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Social learning influences the preferences of domestic hens for novel food

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It has been argued that social learning helps animals either avoid noxious substances or identify food items, but evidence suggests that avian social learning is fundamentally different from that of mammals. In two experiments, we investigated whether the preferences of domestic hens, *Gallus g. domesticus*, for novel food were influenced by observing the feeding behaviour of conspecifics. In experiment 1, we attempted to confirm that birds can develop socially learnt aversions to unpalatable foods. Despite demonstrators showing a highly visible 'disgust reaction' after eating unpalatable coloured food, observers did not develop aversions to similarly coloured food. In experiment 2, we aimed to determine whether preferences for palatable food were socially learnt, and whether the extent of a demonstrator's preference for novel food affected the magnitude of the observer's socially learned preference. Demonstrators ate coloured food of standard or high palatability, or did not peck food at all. When the demonstrators pecked more frequently or fed more quickly from the food, the observers consumed a greater proportion of food of the same colour; however, this was only when the food was red, not green. We argue this indicates an unlearned aversion to red food, overcome by social learning of the food being highly palatable. The results provide no evidence that adult hens learn aversions through observing disgust reactions, but show that hens are sensitive to the extent of demonstrator preferences for palatable food. The data do not support the hypothesis that avian social learning is fundamentally different from that of mammals.

Social learning is said to occur when direct or indirect social interaction facilitates the acquisition of a novel pattern of behaviour. It usually takes the form of an experienced animal (the demonstrator) performing a behaviour such that the naïve animal (the observer) subsequently expresses the same novel behaviour sooner, or more completely, than it would have done using individual learning. One example of social learning is the acquisition of preferences for novel food. By watching the behaviour of others, individuals of a wide variety of species can learn about the acceptability of novel foods (Nicol 1995; Heyes & Galef 1996; Choleris & Kavaliers 1999; Galef & Giraldeau 2001). There is debate and equivocal evidence about the function of social learning of preferences for novel foods. Data from birds indicate that social learning helps animals avoid toxic or noxious substances (Mason et al. 1984), although it has been argued (Galef 1996) that data from rats, *Rattus norvegicus*, indicate social learning facilitates the identification of potential food items, rather than potential poisons. There is evidence to support both of these views; however, this evidence might also indicate a fundamental difference between avian and nonavian species in the social learning of food preferences.

Evidence that social learning helps avian species identify potential poisons comes from several sources. Mason & Reidinger (1982, 1983) showed that if red-winged blackbirds, *Agelaius phoeniceus*, observed conspecifics consume a coloured food (or food in a distinctively marked container) paired with toxin-induced illness, they subsequently avoided food associated with that colour or container. Similarly, Fryday & Grieg-Smith (1994) showed that house sparrows, *Passer domesticus*, consumed less red food after they observed others eat quinine-treated red food, although the authors noted a significant positive correlation between consumption by the experienced bird and the observer and suggested this effect might have been social facilitation rather than a

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learned avoidance. In both these studies wild-caught birds were used, meaning that previous experience (e.g. coloured foods, illness, taste preferences) could not be accounted for. Perhaps more convincingly, when domestic layer strain chicks, *Gallus g. domesticus*, observed other chicks pecking beads dipped in bitter-tasting methyl anthranilate, they subsequently avoided pecking beads of that colour (Johnston et al. 1998). However, studies on social learning of aversions in nonavian species have been unable to corroborate these results.

After reviewing a series of laboratory studies on rats, Galef (1996, page 51) concluded there is ‘no evidence consistent with the view that food preferences induced in observer rats by demonstrators are influenced by the state of health of those demonstrators’. Similarly, Visalberghi & Addessi (2000) found that capuchin monkeys, *Cebus apella*, rely on their own experience and not on what they see other group members doing in response to a decrease in food palatability. Although social learning would be particularly advantageous when foods are poisonous, several studies have shown that Japanese macaques, *Macacca fuscata*, do not learn to avoid a poisonous food by observing another’s rejection of it (reviewed by Visalberghi 1994). This raises the question whether social learning does confer aversions to noxious foods, or whether this occurs in avian species but not others, that is, there is a genuine phylogenetic difference in behaviour. An additional complication in interpreting studies on birds is that some show unlearned preferences for colour (e.g. Mastrota & Mench 1994; Guilford & Rowe 1996) although the extent of these in adult domestic hens is unknown. Therefore, in experiment 1 we attempted to confirm previous findings that avian species can develop socially learnt aversions to unpalatable foods by studying, for the first time, adult birds with known previous experience.

There is also evidence that social learning helps animals identify potential food items. First, there is direct evidence that after a naïve animal interacts with a recently fed conspecific, the naïve animal shows an enhanced preference for whatever food the other has eaten (Fryday & Grieg-Smith 1994; Cadieu et al. 1995; Galef 1996; Choleris et al. 1998; but also see Hatch & Lefebvre 1997). Second, animals with learned flavour aversions quickly reverse these when they observe or interact with naïve animals eating the food (Klopfer 1959; Galef 1986; Provenza & Burritt 1991; Yoerg 1991; Meunier-Salaun et al. 1997), termed ‘social blockade’ by Heyes & Durlach (1990). Third, adult behaviour towards offspring is suggestive of attempts to teach young about potential food (Nicol & Pope 1996; Fritz et al. 2000; Midford et al. 2000), or, at least, offspring develop preferences for the same food as adults when feeding socially (Hikama et al. 1990; Provenza et al. 1993). Fourth, a wide variety of studies on many species have used food as the reinforcement for social learning of operant or novel responses (e.g. Nicol 1995; Heyes & Galef 1996; Nicol & Pope 1999; Fritz et al. 2000); presumably, learning of the response is motivated by the desire to gain the potential (although familiar) food. One question regarding socially learnt preferences is whether the extent of a demonstrator’s preference for a novel food can influence the magnitude of the preference that observers acquire by social learning; this does not appear to have been examined in either avian or nonavian species.

The feeding behaviour of domestic hens indicates they are likely to be a good model for examining the social learning of food preferences. Adult domestic hens feed gregariously, thus providing the opportunity for social learning. If an individual encounters an apparently highly palatable item, she increases her rate of pecking and scratching in an obviously excited manner which often attracts the attention of other hens who run and feed from the same location, or chase the other hen if she happens to pick up the item and run away. Alternatively, if a hen ingests an unpalatable item, she often begins vigorous head shaking, bill wiping and gaping, the so-called ‘disgust reaction’. There is much evidence for social learning and facilitation of feeding in this species. The pecking preferences of layer hen chicks are easily modified in the first few days of life by a wide variety of stimuli including adult bird behaviour (Stokes 1971; Sherry 1977; Nicol & Pope 1996), chicks of the same age (Tolman 1964; Tolman & Wilson 1965; Johnston et al. 1998), model hens (Turner 1964; Tolman 1967) or a model beak performing ‘pecking’ activity (Suboski & Bartashunas 1984); for a related species, the Burmese fowl, *Gallus g. spadiceus*, real or videotaped images of feeding conspecifics also influence pecking preferences of adults and chicks (McQuoid & Galef 1992, 1993; Moffat & Hogan 1992). Operant studies on adult domestic hens have provided evidence for social learning of pecking preferences (Nicol & Pope 1992, 1993, 1994); however, it is not known whether social learning amongst adult hens facilitates the acceptance or rejection of novel foods.

EXPERIMENT 1

In experiment 1, we aimed to extend previous findings that birds can develop socially learnt aversions to unpalatable food. To achieve this, we used a 2 × 2 factorial design in which we tested whether observer birds were influenced by watching demonstrators eat either unpalatable or standard palatability food, of either red or green coloration.

Methods

Animals, husbandry and treatments

Eighty layer-strain hens were obtained at 9 weeks of age from a commercial breeder and housed in pairs in wooden cages (100 × 45 cm and 60 cm high) with a wood-shavings floor substrate. Each cage incorporated a perch, plastic nestbox, two overhead drinking nipples and a supplementary free-standing tower drinker. The cages were located in four rooms of a suite with a common passageway and common airspace. The light regimen was 12:12 h light:dark and the room temperature was maintained at 22–24°C. The birds were fed standard commercial layer’s mash ad libitum from a trough at the front of the cage.

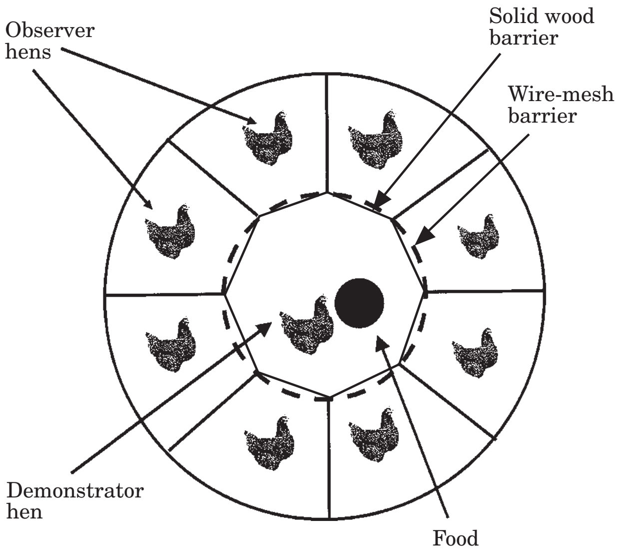

Figure 1. The apparatus used to expose hens to demonstrations of eating food of various palatabilites and subsequent testing of preferences of observers. The wire-mesh barriers were present during the demonstrations but were replaced by solid wooden barriers during testing of the observers.

We designated 64 birds as 'observers' and randomly allocated them to one of four demonstration treatments: demonstrators eating unpalatable red or unpalatable green food, or eating standard palatability red or standard palatability green food. The 16 observers for each treatment were exposed to the demonstrators in two subgroups of eight in a novel apparatus (Fig. 1). We designated 16 birds as demonstrators, four per treatment. Thus each subgroup of observers saw two different demonstrators to ensure they were exposed to an appropriate response. The demonstrators were housed together in one of the rooms to avoid the observers seeing them eating coloured food during habituation. During habituation and the procedure, the same birds comprised each group of eight and were always exposed to the same pair of demonstrators.

Apparatus and food preparation

The apparatus (Fig. 1) comprised two concentric rings (165 and 65 cm diameter) with eight wooden panels connecting the inner and outer rings. These divided the outer ring into eight equally sized pens into which we could place an observer hen. The inner circle was constructed of wire mesh and housed the demonstrator during habituation and the procedure. To prevent observer birds seeing each other during the preference tests (see below), we placed a wooden panel into the end wall of each pen nearest the inner ring circle. All walls were 60 cm high and the birds were kept in the pens by a sheet of metal mesh placed on the top of the pen. All food dishes used during habituation, demonstration and the preference tests were transparent, circular glass bowls measuring 10 cm in diameter with a wire-mesh (3-cm aperture) top to prevent the birds flicking food out of the bowl. The apparatus was located in the central corridor of the suite of rooms housing the birds.

We prepared standard-palatability dyed food by thoroughly mixing 100 g of standard layers mash with 20 ml of either red (artificial cochineal) or green (apple green) food dye (L. Noel and Sons Ltd, Oswaldtwistle, Lancashire, U.K.) in 40 ml of water, drying the mixture in an oven at 100°C overnight and then crushing any clumps larger than 3 mm. We prepared unpalatable food by substituting the 40 ml of water with an 80% w/v solution of methyl anthranilate (MeA), that is, the minimum concentration known reliably to evoke a disgust reaction.

Habituation and training

Both demonstrators and observers were habituated to the apparatus and aspects of the procedure in the following way. We placed each group of eight observers and a relevant demonstrator into the apparatus. After 25 min, we removed the demonstrator and inserted wooden panels into the end section of each observer pen. After 5 min, we removed the wooden panels and repeated the procedure using the other bird of the pair of demonstrators. We did this four times during the 14 days prior to the demonstration and preference tests. We habituated demonstrators to eat either red or green food by placing a bowl of the coloured food at the front of the home cage on at least 10 occasions prior to the demonstration and preference tests, by which time the birds readily consumed the coloured food immediately upon its presentation.

Demonstration and preference test procedure

We placed a dish containing 150 g of food dyed the colour to which the relevant demonstrators had been trained, in the centre of the demonstration pen. We then placed each observer of a group of eight into an observer pen (which did not contain food during the demonstrations) and one bird of the demonstrator pair in the demonstrator pen. After 5 min we replaced the demonstrator in the home cage and substituted the other bird of the pair for a further 5 min. The food was not replenished, as the amount consumed during this time was only a small proportion of the 150 g. We recorded demonstrations on video. We then removed the second demonstrator, placed wooden panels in the inner end sections of each observer pen, to prevent the observers seeing each other, and a dish containing red standard-palatability food and a dish containing green standard-palatability food close to the wall of the outer circumference of the observer circle ca. 10 cm apart. The position and temporal order of placing the dishes were balanced for left and right positions. We video recorded the behaviour of the observers for 60 min with a camera positioned directly above the apparatus. After the 60-min preference test, we returned the observers to their home pens, and washed the apparatus and floor. About 1 h later, we repeated the demonstration and preference test for a different treatment selected at random (with the condition that it was not the same treatment as tested previously on that day). We did all demonstrations and preference tests within a 7-day period between 1300 and 1800 hours.

From the videotapes we assessed the quality of the demonstration by recording the latency to peck and number of pecks at the food, the number of head-shakes and number of bill-wipes. We determined the food preferences of the observers by recording the first and second food colour pecked, the latency to peck each colour and the amount of each colour consumed throughout the 60 min (because of minor spillage by the birds, when the measured amount of food consumed was less than 1.0 g, this was entered into the analysis as 0.0 g).

A dish of unpalatable food was placed near the exit of a ventilation duct above the apparatus to flood the area with the smell of MeA and standardize the olfactory environment for each demonstration.

Statistical analysis

The amount of red or green food eaten by the observers was expressed as a proportion of the total eaten, and the latency to peck as a proportion of the 1-h observation period. In each case, the proportion data were subjected to arcsine square root transformation prior to two-way ANOVA, as recommended by Sokal & Rohlf (1981). Except where stated, all analyses were two-way ANOVA with palatability and colour entered as the treatments. Data presented in tables are nontransformed data.

Ethical note

Methyl anthranilate is widely used to make ingestive stimuli taste aversive in studies of visually mediated passive avoidance learning in chicks (e.g. Marples & Roper 1997; Johnston et al. 1998). In pilot trials, we determined that a minimum concentration of 80% w/v was required to ensure an immediate and obvious ‘disgust reaction’ (i.e. bill wiping and head shaking) in five of six nonexperimental birds tested. The effects of tasting the MeA lasted only a few seconds in both the pilot trials and in subsequent demonstrations. There were no obvious long-term consequences of tasting MeA, for example growth, egg laying and behaviour all appeared normal. We used a minimum number of animals to ensure valid demonstrations whilst minimizing exposure to MeA.

Results

Behaviour of demonstrators

The palatability of the food eaten by the demonstrators had a significant effect on their behaviour. The presence of MeA in the food resulted in a significant increase in the number of head-shakes ($F_{1,12}$=9.6, P=0.009) and the number of bill-wipes ($F_{1,12}$=9.4, P=0.009), but there was no significant effect of food colour on either behaviour (head-shakes: $F_{1,12}$=0.1, P=0.83; bill-wipes: $F_{1,12}$=0.6, P=0.45; Table 1). Both the latency to peck the food and the number of pecks were highly variable amongst the demonstrators, which resulted in there being no significant effect of treatment on either behaviour.

Table 1. Behaviour of demonstrator hens given either red or green food that was either of standard palatability or unpalatable

Treatment	Head-shakes	Bill-wipes
Unpalatable red	34.8±5.6	24.0±2.5
Standard red	13.0±4.3	2.5±2.5
Unpalatable green	34.0±8.0	16.8±11.9
Standard green	16.5±6.8	0.0±0.0

Values are means±SE with data derived from N=4 demonstrator hens for each treatment.

Table 2. Observer hens’ consumption of food (proportion eaten of the same colour given to the demonstrator) after having observed demonstrator hens given unpalatable or standard-palatability food coloured either red or green

Treatment	Total eaten (g)	Proportion eaten
Unpalatable red	19.6±1.9	0.32±0.05
Standard red	17.1±2.1	0.35±0.05
Unpalatable green	18.5±1.6	0.69±0.06
Standard green	17.8±2.4	0.77±0.04

Values are means±SE.

Whilst feeding, the demonstrators frequently moved position indicating that all observers would at some time during the demonstration have been able to see clearly the pecking behaviour of the demonstrators.

Behaviour of observers

The total amount of food eaten by the observers was not significantly affected by either the palatability ($F_{1,60}$=0.66, P=0.41) or colour ($F_{1,60}$=0.9, P=0.93) of the food eaten by the demonstrators (Table 2). However, there was a highly significant effect of colour on the proportion of food eaten by the observers that was the same colour as given to the demonstrators, termed the ‘correct’ colour ($F_{1,60}$=45.7, P=0.0001). When the data are considered separately for each of the palatabilities, there was a significant effect of colour on the proportion of the correct colour eaten by the observers for both the unpalatable ($F_{1,31}$=21.4, P=0.0001) and standard-palatability ($F_{1,30}$=33.9, P=0.0001) treatments.

There was no significant effect of palatability or colour on the behaviour of observers with respect to their latency to peck red (palatability: $F_{1,13}$=0.02, P=0.88; colour: $F_{1,13}$=0.56, P=0.46) or green (palatability: $F_{1,41}$=1.44, P=0.23; colour: $F_{1,41}$=1.94, P=0.17) as the first colour pecked. Similarly, there was no significant effect of palatability or colour to peck either colour first, although the effect of palatability only just failed to reach statistical significance (palatability: $F_{1,60}$=3.16, P=0.08; colour: $F_{1,60}$=0.41, P=0.52). There was also no significant effect of palatability or colour on the latency to peck the correct colour when this was the first colour pecked (palatability: $F_{1,26}$=0.40, P=0.53; colour: $F_{1,26}$=0.71, P=0.40; Table 3).

Table 3. Number of birds that pecked first at red or green food after having observed demonstrator hens given either red or green unpalatable or standard-palatability food

Treatment	N	No. pecking red food first	No. pecking green food first	No. that did not peck
Unpalatable red	16	5	11	0
Standard red	16	3	12	1
Unpalatable green	16	4	12	0
Standard green	16	5	10	1
Total	64	17	45	2

The number of hens to peck green as the first colour was significantly greater than expected if an equal number of hens within each treatment had pecked red or green first (chi-square: $\chi^2_3=22.4$, $P<0.001$; Table 3).

Because each group of eight observers was exposed to a different pair of demonstrators, interdemonstrator differences might have caused variable behaviour between the observers and obscured any social learning relationship. We therefore analysed the data by calculating the regressions of the behaviour of observers on the data averaged for the two demonstrators they saw. This analysis shows that there was no statistically significant regression of the proportion of food eaten by the observers that was the correct colour on the number of pecks ($r^2=0.003$, $P=0.95$), the latency to peck ($r^2=0.145$, $P=0.35$), the number of bill-wipes ($r^2=0.141$, $P=0.36$) or the number of head-shakes ($r^2=0.028$, $P=0.69$) by the demonstrators.

In brief, the results of experiment 1 showed that giving unpalatable food to demonstrator hens had little effect on the socially learnt food preferences of observer birds. We therefore failed to confirm previous findings that birds can develop socially learned aversions to unpalatable food.

EXPERIMENT 2

In experiment 2, we aimed to determine whether the extent of a demonstrator's preference for a novel food can influence the magnitude of the preference that observers acquire by social learning, and, in addition, extend the findings of experiment 1 by determining whether preferences for palatable food can be socially learnt by hens. To achieve this, we used a 3 × 2 factorial design in which we tested whether observer birds were influenced by watching demonstrators either eat standard food, highly palatable food, or stand near food but not peck at this (nonfeeding) when the food was either red or green.

Methods

In general, the methods used in experiment 2 were identical to those used in experiment 1. Differences between the two experiments are detailed below.

Treatments

We designated 80 hens (housed as triplets) as 'observers' to one of 10 groups. Each group watched one of six demonstrations (treatments), that is, observing demonstrators eat highly palatable red or green food ($N=16$ observers/treatment) or standard-palatability red or green food ($N=16$ observers/treatment), or not eat red or green food ($N=8$ observers/treatment). We designated 30 hens (also housed as triplets) as demonstrators, although only two of each triplet were subsequently used in the procedure (see below).

Food preparation, habituation, training and demonstrator selection

We created highly palatable food by placing mealworms, a food item known to be much preferred by hens, into a bowl of coloured, standard-palatability food. Three demonstrators randomly selected to demonstrate consumption of high-palatability food were given a bowl of the appropriately coloured highly palatable food in the home cage until each hen had been seen to consume at least one mealworm. Three nonfeeding demonstrator hens selected to demonstrate 'not pecking at food' were given a dish of the appropriately coloured food covered with a tightly fitting transparent Perspex lid for a 3-h period. For both types of demonstration, this was done on four occasions before selection of demonstrators.

Ten days prior to the preference test, we selected the two best demonstrators from each group of three by placing them individually into the apparatus and giving them a bowl of the appropriate food for 5 min, thus simulating the test procedure. We counted the number of pecks at the food and selected the two birds from each triplet that pecked in the most desired manner (frequently for the highly palatable, not at all for the nonfeeding, and intermediate for the standard palatability) for the subsequent demonstrations.

Demonstration and preference test procedure

The same procedure for experiment 1 was used in experiment 2. The dishes for the demonstrators of highly palatable food did not contain mealworms during the demonstration itself, to avoid giving visual cues to the observers. A dish of highly palatable food was placed near the exit opening of a ventilation duct above the apparatus to flood the area with the smell of mealworms and standardize the olfactory environment for each demonstration.

Table 4. Behaviour of demonstrator hens given either red or green food of high palatability, standard palatability or covered with a Perspex lid (nonfeeding)

Treatment	Latency to peck (s)	No. of pecks
Highly palatable red	0.8±0.8^a	272±80
Standard red	103.3±53.4^b	51±19
Highly palatable green	0.0±0.0	308±55
Standard green	2.5±2.2	200±72

Values are means±SE with data derived from N=4 demonstrator hens for each treatment. Means within each colour of demonstration with different superscripts differ significantly (one-way ANOVA, PLSD) at P<0.05 (see text for details). None of the nonfeeding demonstrators pecked at the bowls or food.

Results

Behaviour of demonstrators

Nonfeeding demonstrators (given bowls with Perspex lids on) did not peck at the bowls and therefore had the maximum latency and zero pecks. When only data from the high- and standard-palatability demonstrators were considered (i.e. data from the nonpecking demonstrators were not included in the ANOVA), the behaviour of the demonstrator birds was significantly affected by the palatability of the food. Two-way ANOVA showed that demonstrators that had been pretrained with high-palatability food had a shorter latency to peck the food ($F_{1,12}$=7.2, P=0.02) and pecked more frequently at the food ($F_{1,12}$=7.1, P=0.02) than standard-palatability demonstrators (Table 4). There was no significant effect of colour on the number of pecks given by the demonstrators ($F_{1,12}$=2.2, P=0.16) but there was a significant effect on the latency to peck ($F_{1,12}$=5.68, P=0.03); therefore, data for each of the colours were considered separately in a one-way ANOVA. Table 4 shows that there was a significant effect of palatability on latency to peck when the food was red (latency: $F_{1,7}$=6.06, P=0.048) but not when it was green (latency: $F_{1,7}$=1.9, P=0.21). Data for the number of pecks followed similar colour-influenced trends.

Behaviour of observers

There was no significant effect of palatability ($F_{2,68}$=2.9, P=0.06) or colour ($F_{2,68}$=0.3, P=0.58) on the total amount of food eaten by the observers (Table 5). Because this analysis showed that the effect of palatability only slightly missed being statistically significant and there was no significant effect of colour or interaction, we pooled data for the colours and did a one-way ANOVA followed by Fisher's PLSD to determine the overall effects of palatability. This showed that palatability had a significant effect on the total amount of food eaten ($F_{2,71}$=3.12, P=0.048). The least total amount was eaten by observers that saw highly palatable food being eaten ($\bar{X}\pm$SE=4.0 ± 1.1 g), which was significantly less than when observers saw standard-palatability food being eaten (10.3 ± 2.1 g); both were not significantly different from the total amount eaten after observing nonfeeding demonstrators (8.7 ± 2.9 g).

Table 5. Observer hens' consumption of red and green coloured food (proportion eaten of the same colour given to the demonstrator) after having observed demonstrator hens given red or green food of high palatability, standard palatability or covered with a Perspex lid (nonfeeding)

Treatment	Total eaten (g)	Proportion eaten
Highly palatable red	2.7±1.0	0.73±0.12^a
Standard red	10.7±2.9	0.32±0.13^b
Nonfeeding red	7.8±4.0	0.07±0.04^b
Highly palatable green	5.6±2.1	0.75±0.13^y
Standard green	10.0±3.2	0.76±0.10^y
Nonfeeding green	9.6±4.4	0.27±0.11^z

Values are means±SE. Means within each colour of demonstration with different superscripts differ significantly (one-way ANOVA, PLSD) at P<0.05 (see text for details).

Table 5 also shows that the palatability ($F_{2,38}$=6.1, P=0.005) but not the colour ($F_{2,38}$=3.1, P=0.082) of food given to the demonstrators had a significant effect on the proportion of food eaten by the observers that was the correct colour. The effect of colour approached statistical significance; therefore we subjected the data for each demonstrated colour separately to one-way ANOVA followed by Fisher's PLSD. This showed that palatability had a significant effect on consumption (red given to demonstrator: $F_{2,21}$=4.4; P=0.03; green given to demonstrator: $F_{2,21}$=3.9, P=0.04). Increasing the palatability of the demonstrators' food from standard to high palatability resulted in the proportion of correct coloured food eaten by the observers being significantly different when the demonstrators ate red, but not green.

There was no significant effect of the palatability or colour of food given to the demonstrators on the behaviour of observers with respect to their latency to peck red (palatability: $F_{2,35}$=0.52, P=0.59; colour: $F_{2,35}$=1.1, P=0.29), green (palatability: $F_{2,24}$=1.97, P=0.16; colour: $F_{2,24}$=0.13, P=0.73) or either colour (palatability: $F_{2,44}$=0.91, P=0.4; colour: $F_{2,44}$=0.93, P=0.34) as the first colour pecked. There was also no significant effect of the palatability or colour of food given to the demonstrators on the latency of observers to peck the first colour when this was the correct colour ($F_{2,23}$=0.87, P=0.43; $F_{2,23}$=1.9, P=0.17; Table 6). Pooling the data for the two colours and analysing with one-way ANOVA revealed no significant effect of palatability on any of these measures of latency to peck.

The number of hens to peck first at green was not significantly greater than expected if an equal number of hens within each treatment pecked red or green first (chi-square: χ^2_3=7.82, NS; Table 6).

There was a significant regression of the proportion of food eaten by the observers that was the correct colour on the number of pecks by the demonstrators (r^2=0.852, P=0.0001; Fig. 2a) and on the latency to peck by the demonstrators (r^2=0.665, P=0.0044; Fig. 2b), that is, if the demonstrator hens pecked more quickly or more frequently at coloured food, this significantly increased the observers' proportional consumption of food of that colour.

Table 6. Number of birds that pecked first at red or green food after having observed demonstrator hens given either red or green food of high palatability, standard palatability or covered with a Perspex lid (nonfeeding)

Treatment	*N*	No. pecking red food first	No. pecking green food first	No that did not peck
Highly palatable red	16	5	4	7
Standard red	16	5	7	4
Nonfeeding red	8	2	2	4
Highly palatable green	16	2	6	8
Standard green	16	3	9	4
Nonfeeding green	8	3	2	3
Total	80	20	30	30

DISCUSSION

Our results do not support Mason et al.'s (1984) suggestion that social learning facilitates aversions to noxious or toxic novel foods. We examined whether observer hens, by watching other hens (demonstrators) interact with coloured unpalatable food, learned this food was unpalatable and subsequently avoided it. Despite the demonstrators showing obvious disgust reactions by vigorous head shaking and bill wiping, there was no evidence that the observers avoided eating the food as indicated by consumption and latency to peck the food. This apparent failure to learn socially an avoidance of unpalatable food contrasts with a previous study on domestic hen chicks (Johnston et al. 1998) and might indicate an age-related influence of social learning. Social learning of aversions may be of greatest benefit to young animals that have had insufficient time to develop experience of foods and would benefit by observing the behaviour of others, whereas adults will have had the opportunity to acquire experience and might make decisions based on this, rather than the behaviour of other individuals. This would certainly be advantageous in *Gallus domesticus* because neophobia does not prevent chicks (in the absence of adults) from ingesting large quantities of coloured LiCl soloution upon initial exposure, and ingestion of lethal quantites upon later presentation, despite the solution's obvious coloration (Hayne et al. 1996). Alternatively, ecological or social constraints during the evolution of this species might have resulted in there being little benefit from the social learning of unpalatability. For instance, selective pressure for this mode of learning would be reduced if these animals rarely encountered toxic food, the consequences of ingestion were low, or the birds rarely interacted after consumption of such items (Noble et al. 2001). Studies on the effects of age on social learning are required. In combination with previous results, the present data might indicate that social learning of avoiding noxious substances occurs in domestic hen chicks (Johnston et al. 1998), but the effectiveness of this wanes with maturation (present results).

In experiment 1, demonstrators that ate unpalatable food shook their heads and wiped their bills significantly more than those that ate standard-palatability food, but the behaviour of the observers was unaffected by this difference in demonstration. So, even when a disgust

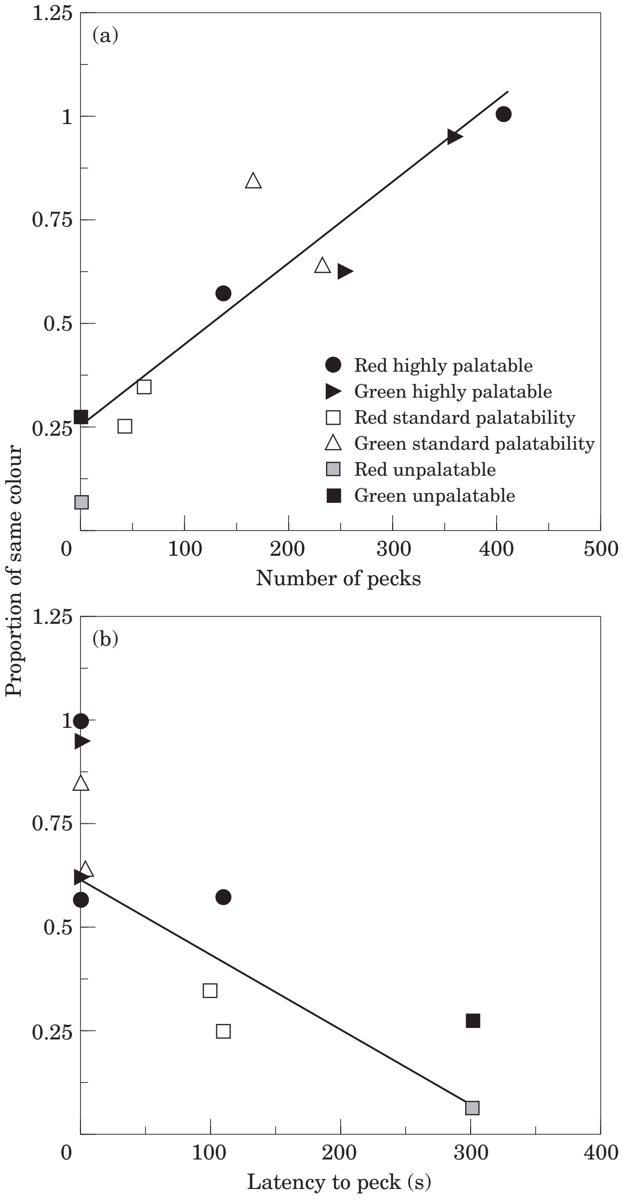

Figure 2. Correlation between (a) the number of pecks and (b) the latency to peck by demonstrators that were either given coloured food that was highly palatable or of standard palatability, or were standing near food but not eating this (nonfeeding) and the proportion of food eaten by observers that was the same colour given to the demonstrator.

reaction was readily observable, this had little effect on the learning of avoidance in observers. Possibly, animals using social learning do not attend to aspects of behaviour that appear highly informative to human observers. In our experiment 1, the number of pecks to the food by the demonstrators did not differ significantly between treatments, raising the possibility that the observers attended to the number of pecks, or perhaps simply the fact that the food was pecked, as the salient indicator of palatability, rather than bill wiping or head shaking. The results of experiment 2 also suggest that if social learning of food avoidance occurs, this might be unrelated to the disgust reaction. When observers saw demonstrators standing near coloured food but not pecking at it, the observers subsequently avoided food of this colour (Fig. 2a). This appears contrary to Visalberghi & Fragaszy's (1996) view that social learning requires a behaviour to be performed (e.g. eating) while the absence of the behaviour (e.g. not eating) is not likely to lead to social learning, unless behaviours that are cognitively demanding (e.g. active teaching) are also present. In the present study it remains to be elucidated whether the (in)action of not pecking at food by demonstrators is interpreted by observers as indicating 'this is noxious' or simply 'this is not a food item'.

In experiment 2, we tested Galef's (1996) suggestion that social learning aids learning of potential food items. We found this to be true. If observers watched demonstrators given coloured food of different palatabilities, the observers ate a greater proportion of the colour if this was demonstrated as more highly palatable. This was related to the pecking behaviour of the demonstrators. When demonstrator hens pecked more frequently (Fig. 2a) or fed more quickly (Fig. 2b) from coloured food, observers subsequently consumed a greater proportion of food of the same colour. Social learning by birds can be influenced by a wide range of factors such as maturation (Midford et al. 2000), type of food (Cadieu et al. 1995), duration of food deprivation (Nicol & Pope 1993), social status or relatedness of demonstrator (Coussi-Korbel & Fragaszy 1995; Hatch & Lefebvre 1997; Nicol & Pope 1999; Fritz et al. 2000; Midford et al. 2000) and the opportunity for scrounging (Giraldeau & Templeton 1991; Midford et al. 2000): we can now add the extent of the demonstrator's preference to this list.

Observers developed preferences for highly palatable food based on the behaviour of demonstrators given this food; however, this effect was influenced by the colour of the food. When the observers had seen demonstrators given red food, the proportion of red food that they subsequently ate increased with increasing demonstrated palatability, but, when the demonstrators were given green food there was no significant difference between high- and standard-palatability treatments in the consumption of green food. We suggest that this interaction results from an unlearned avoidance of red food by the observers which was overcome by a demonstration of high palatability. Some colours, red and yellow, are particularly effective at signalling unpalatability (Guilford & Rowe 1996; Rowe & Guilford 1999). This is evident in the feeding behaviour of hens. They will consume more green food than red when offered the choice (Hurnik et al. 1971), they pecked preferentially first at green food rather than red (present results), and, in experiment 2, observers (naïve to coloured food) that saw nonfeeding demonstrators giving no indication of palatability of either colour consumed a considerably greater proportion of green food than red, which was almost totally avoided. We suggest that adult hens have an unlearned aversion to eat red food and that to overcome this aversion completely, it was necessary for the observers to see the heightened intensity of the demonstration given when eating highly palatable food. It was only after observing this demonstration that the hens increased the consumption of red food to a similar proportion to that recorded for standard or highly palatable green food. What is particularly clear is that when we compared the observers' consumption of the correct food colour (Table 5) with the latency to peck by the demonstrators (Table 4), the responses of the observers obviously reflected those of the relevant demonstrators, that is, increasing palatability from standard to high had a significant effect for red food but not green.

In experiment 2, hens that observed demonstrators eating highly palatable food subsequently ate less than hens that observed demonstrators eating standard food or demonstrators not eating at all. This suggests, paradoxically, that some aspect of the demonstrator's behaviour when eating highly palatable food reduced food consumption by observers. When hens peck at food, some pecks are exploratory (foraging) rather than ingestive (e.g. Yo et al. 1997). Possibly, the high-palatability demonstrators whilst searching for mealworms demonstrated foraging behaviour rather than ingestive pecking, and, as a consequence, the high-palatability observers also foraged in the food rather than ingested it.

Observers learned of the palatability of food by watching demonstrators located in a central pen, but were subsequently given bowls of food ca. 1 m away at the periphery of their own pen and had to turn 180 degrees to feed (see Fig. 1). Since the observers were not given the same food and bowls in the same places as the demonstrators, the phenomenon, by definition, could not be local enhancement. Expression of learned preferences at a site remote from the locality in which the demonstration was observed indicates the hens learned a characteristic of the food itself, rather than of the site at which the food was consumed. This could have been stimulus enhancement or observational conditioning. Learned aversions might, in contrast, be mediated by local enhancement (this could explain why we found no such learning of aversion in experiment 1), a possibility worthy of further investigation.

In summary, we have shown that adult hens developed preferences for novel food by watching the feeding behaviour of conspecifics. This form of social learning was complex. Information indicating a food was unpalatable was apparently not learned when demonstrators showed a highly visible disgust reaction; however, observers seeing a demonstrator not pecking at coloured food avoided this colour when it subsequently became available. Information indicating a food is highly palatable was learned and caused coloured food demonstrated as ‘highly palatable’ to be selected preferentially by observers; however, this was markedly influenced by the colour of the food and might only be applicable to colours for which hens have an unlearned aversion. The results of the two experiments combined (1) provide no evidence that hens learn aversions through observing disgust reactions, (2) confirm that avian species can develop preferences for palatable food through social learning, and (3) show that hens are sensitive to the extent of demonstrator preference. These results are consistent with what has been observed in several nonavian species, and are therefore at odds with the hypothesis that avian social learning is fundamentally different from that of mammals.

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