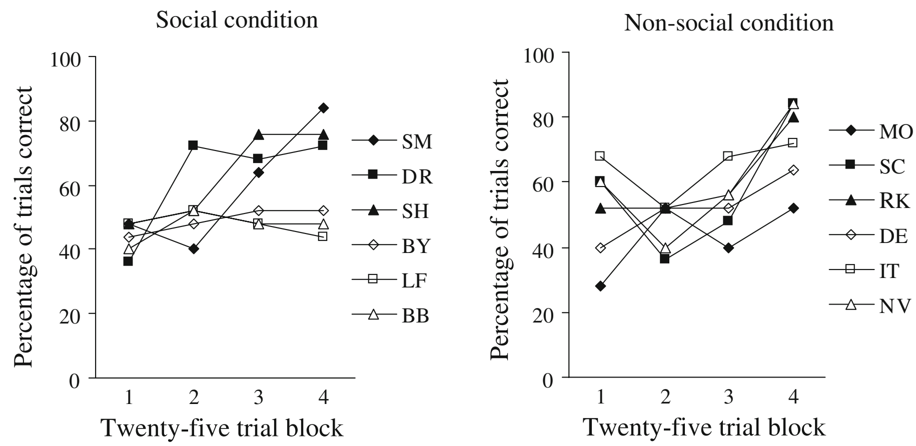

Fig. 3 The percentage of trials in which observers chose the nut-containing pot first during each block of trials in the social and non-social conditions. *Open symbols* show squirrels in the FP groups and *filled symbols* show squirrels in the FN groups

correctly on 28% of left trials but 86% of right trials). All other squirrels chose correctly on 38–64% of left trials and 54–66% of right trials.

There was no significant difference between the FN and FP groups (mean ± SE: FN group = 53.33 ± 5.24; FP group = 59 ± 3.79; $F_{1,4} = 1.13$, $P = 0.348$), but there was a significant effect of trial block ($F_{3,12} = 7.31$, $P = 0.005$) showing that squirrels improved over the course of the study (Fig. 3b). There was no significant trial block by group interaction ($F_{3,12} = 0.23$, $P = 0.87$).

Discussion

The results show that squirrels performed differently when social and non-social cues were presented in a simultaneous discrimination task. Squirrels in both conditions chose the correct pot more frequently over the course of the trials but the different conditions had differing effects on the performance of the FP and FN groups. In the social condition, squirrels that were rewarded for choosing the opposite pot to the one they had observed being emptied by a conspecific chose correctly more frequently than expected by chance by the end of the experiment and more frequently than squirrels that were rewarded for choosing the same pot as the conspecific. These squirrels continued to choose at chance levels in the last block of trials, resulting in a FNE in the social condition. In the non-social condition, only four of the six squirrels performed significantly better than expected by chance in the last block of trials but, squirrels for which the pot in front of the coloured card was the rewarded one chose correctly as frequently as squirrels that had to choose the pot that was not in front of the card to obtain the reward, so that neither a FNE nor a FPE developed.

Social condition

The finding that squirrels learned to choose the opposite pot to the conspecific demonstrator more readily than they learned to choose the same pot supports the findings of previous social learning studies with other species (Darby and Riopelle 1959; Templeton 1998). These previous studies were complicated by the fact the demonstrator provided different information (finding food vs. not finding food) to the FP and FN groups but the current study suggests that even when the demonstrator provides all observers with the same information about the availability of food a FNE develops.

The results also support the anecdotal evidence that wild scatter-hoarding mammals are capable of learning about the whereabouts of hidden food by observing conspecifics (kangaroo rats, Daly et al. 1992; squirrels, Steele et al. 2008), and the findings of a study with captive American red squirrels (*Tamiasciurus hudsonicus*) in which juveniles learned to open hickory nuts more efficiently if they had first seen an adult perform the task (Weigl and Hanson 1980).

This experiment provides a further example of a case in which animals respond in line with the information provided by a demonstrator rather than simply copying them (Giraldeau et al. 2002). The result also suggests that information generated by conspecifics that is consistent with the previous experience and/or ecology of an individual continues to have control over their behaviour, even when it leads to making incorrect choices, at least in the case of social learning tasks.

It is possible that the observer could have used olfactory cues, either left by the demonstrator, or from the nut in the pot in order to decide which pot to open but this seems unlikely. Firstly, the demonstrator was free to move about anywhere in the demonstration cage and to touch or open both pots (the second always behind the curtain, out of view of the observer). This made it impossible for the observers to use odour from the demonstrator as a reliable cue as to which pot to choose. Secondly, the observers' behaviour did not suggest that they were relying on odour cues; they showed no signs of following scent trails, e.g. by sniffing along the ground, and they were never seen to sniff in the direction of both pots before choosing one. The squirrels' choice was always recorded as the first pot they touched rather than necessarily fully opened so they could not inspect the pots for olfactory cues very closely before choosing one.

Non-social condition

When the feature was non-social, squirrels in both the FP and FN groups chose the correct pot increasingly frequently over the course of the experiment but to an equal extent so that neither a FPE nor a FNE developed.

The only previous studies on the FPE in non-social discrimination learning using simultaneously presented stimuli involved children responding to abstract shapes on monitors (Sainsbury 1971b, 1973) and they found a FPE in young children, possibly because they were unable to withhold their responses to the feature in the FN-discrimination condition. In the current study, to equate the non-social condition to the social condition as far as possible, the card was removed before the choice phase so the squirrels did not have the opportunity to attend to it whilst opening a pot. The squirrels were also prevented from responding immediately because there was a delay between the observation phase and the choice stage and this may have helped at least some of them to make more considered choices so that squirrels in the FN group performed as well as squirrels in the FP group.

The result of the non-social test indicates that the action of the nut being removed from a pot, without the presence of a conspecific, was not sufficient to produce the FNE.

Feature-discrimination learning with different types of features

The difference in the squirrels' tendency to associate the conspecific and card with the presence or absence of food is consistent with their differing familiarity with the two features. The squirrels had previous experience of the relationship between conspecifics and food or caches (both in their home cages and in the wild or at the sanctuary) but not between the card and food. When caching in the wild, squirrels store individual items of food in individual caches so the sight of a conspecific removing food from a hidden location should act as a reliable predictor of the absence of food. In the non-social condition, the card is not a natural, reliable predictor of the presence or absence of food and so squirrels had no particular predisposition when learning with it.

It is worth pointing out that although the squirrels had both a conspecific and card present in their cages or a neighbouring cage, five of the six squirrels used in the social condition were no more familiar with the demonstrator squirrel than the squirrels used in the non-social test were with the specific piece of red and black card. This suggests that the squirrels were readily able to generalise from past experience of one conspecific to the conspecific in the current study.

Further investigations would need to control squirrels' experience of the relationship between conspecifics and food before the test or provide subjects with prior experience of different cards associated with the presence or absence of food to determine whether familiarity of the relationship between the feature and outcome is necessary for a FNE to develop and whether that alone can lead to a FNE.

The results of the current experiments may also relate to a difference between learning in social and non-social situations. Animals may be able to use more advanced cognition in social situations than in non-social ones (e.g. Jolly 1966). In the social learning experiment the squirrels may have understood that the demonstrator's chosen pot was now empty but in the non-social test, the squirrels either did not or could not interpret the nut moving out of the pot. It is possible that the information generated during the observation phase in the non-social condition could not be interpreted because the nut remained visible on the floor of the D-cage once it had been pulled out of the pot whilst in the social condition it was clearly no longer available as it was eaten or carried away. Difficulty in interpreting the action of the nut in the non-social condition may explain why two squirrels never chose correctly at above chance levels. Instead, the squirrels could recall the position of the card as a simple cue that perfectly predicted the location of the nut, enabling some of them to learn either the FP or FN discriminations.

Further experiments may determine exactly what the squirrels learn by observing conspecifics. This could be achieved by altering what the observer has to learn from the demonstrator, e.g. they must choose the same or a differently patterned pot rather than pot location as the demonstrator; this would help to separate out whether squirrels respond to the same cue-reward association as the demonstrator or use the demonstrator itself as a simple cue. The extent to which observer squirrels can interpret information generated during the demonstration phase could be also investigated further by manipulating the type of information provided, e.g. have the demonstrator squirrel store a nut rather than remove it, which, if the actions of the conspecific are important, should lead to the development of a FPE.

The results of these experiments suggest that grey squirrels, like other scatter-hoarders, can learn by observing a conspecific and give further support to previous findings that a FNE develops in the social learning of a simultaneous discrimination. The experiments indicate a potential difference between social and non-social learning which should be investigated further. Although social learning is categorized separately from other, non-social forms of learning the actual differences between the two are not well described or understood (Seligman 1970; Heyes 1994). Further work should aim to distinguish between the possibilities that the difference is due to differences in the familiarity of the relationship between the social and non-social stimuli and the outcome or in the ability of squirrels to interpret socially and non-socially generated information.

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