Behavioural Processes 169 (2019) 103983

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Does demonstrator relevance affect social preferences and the social transmission of food preferences in female mice (*Mus musculus*)?

Lindsey Kitchenham[a,*], Kelsy Ervin[a], Melissa Tigert[a,1], Georgia Mason[b], Elena Choleris[a]

[a] Department of Psychology, University of Guelph, Guelph, ON, Canada
[b] Department of Animal Biosciences, University of Guelph, Guelph, ON, Canada

ARTICLE INFO

Keywords:
Food preferences
Mus musculus
Social behaviour
Social learning

ABSTRACT

This study examined whether a history of beneficial social learning experiences affects social partner preferences in laboratory mice (*Mus musculus*) and whether observer mice acquire adaptive model-based social learning strategies through associative learning. We tested whether observers would come to socially prefer demonstrators who provide beneficial information through the social transmission of food preference (STFP), over demonstrators who do not; and whether they would preferentially attend to and learn from such demonstrators. Observers were given repeated exposures to two demonstrators who differed in whether or not they consistently provided beneficial information (which increased observers' ingestion of food via the STFP). After multiple social learning experiences with a "relevant demonstrator" (our CS+) whose demonstrated food was available for consumption (our US) by the observer and a "non-relevant demonstrator" whose demonstrated food was never encountered, neither demonstrator was preferred over the other. Furthermore, observers learned equally well from both relevant and non-relevant demonstrators. The present findings suggest that adaptive model-based social learning strategies are not followed in the STFP, although we recommend further testing of the social preference hypothesis.

1. Introduction

Group living can have many benefits, including enhanced abilities to detect predators and food sources, and opportunities for social learning. Social learning is an adaptive strategy for acquiring new useful information in which "learning is influenced by observation of, or interaction with, a conspecific or its products" (Heyes, 1994, p. 207; see also Hoppitt and Laland, 2008; Nicol, 1995). It allows 'observer' individuals to reap fitness benefits by copying others ('demonstrators'), so avoiding the costs (e.g. risks of poisoning or predation) associated with trial-and-error learning (Boyd and Richerson, 1985). Within a social group, however, interactions between group-living conspecifics are typically not random (e.g. Holmes, 1988; Seyfarth and Cheney, 2012). Instead, some social partners are generally preferred over others, such that greater amounts of time, proximity, energy or affiliation are allocated to some individuals over others (Seyfarth and Cheney, 2012; Terranova et al., 2000); and opportunities for social learning from different group-mates thus differ too (Coussi-Korbel and Fragaszy, 1995).

Dugatkin and Sih (1995) hypothesized that such social partner preferences are likely whenever choosing particular partners benefits an individual's fitness (e.g. by enhancing the chooser's own foraging success). For example, consistent with this idea, guppies develop preferences for trained conspecifics who had successfully employed a task to gain food (Lachlan et al., 1998); and long-tailed macaques (*Macaca fascicularis*) preferentially interact with proficient tool users, when foraging for hard-shelled invertebrates, fruit, and seeds (Tan et al., 2018). Associative learning is one possible mechanism for the emergence of such preferences. After all, social partner preferences can be experimentally conditioned in the laboratory by repeatedly pairing a particular individual (the CS+) with a pleasant experience, the US (e.g. Coria-Avila, 2012): a form of Evaluative Conditioning (cf. De Houwer, 2011), known as 'Conditioned Social Preference' (e.g. evident in both mice [Kent et al., 2014, 2013] and rats [Coria-Avila et al., 2005; Tecamachaltzi-Silvaran et al., 2017]). One principle aim of this current study was to therefore see if social partner preference could similarly be

Abbreviations: STFP, social transmission of food preferences; SLEs, social learning experiences

* Corresponding author. Present address: Department of Animal Biosciences, University of Guelph, Guelph, ON, Canada.
E-mail addresses: lkitchen@uoguelph.ca (L. Kitchenham), kervin@uoguelph.ca (K. Ervin), melissa.tigert@mail.utoronto.ca (M. Tigert), gmason@uoguelph.ca (G. Mason), echoleri@uoguelph.ca (E. Choleris).
[1] Present address: Faculty of Medicine, University of Toronto, Toronto, ON, Canada.

https://doi.org/10.1016/j.beproc.2019.103983
Received 20 December 2018; Received in revised form 17 September 2019; Accepted 8 October 2019
Available online 14 October 2019
0376-6357/

conditioned in mice, but via social learning, because, as we review next, social animals should have evolved mechanisms for detecting and responding to those demonstrators whose information is most likely to benefit them.

In any group, individuals will differ in their foraging abilities (e.g. Giraldeau, 1984). Using social information is therefore not always beneficial (Boyd and Richerson, 1985; Giraldeau et al., 2002; Kendal et al., 2005): socially acquired information may sometimes provide no benefit to the observer, or even be costly (e.g. resulting in lost opportunities, time and energy that the observer could have spent elsewhere). Laland (2004)'s Social Learning Strategy theory therefore proposes that social learning is not indiscriminate between demonstrators, but instead strategic, with observers using various heuristics to inform from whom they should learn ("who" or "model-based" strategies). For example, observers should preferentially attend to and learn from more *knowledgeable* and/or *successful* demonstrators (as indicated by the pay-off the demonstrator gains from a behaviour, or via proxies of success such as age and/or social status: Boyd and Richerson, 1985; Mesoudi, 2008) over unknowledgeable and/or unsuccessful ones because, theoretically, such strategies are likely to increase their probabilities of acquiring beneficial information (Kendal et al., 2018; Laland, 2004). Evidence for this comes primarily from primates (cf. Kendal et al., 2018). For instance, chimpanzees (*Pan troglodytes*) preferentially attend to the oldest, highest-ranking individuals (Kendal et al., 2015) as well as trained over untrained demonstrators (Kendal et al., 2015); vervet monkeys (*Chlorocebus pygerythrus*) preferentially attend to and copy the foraging tactics of the philopatric sex, perhaps because they have more knowledge of the local environment (van de Waal et al., 2010); and tufted capuchins (*Sapajus* spp.) learning to break open nuts, preferentially attend to proficient, productive nut-crackers (Coelho et al., 2015). But perhaps more important than demonstrator attributes alone is that when observers preferentially attend to certain demonstrators, doing so should increase their own rate of reward. Observers are thus likely to learn who provides beneficial information via associative learning (Heyes and Pearce, 2015; Heyes, 2016). Selective attention to the most proficient nut-crackers in tufted capuchins for example, was likely because the most nuts could be scrounged from these individuals (Coelho et al., 2015; see also Ottoni et al., 2005; Tan et al., 2018 for similar examples). Such associative learning effects should then cause observers to preferentially attend to, copy, and seek out the most relevant demonstrators, thereby increasing proximity and thus further opportunities for social learning (see Coussi-Korbel and Fragaszy, 1995).

In laboratory rodents, social learning research often focuses on the social transmission of food preference (STFP). Here, naturally food neophobic rodents, most commonly Norway rats (*Rattus norvegicus*: e.g. Galef, 1996; Galef and Wigmore, 1983) and house mice (*Mus musculus*: e.g. Valsecchi and Galef, 1989), develop preferences for novel foods whose odours are detected on the breath of a conspecific. The food odour must be encountered on the breath of a living demonstrator: carbon disulfide (CS_2), a gas found at high concentrations in expired breath, drives the STFP (Bean et al., 1988; Galef et al., 1988). Thus, exposure to a novel food on its own, or with a conspecific simply nearby is not sufficient to induce a preference (e.g. Choleris et al., 2011; Ervin et al., 2015; Valsecchi and Galef, 1989). STFP arguably functions to expand feeding repertoires and can be particularly useful when such animals forage from a central place (e.g. a nest), especially when food availability and distribution are unpredictable (e.g. Ward and Zahavi, 1973). Thus in theory, when successful foragers return to the colony after exploiting a novel food patch, observer rodents can use this information to facilitate their own consumption of these novel foods during their own future foraging attempts; observers thereby increase their own rates of foraging due to reduced food neophobia (for evidence see Galef, 1983; Galef and Wigmore, 1983; Valone, 1989).

However, foraging efficiency is only increased if the observers are able to access this novel food and so reap these benefits of the STFP. Consequently, the benefits of learning from successful foragers may not be equal: demonstrators accessing large, close or rapidly replenishing patches of food which subsequent observers can then exploit would be very beneficial to attend to, compared to demonstrators who access distant, small or depleted sources that are difficult or impossible for observers to exploit themselves. Thus, observers should – if strategic – learn which individuals regularly carry beneficial information, demonstrating novel foodstuffs that observers can not only actually obtain for themselves, but also readily exploit thanks to the neophobia-reducing effects of STFP. We will term such individuals "relevant demonstrators".

Thus, in principle, adaptive model-based Social Learning Strategies would be advantageous for rodents using the STFP, assuming that colony-members differ in their provision of beneficial information. Despite this, the STFP was not discussed in the most recent review of Social Learning Strategy theory (Kendal et al., 2018). Furthermore, experimental investigation into the use of such model-based strategies in STFP has to date yielded equivocal results, at least in rats. For example, some studies indicate that observer rats will preferentially learn from healthy demonstrators, over sick ones (Hishimura, 2000; Kuan and Colwill, 1997). However, other studies indicate that rats learn equally well from both (Galef et al., 1990b, 1983; Galef and Whiskin, 2000); and also that they will learn from demonstrators rendered unconscious via anesthesia (Burne et al., 2009; Galef et al., 1983; Nicol et al., 2014). Furthermore, observer rats will even continue to learn from demonstrators whose information has made the observer sick (Galef et al., 1999; Agee and Monfils, 2018). In contrast, the few studies done with house mice suggest they may use model-based strategies in the STFP: behaviourally abnormal mice exhibiting high levels of stereotypic behaviour (e.g. repetitive route-tracing or bar-mouthing) tend to be less effective demonstrators than non-stereotypic mice (Harper et al., 2015); and pups are less efficient demonstrators than adult mice (Choleris et al., 1997). The STFP can also be modulated by familiarity between observers and demonstrators in mice (Forestier et al., 2018) as well as in rats (Galef et al., 1998; Galef and Whiskin, 2008; Agee and Monfils, 2018) and gerbils (*Meriones unguiculatus*: Valsecchi et al., 1996). The adaptive value is unclear in these last examples (they might better be termed 'biases' than 'strategies': S.J. Shettleworth, personal communication), but they do at least confirm that the STFP is sensitive to effects of demonstrator identity.

Here, we therefore investigate whether laboratory mice (*Mus musculus*) learn, via associative mechanisms, to use "copy relevant foragers" (demonstrators who consistently carry beneficial information), and/or "do not copy irrelevant foragers" (demonstrators who consistently carry information that is not beneficial), as model-based strategies in the STFP. We also investigate whether they would acquire a social preference for the proximity of relevant demonstrators. Our experiments involved female mice, who reliably display robust STFP (e.g. Choleris et al., 2011; Clipperton et al., 2008; Ervin et al., 2015; Phan et al., 2012, 2011; Valsecchi and Galef, 1989). They are also highly sociable, and have non-random individual partner preferences for other females (e.g. Weidt et al., 2014, 2008). Experiment 1 is a pilot in which we tested whether we could condition a social preference for a "relevant demonstrator" with the STFP. In summary, observer mice were given the opportunity to learn who provides beneficial information (i.e. by increasing observers' ingestion of food via the STFP) by repeatedly interacting with a "relevant demonstrator" (our CS+) who consistently provided information about safe novel foods which were then made available for consumption (our US) by the observer; as well as with a "non-relevant demonstrator" (our CS-) who only ever provided information about novel foods which the observers then never encountered. We hypothesised that if social learning influences partner preferences in an adaptive way, such that a history of relevant flavour demonstration induces social preferences in observer mice, and/or a history of irrelevant flavour demonstration induces avoidance, then "relevant demonstrators" should come to be socially preferred over "non-relevant demonstrators". Experiment 2 replicates Experiment 1

with similar but improved methodology and larger sample size. Experiment 2 also tests the hypothesis that demonstrator relevance shapes which individuals observer mice will learn food preferences from; this predicts that when given a choice, observers should preferentially learn from relevant and/or discount non-relevant demonstrators, such that flavour preferences acquired from the formerly "relevant demonstrators" are stronger and/or food preferences from the formerly "non-relevant demonstrators" are weaker or even absent. Combined, the two studies then provide a more robust test of our hypotheses by both increasing sample size and thus statistical power, and demonstrating the replicability of our results.

2. Methods

2.1. Experiment 1 (Pilot)

2.1.1. Study animals and housing

We used CD1 mice because they are gregarious (e.g. Terranova et al., 1963), and females as the more affiliative sex (Terranova et al., 1963). All mice were purchased from Charles River Laboratories (Quebec, Canada). To reduce the number of animals, demonstrator mice (N = 22) were re-used from a previous experiment in which they had been ovariectomized at around 10 weeks of age (as have been used successfully in past work: Clipperton et al., 2008; Ervin et al., 2015; Phan et al., 2011, 2012). They were 20–24 weeks old at the start of this study. Observer mice (N = 11) were purchased for this experiment and upon arrival, left undisturbed for a 2-week acclimation period; left gonadally intact; and approximately 10 weeks of age at the start of the study. After acclimation, and five days before testing, mice were housed in groups of three with one observer and two demonstrators (one randomly assigned to be the relevant demonstrator, and the other the non-relevant). Mice lived in these trios for the 19 days of the experiment. Since familiarity influences mouse social preferences (e.g. Nagy, 1965) all procedures were run with both demonstrators present with their observer, except during experimental feeding when all mice were fed individually. Thus, at the time of testing, both demonstrators were equally familiar to their observer.

Mice were housed in polyethylene laboratory cages measuring 27 × 16 × 12 cm (length × width × height, Allentown Inc.), furnished with corn cob bedding and nesting material (Envigo, Mississauga, Ontario, Canada), a paper cup for shelter and a wood tongue depressor for chewing (Fisher Scientific, Ottawa, Ontario, Canada). Rooms were maintained at 21 ± 1 °C and on a 12:12 reversed dark/light cycle, with lights off at 0800 h so that daytime testing corresponded with the nocturnal mouse active period. Food and water were given *ad libitum* (except during food deprivation: see below); mice were fed a maintenance laboratory rodent diet (Harlan® Teklad Global Diet, Mississauga, ON, Canada [14% protein]). On each experimental day, all mice were moved from the colony room to the experimental room 12 h before testing to habituate. Over the course of the experiment, observer body weights and home cage food consumption were measured each night (2000 h) to monitor the effects of food deprivation. Procedures were approved by the Animal Care Committee of the University of Guelph (AUP # 3302) in accordance with the Canadian Council on Animal Care recommendations.

2.1.2. Baseline social preference

A baseline assessment of observers' preferences for their two demonstrators was conducted on Day 1 of experimentation. Demonstrators were removed from the home cage 24 h beforehand to ensure pronounced social investigation upon reunion (e.g. Lister and Hilakivi, 1988). For the test, demonstrators were contained in clear Plexiglas cylinders (7 cm diameter, 12 cm high) with 36 holes (4 mm diameter) drilled into the bottom allowing for the passage of olfactory cues (Choleris et al., 2006). Demonstrators were habituated to these cylinders three days before Day 1 of experimentation by repeated bouts of containment increasing in duration (starting with 2 min. ending with 20 min.) until they showed no visible signs of distress. The two demonstrator containing cylinders were simultaneously placed into their respective observer's home cage, counterbalanced by side (left, right) across cages for a 20 min investigation period (as is common in social preference studies; e.g. Crusio, 2001), that was recorded under red light with an Everio camcorder (JVC, Mississauga, ON, Canada) mounted on a tripod approximately 30 cm above the cage. The recorded interactions were then scored for investigation of each demonstrator (active sniffing within ~2 mm of the perforations of the stimulus cylinders) and cylinder-directed activity (including sniffing the part of stimulus cylinder without holes, digging at the base of the cylinder, biting the perforations, and burying the cylinder with bedding: e.g. Phan et al., 2012, 2011), all using Observer Video Analysis software (Noldus Information Technology, Wageningen, The Netherlands).

2.1.3. Social learning experiences

Starting on Day 2 of experimentation, seven social learning experiences (SLEs), provided observers with opportunities to learn, through the STFP, the predictive value of their relevant demonstrator (CS+) whose breath odour predicted a novel food the observer could consume (US), versus the non-relevant demonstrator (CS-) whose breath odour did not predict this US. Both demonstrators provided olfactory cues about novel foods to the observer. This design was opted for (rather than having the non-relevant demonstrator smell of nothing or a familiar scent) to avoid effects of novelty preference, which would otherwise have been a confound. This number of pairings should be sufficient to condition social preferences (e.g. Kent et al., 2013 and Wood et al., 2015 successfully used as few as four pairings of a social stimulus with a highly salient US, such as ethanol or oxytocin).

Each demonstrator (relevant and non-relevant) was fed one of two novel foods (made fresh every morning by mixing powdered rodent chow with the flavourings [proportions by weight]) for each SLE, which were counterbalanced for demonstrator relevance (e.g. on SLE 1 half of the relevant demonstrators were fed anise, with the corresponding non-relevant demonstrator fed marjoram, the other half of the relevant demonstrators were fed marjoram and the corresponding non-relevant fed anise). Flavours were presented in this order: anise (2%) and marjoram (2%) for SLE 1, clove (1%) and cumin (1%) for SLE 2, ginger (1%) and coriander (1%) for SLE 3, mint (1%) and oregano (1%) for SLE 4, sage (1%) and onion (1%) for SLE 5, garlic (1%) and nutmeg (1%) for SLE 6, and basil (1%) and mustard (1%) for SLE 7. Flavours were mostly chosen from the existing literature on the STFP in rats and mice (e.g. Herrera et al., 2008; Strupp et al., 1990; Vale-Martõ Ânez et al., 2002), but flavour pairings and concentrations used were not tested for equipalatabilty. The SLEs were run consecutively (one SLE a day) except for a 24 h break after SLE 4 when cages were cleaned since this procedure can be stressful to the mice (e.g. Balcombe et al., 2004). All mice were food deprived for 12 h each night before a SLE (during the light phase when food consumption is normally low; e.g. Clipperton et al., 2008) to ensure adequate food consumption the following morning.

The demonstrators were fed individually in clean polyethylene cages (27 × 16 × 12 cm) for 1 h. Flavoured food was presented in a cylindrical glass jar 5 cm high and 7.5 cm in diameter (Dyets Inc., Bethlehem, PA), with a stainless-steel cover with a hole (2.5 cm diameter) and a perforated stainless-steel disk being placed on top of the powdered food to reduce digging and spillage, and ensure accurate measures of food consumption (Clipperton et al., 2008). Food intake was determined by weight to 0.01 g precision with a digital scale (Sartorius Corp., Edgewood, NY) and demonstrators were required to eat a minimum of 0.10 g of food. Demonstrators met this criterion on all but one instance (average consumption 0.74 g; range of 0.08–1.60 across SLEs). After feeding, the demonstrators were placed in the Plexiglas cylinders and simultaneously presented to the observers in the home cage (counterbalanced by side) for a 20 min investigation period

that was video recorded and scored for observers' relative investigation – namely, active sniffing within ~2 mm of the perforations of the stimulus cylinders (Phan et al., 2011, 2012) – of each demonstrator (relevant, non-relevant) using Observer Video Analysis software. After each investigation period, the observers were immediately fed (from the glass jars like those used for the demonstrators) the same food that had been fed to their relevant demonstrator for 1 h. The observers were never given the food consumed by the non-relevant demonstrator. Thus, the relevant demonstrator provided multiple opportunities for observers to utilize their social learning, while the non-relevant demonstrator did not. Observer food intake was checked by weight of the food jars to 0.01 g precision. Observer mice ate on average 0.69 g of food in the 1-h feeding period (range: 0.10–1.25 g). This procedure was repeated for all seven SLEs.

2.1.4. Final social preference

To re-assess the observers' relative preferences for the two demonstrator types, the same procedures were followed as for the baseline social preference test. But here, removing demonstrators from the home cages for 24 h beforehand was done not only to ensure social investigation, as before, but also to allow any dietary olfactory cues on their breath to dissipate to a level undetectable by observers (validated in pilot testing), as to not influence observers' investigation of their demonstrators. Video recorded interactions were scored as described in the baseline social preference test.

2.2. Methods experiment 2

2.2.1. Study animals and housing

As in Experiment 1, female CD1 mice from Charles River Laboratories were used. Observers (N = 30) were between 10 and 12 weeks of age at the start of the experiment, while the demonstrators (N = 60) were aged 12–15 and 14–17 weeks. Demonstrator mice were re-used from a previous experiment (except this time they were gonadally intact, as in Choleris et al., 2011, 1997), while observer mice were purchased. Because of the larger sample size, mice were run in two successive cohorts to which observers were randomly assigned (n = 15 per cohort). Experimentation lasted 15 days/cohort (total 30 days of experimentation). As in Experiment 1, procedures were always run with both demonstrators in the presence of their observer, except for experimental feeding, where all mice (observers and demonstrators) were fed individually. Housing, lighting, and feeding, and general experimental procedures followed Experiment 1. Body weights and home cage food consumption were not monitored because they had not been affected in Experiment 1.

2.2.2. Baseline social preference

Like in Experiment 1, we took a baseline measure of observers' preferences for each of their demonstrators (relevant and non-relevant demonstrators). Procedures followed those of Experiment 1, with one exception: only the first 10 min of the social interaction was video recorded because in Experiment 1, observer investigation of demonstrators during the first 10 min of social interaction strongly predicted their investigation over the full 20 min interaction period ($r = 0.82$, $t(117) = 19.62$, $p = 0.000$). The video recorded interactions were again scored as previously described for the baseline social preference test in Experiment 1, and by the same experimenter, but this time the experimenter was blind to the identity of each demonstrator.

2.2.3. Social learning experiences

The SLEs commenced the next day. We increased the number of flavours used for each SLE from 2 to 4 (each observer receiving 1 of the 4 flavours per SLE), so increasing the variation in palatability and attractivity of the foods each day; and we also increased the number of SLEs from seven to eight. For practicality, observers and their respective demonstrators were randomly divided into two batches (Batch 1 n = 8; Batch 2 n = 7 observers) run one after the other on the same experimental day. Batch 1 received their novel food (counterbalanced for demonstrator relevance as outlined in Experiment 1) in this order: parsley (2%) and rosemary (1%) for SLE1, anise (2%) and marjoram (2%) for SLE 2, ginger (1%) and coriander (1%) for SLE 3, sage (1%) and onion (1%) for SLE 4, basil (1%) and mustard (1%) for SLET 5, clove (1%) and cumin (1%) for SLE 6, mint (1%) and oregano (1%) for SLE 7, and garlic (1%) and nutmeg (1%) for SLE 8; Batch 2 received these flavours (counterbalanced for demonstrator relevance as outlined in Experiment 1) in the reversed order.

All mice were food deprived for 12 h before each SLE. On the morning of testing, Batch 1 demonstrator mice were fed first (0800 h) in clean polyethylene cages for 1 h, using the same feeding jars described in Experiment 1. Batch 2 demonstrator mice were fed after (1000 h), with cleaned cages (50% ethanol and water) re-used from Batch 1 and feeding jars (cleaned with unscented soap, baking soda, and water). Demonstrators were again required to eat a minimum of 0.10 g of food. Demonstrator mice ate on average 0.85 g (range 0–3.62 g). The relevant demonstrator for Observer 22 ate 0 g on SLE 5 & 6, and thus Observer 22 was excluded from all analyses. Observer mice ate on average 1.00 g of food in the 1-hr feeding period (range: 0.10–3.50 g). A "break" (48 h) in the SLEs was implemented after SLE 4 for cage changes. The same experimenter as in Experiment 1 scored the interactions as previously described for the SLEs in Experiment 1, this time using JWatcher Version 1.0 (Sinauer Associates Inc., Massachusetts, United States).

2.2.4. Final social preference

After the last SLEs demonstrators were removed from their observers' home cage 24 h before the final social preference test. Procedures were the same as in Experiment 1. Observer investigation of their demonstrators and cylinder-directed activity was scored by the same experimenter, but this time blind to demonstrator identity, using Observer Video Analysis software

2.2.5. The social transmission of food preference (STFP)

After the last social learning experience, we assessed the observers' preferences for the foods eaten by each of their demonstrators (relevant and non-relevant). All mice were food deprived for 12 h before the test. On the morning of testing, demonstrator mice were individually fed novel foods from the same jars used in the SLEs in clean polyethylene cages for 1 h. All demonstrators (relevant and non-relevant) were fed either 2% cocoa (Fry's Premium Cocoa, Cadbury Ltd., Mississauga, Canada) (n = 30) or 1% cinnamon (McCormick Ground Cinnamon, McCormick Canada, London, Canada) (n = 30) counterbalanced for demonstrator type. The cinnamon and cocoa flavoured diets were previously established as generally equipalatable to female CD1 mice obtained from Charles Rivers (Choleris et al., 2011; Clipperton et al., 2008) but we counterbalanced the use of these two flavours between relevant and non-relevant demonstrators because palatability variations in different batches of mice are common. Food intake was determined by weight to 0.01 g precision and demonstrators were required to eat a minimum of 0.10 g of food: none needed to be excluded (average consumption was 0.93 g; range 0.24–2.04 g).

After feeding, demonstrators were placed in the Plexiglas cylinders and placed into the home cage, counterbalanced by side (left, right) for the observers to investigate. This time both demonstrators, not just the relevant one, would predict novels foods that would be presented to the observer. Observers were given 20 min to investigate their demonstrators. This interaction was scored by the same experimenter, blind to demonstrator identity, for observers' investigation – again active sniffing within ~2 mm of the perforations of the stimulus cylinders – of each demonstrator (relevant, non-relevant) using Observer Video Analysis software. After the interaction, the observers were tested for food preferences in polyethylene cages (37 × 21 × 19 cm) with two food magazines affixed to one side (Tecniplast, Varese, Italy), which had removable food trays, each with an apron to catch spills and allow

for precise measurements of intake (Clipperton et al., 2008; Valsecchi and Galef, 1989). Observers were given 1 h of access to 1% cinnamon and 2% cocoa flavoured diets for consumption, and food intake was determined by weight of the food trays to 0.01 g precision. Thus observers were able to consume both flavoured foods demonstrated by the different demonstrators (relevant and non-relevant) (cf. e.g. Galef et al., 1990a; Galef and Whiskin, 2000, 2004; Kuan and Colwill, 1997). Only observers who ate more than 0.01 g were included in the analysis; in practice this meant all of them. Observer mice ate on average 0.81 g of flavoured food in the 1-h food choice test period (range: 0.24–1.91 g).

2.3. Statistical analyses

Statistical analyses were performed using IBM SPSS Statistics, Version 24 and 25 for Windows (SPSS Inc., Chicago, IL) and JMP (SAS Institute Inc. Cary, NC). The Shapiro-Wilk test was used to assess normality of studentized residuals from the General Linear Models. Data with non-normal residuals were transformed using either square-root, logarithmic or Box-Cox transformations. The studentized residuals from each model were plotted against the predicted values to assess fulfillment of the homogeneity of variance assumption for all models. All data appeared homogeneous.

Analyses were conducted to test the following predictions: (1) that after multiple social learning experiences, observers would direct more social investigation towards the relevant demonstrator than the non-relevant demonstrator, during both the final social preference test (in which dietary olfactory cues were absent) and the final STFP interaction (in which dietary olfactory cues were present), and also during the later SLE trials; and (2) that observers will learn the STFP better from the relevant than the non-relevant demonstrator.

2.3.1. Investigation of and preference for relevant and non-relevant demonstrators

Social investigation times were analysed using Mixed General Linear Models with greater investigation durations indicating greater social/investigative preference (Harrison et al., 2016). Separate analyses were run for: the social preference tests (model: test [baseline, final] and demonstrator [relevant, non-relevant] and their interaction as repeated measures, plus observer as a random effect); the social learning experiences (model: SLE [with day as a continuous effect], demonstrator [relevant, non-relevant] and their interaction as repeated measures, with observer as a random effect); and the STFP (model: demonstrator [relevant, non-relevant] as a repeated measure, with observer as a random effect). The first two models were then re-run with Experiment 1 and Experiment 2 combined (blocking by Experiment) to enhance statistical power and to investigate (using the interaction term) whether any effects differed between the two experiments. Observers' social preference for their demonstrators was also re-examined using total cylinder directed activity (the sum of the time spent sniffing the cylinder perforations, sniffing the part of stimulus cylinder without holes, digging at the base of the cylinder, biting the perforations, and burying the cylinder) for the social preference tests (model: test [baseline, final] and demonstrator [relevant, non-relevant] and their interaction as repeated measures, plus observer as a random effect). This was to check that our non-significant findings were not just artefacts of the 'sniffing' variable initially measured.

Observer 33's datum from the final social preference test, the STFP test, and SLE 5–8 was dropped from the analyses because her relevant demonstrator did not eat any food on two of the SLEs (5 and 6). Observer 31 escaped from the cage during observation on SLE 4, and thus her data for SLE 4 was dropped from the analysis on SLEs. Data from Observer 7, 8 & 9 were also missing from SLE 5 due to a lost video file; the missing data were imputed using Multiple Imputation via Linear Regression model and the Monotone method.

2.3.2. The social transmission of food preference (STFP)

Social learning from the relevant versus non-relevant demonstrator was assessed by examining observers' flavour intakes using a Mixed General Linear Model (with demonstrator type [relevant, non-relevant] as the repeated measure, flavour [cinnamon, cocoa] as the between-subjects variable, their interaction, and observer as a random effect). Only demonstrators and observers who ate ≥ 0.10 g of food were included in these analyses (Clipperton et al., 2008).

2.3.3. Power tests on social preference data

To evaluate whether our non-significant preference results could have been Type II errors, we first calculated the effect sizes for partner preference found in Conditioned Social Preference studies where one conspecific was a CS+, another a CS− using female mice as both subjects and stimuli (Kent et al., 2013; Kosaki and Watanabe, 2016; Wood et al., 2015). Effect sizes in these studies were all large (Cohen's $d = 0.97$–2.12). We then used a sample size calculator (Dhand and Khatkar, 2014) to assess our ability to detect effect sizes this large in our own preference tests in Experiment 1 and 2 alone, and across both experiments pooled.

3. Results

3.1. Experiment 1 (Pilot)

3.1.1. Investigation of and preference for relevant and non-relevant demonstrators

3.1.1.1. Social preference tests. Analysis of observers' investigation of relevant and non-relevant demonstrators in the social preference tests found no main effect of test (baseline versus final: F (1, 34.29) = 1.07, $p = 0.308$), nor of demonstrator type ($F(1, 34.29) = 0.28$, $p = 0.600$), and importantly, no interaction between them ($F(1, 34.29) = 0.01$, $p = 0.930$) (Fig. 1). Likewise, observers' total cylinder -directed activity (as an index of social proximity) yielded similar results: observers directed significantly less activity towards their demonstrators in the final test compared to the baseline ($F(1, 36.83) = 5.02$, $p = 0.031$), but did not differentially direct activity towards either demonstrator (relevant versus non-relevant: $F(1, 36.83) = 0{,}22$, $p = 0.639$), with again, no interaction between test and demonstrator type ($F(1, 36.83) = 0.03$, $p = 0.865$). There was thus no *a priori* preference for either demonstrator, and furthermore, preferences did not change by the final social preference test.

3.1.1.2. Social learning experiences. Examination of observers' investigation during the social learning experiences showed a significant decrease in demonstrator investigation duration over all SLEs ($F(1, 85.82) = 100.70$, $p = 0.000$) but with no differences between demonstrators ($F(1, 78.00) = 0.25$, $p = 0.621$), nor any interaction between demonstrator type and SLE number ($F(1, 85.82) = 0.30$, $p = 0.588$) (Fig. 2). Thus, over the course of the SLEs, observers spent less time investigating all demonstrators, regardless of whether they were relevant or non-relevant.

3.2. Experiment 2

3.2.1. Investigation of and preference for relevant and non-relevant demonstrators

3.2.1.1. Social preference tests. Analysis of observers' investigation of relevant and non-relevant demonstrators in the baseline and final social preference tests revealed a significant main effect of test (baseline versus final: $F(1, 110.62) = 3.95$, $p = 0.049$), but no main effect of demonstrator ($F(1, 110.62) = 0.00$, $p = 0.992$), nor any interaction between test and demonstrator type ($F(1, 110.62) = 0.27$, $p = 0.604$) (Fig. 7). The effect of test was explained by the fact that unexpectedly, the relevant demonstrator was investigated significantly more in the baseline than the final test ($t(28) = 2.20$, $p = 0.036$), whereas

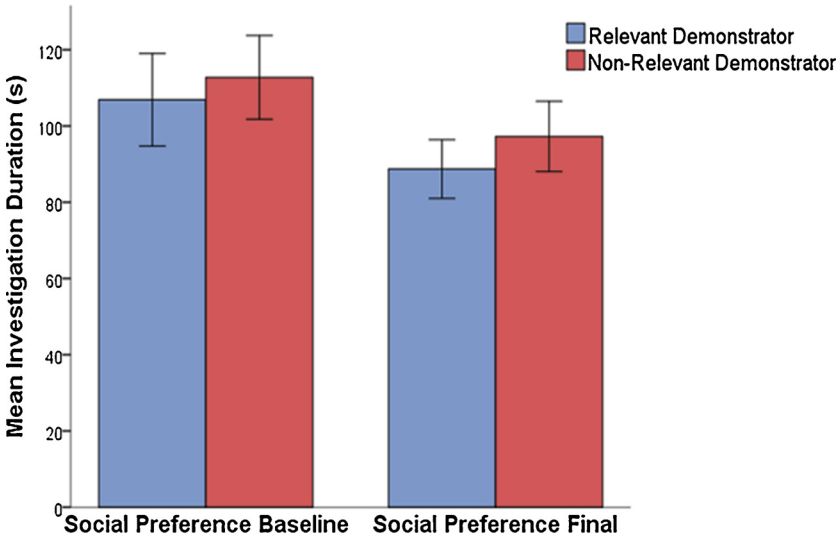

Fig. 1. Investigation duration of relevant and non-relevant demonstrators during the baseline and final (i.e. after seven Social Learning Experiences) social preference tests for Experiment 1 (the pilot) (N = 11 observer mice). Error bars represent ± 1 SE.

investigation of the non-relevant demonstrator did not change ($t(28) = 1.52$, $p = 0.140$) (Fig. 3). But the important result here is that relevant demonstrators did not attract more investigation after the SLEs. Likewise, comparing observers' cylinder-directed activity (indexing social proximity) yielded a significant main effect of test ($F(1, 111.29) = 6.18$, $p = 0.014$, for the same reasons as for sniffing alone) but no main effect of demonstrator ($F(1, 111.29) = 0.07$, $p = 0.68$), nor any effect of the interaction between test and demonstrator type ($F(1, 111.29) = 0.17$, $p = 0.682$). Thus overall, the social learning experiences did not cause the observers to prefer the relevant demonstrators.

3.2.1.2. Social learning experiences. The investigation of both relevant, and non-relevant demonstrators showed a significant decrease over the SLEs ($F(1, 238.96) = 349.34$, $p = 0.000$), but with no effect of demonstrator type ($F(1, 223.36) = 0.53$, $p = 0.470$), nor any interaction between demonstrator type and SLE number ($F(1, 238.96) = 0.00$, $p = 0.990$) (Fig. 4). Thus, as in Experiment 1, demonstrator investigation decreased over time, but similarly for both relevant and non-relevant demonstrators.

3.2.1.3. Investigation during the STFP test. The investigation durations for the relevant and non-relevant demonstrators were again assessed in the final STFP test (run after the SLEs), during which both demonstrators smelled of novel foods (one smelling of cinnamon, the other of cocoa). There was no significant difference in observers' investigation of relevant and non-relevant demonstrators ($F(1, 53.70) = 0.00$, $p = 0.970$) (Fig. 5). Observers thus showed no investigative preference for relevant demonstrators during the STFP test.

3.2.2. The social transmission of food preference (STFP)

Analysis of the observers' flavoured food intake revealed a significant main effect of flavour ($F(1, 53.90) = 18.13$, $p = 0.000$), but no interaction with demonstrator type ($F(1, 53.90) = 1.55$, $p = 0.219$) nor any main effect of demonstrator type ($F(1, 53.90) = 0.68$, $p = 0.414$) (Fig. 6). Thus, observers did not prefer a flavour when demonstrated by relevant demonstrators over the same flavour when demonstrated non-relevant demonstrators.

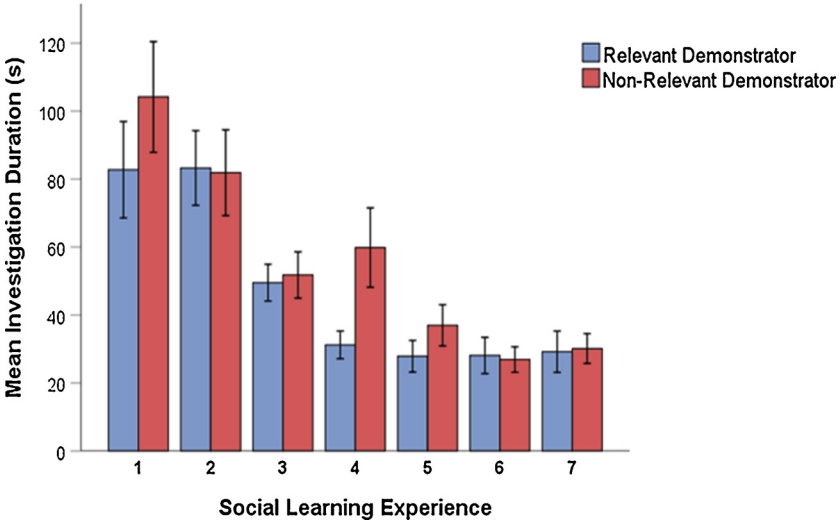

Fig. 2. Mean investigation duration of demonstrators (relevant, non-relevant) during social learning experiences 1 through 7 for Experiment 1 (the pilot) (N = 11 observer mice). Error bars represent ± 1 SE.

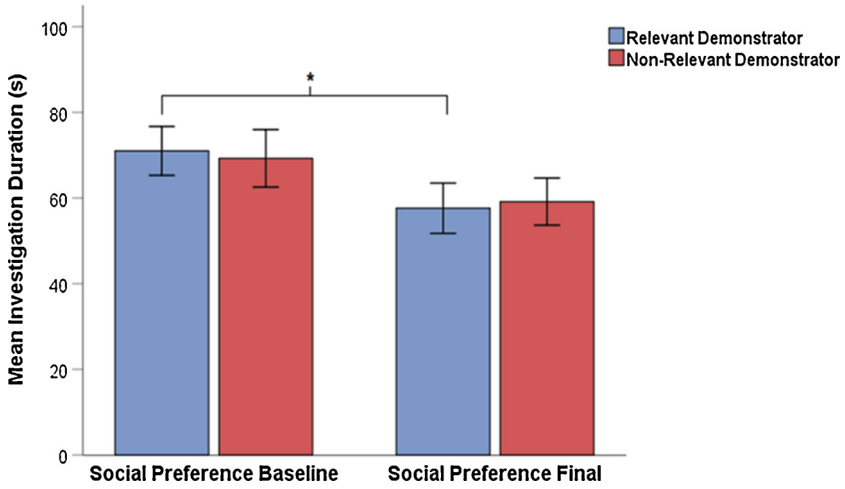

Fig. 3. Investigation duration of the relevant and non-relevant demonstrators during the baseline and final (after eight social learning experiences) social preference tests for Experiment 2 (N = 30 observer mice). Error bars represent ± 1 SE.
*$p < 0.05$.

3.3. Data from experiment 1 and experiment 2 pooled

3.3.1. Investigation of and preference for relevant and non-relevant demonstrators

3.3.1.1. Social preference tests. Combining observers' investigation data from Experiment 1 and Experiment 2 to enhance statistical power revealed a significant effect of test (baseline versus final: $F(1, 150.33) = 4.13$, $p = 0.044$), but again no effect of demonstrator type ($F(1, 150.33) = 0.32$, $p = 0.574$), nor any interaction between demonstrator type and test ($F(1, 150.33) = 0.16$, $p = 0.693$) (Fig. 7). There was a significant effect of experiment ($F(1, 151.52) = 34.29$, $p = 0.000$), but no significant interactions with test ($F(1, 150.33) = 0.00$, $p = .978$) or demonstrator type ($F(1, 150, 33) = 0.31$, $p = 0.581$), nor a 3-way interaction (Experiment x Demonstrator x Test) ($F(1, 150.33) = 0.02$, $p = 0.897$). Thus, the lack of effect of demonstrator relevance on social preference was consistent across our two experiments. Exploration of the main effect of test with a paired sample *t*-test again revealed that the relevant demonstrator was investigated less in the final social preference test than in the baseline test ($t(39) = 2.12$, $p = 0.041$). The non-relevant demonstrator was also investigated less in the final than in the baseline test, but this was only a statistical trend ($t(39) = 1.75$, $p = 0.088$) (Fig. 7). Similarly, examination of total cylinder- directed activity revealed a significant effect of test ($F(1, 153.56) = 11.22$, $p = 0.001$) and experiment ($F(1, 154.38) = 101.36$, $p = .000$), but no effect of demonstrator type ($F(1, 153. 56) = 0.00$, $p = 0.953$), nor any interaction between demonstrator type and test ($F(1, 153.56) = 0.06$, $p = 0.811$).

3.3.1.2. Social learning experiences. Analysis of combined data from Experiment 1 and Experiment 2 confirmed the significant decrease in investigation durations over SLEs ($F(1, 365.65) = 279.41$, $p = 0.000$), but again found no effect of demonstrator type ($F(1, 285.30) = 0.21$, $p = 0.651$) nor any interaction between SLE number and demonstrator type ($F(1, 365.65) = 0.01$, $p = 0.944$) (Fig. 8). There was also a significant main effect of experiment ($F(1, 285.30) = 39.84$, $p = 0.000$) but, again, no interaction with demonstrator type ($F(1, 285.30) = 0.91$, $p = 0.340$) or SLE number ($F(1, 365.5) = 0.87$, $p = 0.350$) nor a 3-way interaction (Experiment x Demonstrator x SLE) ($F(1, 365.65) = 0.01$, $p = 0.965$). Thus, demonstrator relevance did not affect observers' social investigation during the SLEs, consistently across both experiments.

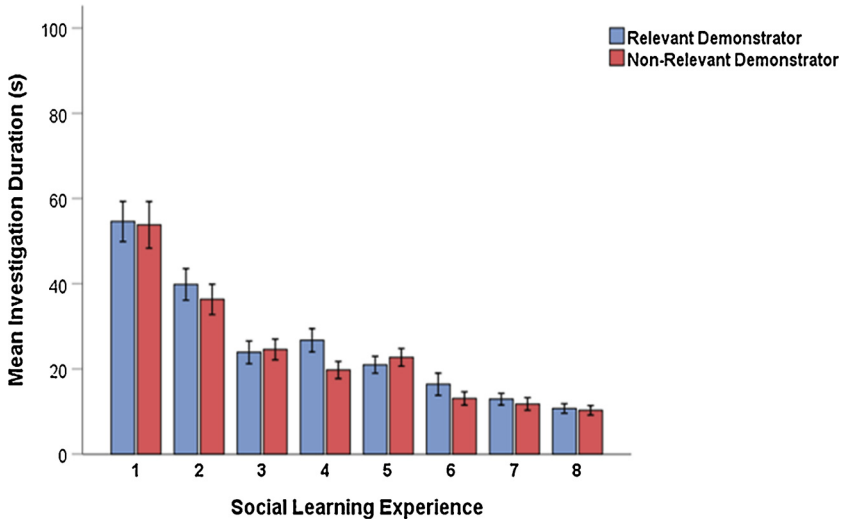

Fig. 4. Investigation duration of demonstrators (relevant, non-relevant) by observers during Social Learning Experiences 1 through 8 in Experiment 2 (N = 30 observer mice). Error bars represent ± 1 SE.

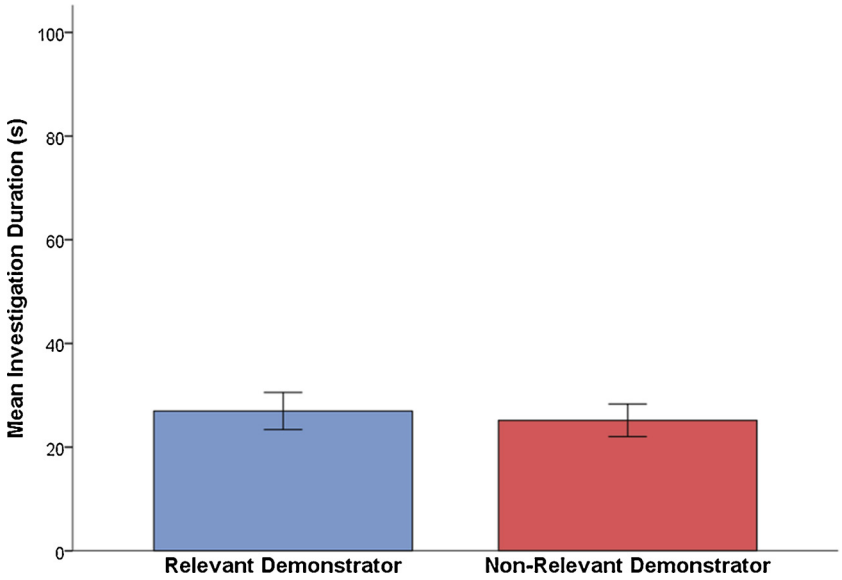

Fig. 5. Demonstrator investigation durations during the STFP test (after eight social learning experiences) for Experiment 2 (n = 29 observer mice). Error bars represent ± 1 SE.

3.3.2. Power tests on social preference data

Power tests (Dhand and Khatkar, 2014) showed that Experiment 1 alone did not have enough power to detect the smallest effect sizes observed in previous conditioned partner preference studies (Cohen's $d = 0.97$). Experiment 2 alone did have enough power to do so and could also have detected smaller effect sizes (Cohen's $d = 0.53$: Medium). However, with our pooled sample size of 41, we not only now had ample power to detect the smallest effect sizes seen in previous conditioned partner preference studies, but we also should have been able to detect effect sizes less than half that size (Cohen's $d = 0.43$: Small-Medium) with 80% power. This indicates that the lack of significant partner preference evident after our SLEs was not a Type II error.

4. Discussion

We hypothesized that if social learning adaptively influences social preferences, then relevant demonstrators, those providing information that always predicted exploitable food (and so was beneficial to the observer) should be preferred over ones providing irrelevant information (not beneficial to the observer because the food the demonstrator had eaten could never be exploited). Additionally, if through associative learning, demonstrator relevance influences who female observer mice learn from in the social transmission of food preference, observers should preferentially learn from demonstrators who have consistently carried relevant olfactory information predicting food reward and learn less well (or not at all) from ones who had only ever carried irrelevant olfactory cues. Neither hypothesis was supported. Below we discuss the possible reasons for these results.

Starting with social preference, even after multiple social learning

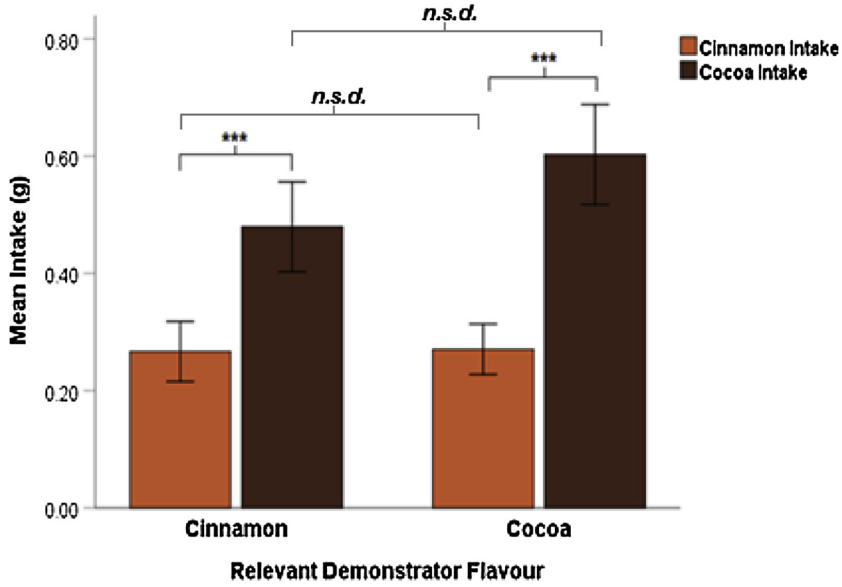

Fig. 6. Amount of cinnamon vs. cocoa flavoured foods consumed by observers whose relevant demonstrator was fed either cocoa or cinnamon for Experiment 2 (n = 29 observer mice). Error bars represent ± 1 SE.
***$p < 0.001$, *n.s.d.* $p > 0.05$.

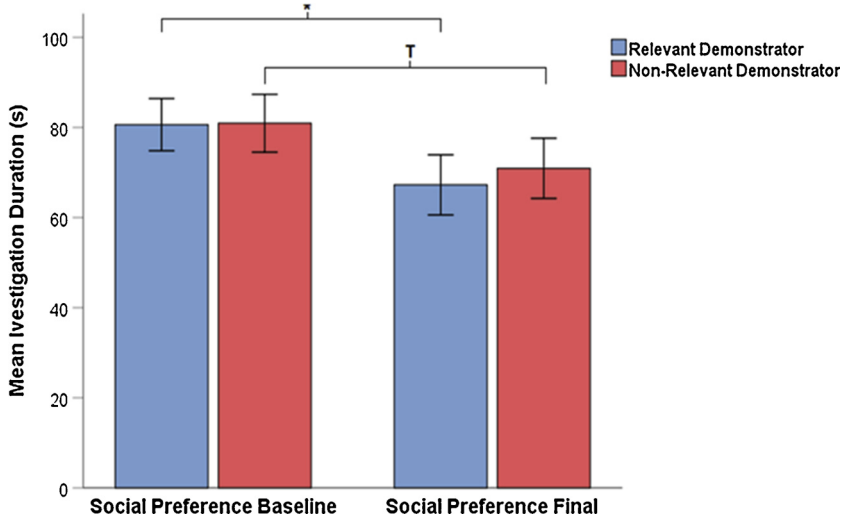

Fig. 7. Investigation duration of the relevant and non-relevant demonstrators during the baseline and final social preference tests for the combined analysis of data from both experiments (N = 41 observer mice). Error bars represent ± 1 SE.
*$p < 0.05$, T = 0.088.

experiences (SLEs), female CD1 mice did not come to direct more social investigation towards the relevant demonstrator than to the non-relevant demonstrator, neither during the final STFP test and SLE trials (in which dietary olfactory cues were present), nor during the final social preference tests (in which dietary olfactory cues were absent). The one notable effect was a decrease in all investigation durations over the course of the SLEs, likely just reflecting both demonstrators' increasing familiarity to the observers (cf. Kareem, 1983). Thus female observer mice did not seem to preferentially seek out, nor spend more time in close proximity with, demonstrators from whom they had successfully learned in the past. Furthermore, our replication of this effect across two experiments, and our power tests, both indicate that this lack of effect was not a Type II error (since we had enough power to detect much smaller effect sizes than those generated by Conditioned Social Preferences in female mice [cf. Kent et al., 2013; Kosaki and Watanabe, 2016; Wood et al., 2015]). Additionally, experiments using food as the US could establish Conditioned Place Preferences in just 6–8 pairings, further suggesting that we had sufficient trials (Chaperon et al., 1998; Maes and Vossen, 1993; Perks and Clifton, 1997). Our results thus resemble those from two other species in which social preferences appear unrelated to foraging outcomes. First, Egyptian fruit bats (*Rousettus aegyptiacus*) who lick fruit residue from the muzzles of others preferentially do this from just 2–3 individuals, but such preferences are unrelated to the chances of acquiring food (Harten et al., 2018). Second, in bearded capuchin monkeys (*Cebus libidinosus)* the foraging proficiency of individuals (i.e. their abilities to open palm nuts, which then leads to the social learning of this task by observers) does not seem to affect how much time others spend close to them (Howard et al., 2018).

Considered together, one interpretation of our finding is therefore that the payoffs gained by an observer from social learning opportunities do not drive social preferences. However, because, to the best of our knowledge, ours is the first study to empirically investigate whether social learning affects social preferences, we urge for more research before this hypothesis is fully rejected. In particular, as a first attempt at testing this idea, our methodology may not have been ideal for promoting the differential association of the relevant demonstrator via successful social learning. This is because the relevant and non-relevant demonstrators were always presented together, and simultaneously predicted a food reward (without any adverse consequence being

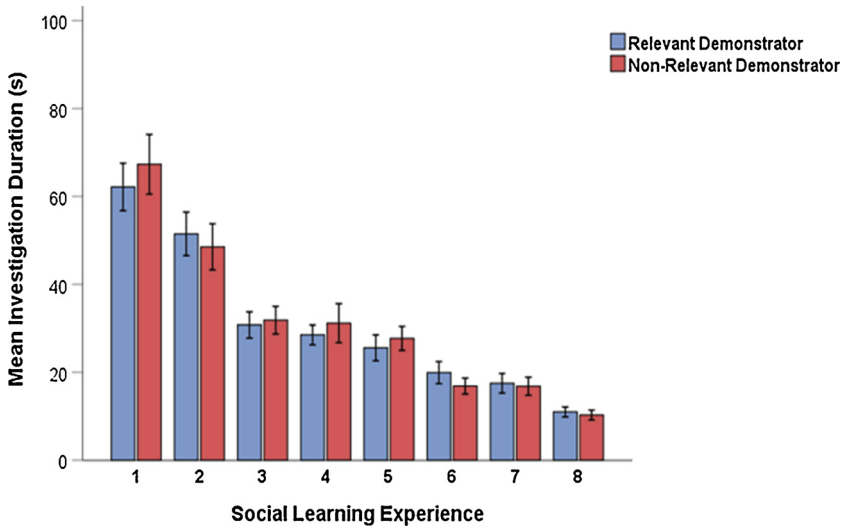

Fig. 8. Investigation duration of demonstrators (relevant, non-relevant) during the social learning experiences for the combined analysis (N = 41 observer mice). Error bars represent ± 1 SE.

associated with the non-relevant demonstrator). The observers could therefore have responded to the two demonstrators as a single compound stimulus. An alternate design would be to present the demonstrators and novel foods sequentially, in separate trials, such that relevant demonstrators are always followed by same-odour novel foods, while non-relevant demonstrators are always followed by no food. This might better allow observer mice to associate dietary olfactory cues on the breath of demonstrators with demonstrator identity and the subsequent presence or absence of food. If methods like these also fail to induce social preferences or aversions, then that would be a more convincing rejection of the hypothesis. Thus, we would urge replication of our study and with alternate methods, before drawing firm final conclusions about how social learning does or does not shape social preferences.

Turning to social learning itself, our hypothesis also predicted that observers would preferentially learn from their relevant demonstrators, such that the STFP effect on observers' novel flavour preferences would be stronger from relevant and weaker (or even absent) from non-relevant demonstrators. This was because even though both demonstrators had previously provided opportunities for social learning during the eight SLEs, only the relevant demonstrators' information could actually be used by the observers. Despite this, in the final STFP trial, when given a choice to now utilize information from both demonstrators, the observers did not appear to respond to them differently, seeming to learn equally from both, thus suggesting that they neither relied more heavily on information from the relevant demonstrators nor discounted information from the non-relevant.

This finding suggests that observer mice do not learn differently from demonstrators who vary in whether they consistently provide information predicting a reward. It also adds to suggestions that adaptive model-based Social Learning Strategies are not followed in the STFP of laboratory rodents (see review by Galef, 2009, and the most recent test of this idea in rats by Agee and Monfils, 2018). Although our Introduction gave examples supporting this idea, all these results are open to alternative explanations. Thus the apparent ineffectiveness of stereotypic demonstrators (Harper et al., 2015) was only a statistical trend, could not be replicated by a subsequent study (Pond, Ervin, Choleris, Walker, & Mason unpublished data) and therefore may not be a true effect; while the mouse pups were judged less efficient demonstrators, not because they did not induce STFP, but because the preferences they induced did not last as long as those from adults (Choleris et al., 1997): in terms of immediate STFP, they were actually as effective as adults. Turning to the three studies in which sick conspecifics failed to be effective demonstrators in the STFP, one (Kuan and Colwill, 1997) used male rats, finding an effect that could not be replicated in females (Galef and Whiskin (2000), as if perhaps sex-specific; while the other (Hishimura, 2000) could instead be explained by observers experiencing the post-ingestion consequences of a sick demonstrators' food prior to social interaction. There is far *more* evidence that observers are rather indiscriminate about demonstrators in the STFP. For instance, as well as the many sickness examples given in the Introduction, observer rats will copy juveniles just as readily as older demonstrators (Galef et al., 1984; Galef and Whiskin, 1998, 2004; and see also Choleris et al., 1997 on mice). Likewise, indicators of foraging success such as the size (Galef et al., 1999) or nutritive quality of the food source being exploited (Galef et al., 1999) do not affect the STFP in rats. Overall, it appears that adaptive model-based Social Learning Strategies have not been selected for in the STFP, at least in laboratory mice and rats.

Why not, in terms of both evolutionary function and underlying mechanism, should be addressed in future Social Learning Strategy research: to date, the STFP has largely been overlooked by these theorists (cf. Kendal et al., 2018). Future studies should also consider increasing the cost of information acquisition and misinformation to both make observers more discriminating (as hypothesized by Koops, 2004) and better approximate the conditions wild animals are likely to experience. Furthermore, more empirical studies on adaptive model-based strategies in the STFP should examine different species with varying social systems (e.g. monogamous gerbils, or the socially-flexible African striped mouse, *Rhabdomys*); while future studies on adaptive model-based strategies in rats and mice should examine different forms of social learning (e.g. observational conditioning or response facilitation).

5. Conclusions

We found no evidence that a history of beneficial social learning experiences influences observers' social preferences for their demonstrators, with relevant demonstrators not coming to be preferred over irrelevant ones. This is a novel hypothesis, however, and should be retested before being rejected after just one study (using methodologies that might better enable observers to learn the differential value of their demonstrators). Furthermore, our findings also did not support the hypothesis that past experiences with a demonstrator who consistently provides relevant, beneficial information directs and enhances female mouse observers' subsequent social learning of food preferences from them. Our results instead add to a growing body of data suggesting that the STFP is typically not modulated by adaptive model-based Social Learning Strategies in laboratory rats and mice. This is a challenge for Social Learning Strategy theories. However, adaptive model-based strategies may still occur in rodents for forms of social learning other than the STFP: an interesting avenue for future work.

Funding

This work was supported by the National Sciences and Engineering Research Council [grant number 400212]. The funding source was not involved in study design; in the collection, analysis and interpretation of data; in the writing of the report; nor in the decision to submit the article for publication.

Declaration of Competing Interest

None.

Acknowledgements

The authors would like to thank our funder, NSERC (grant #400212); the 123 mice who were used in these experiments and the 116 mice used in our pilots; our animal care technicians Michelle Cieplak and Janet Gugan; research assistants who helped run the experiments (Aimee Adcock, Aileen MacLellan, and Basma Nazal); Robert Kitchenham for computer and programing support; and two very helpful anonymous referees.

References

Agee, L.A., Monfils, M.-H., 2018. Effect of demonstrator reliability and recency of last demonstration on acquisition of a socially transmitted food preference. R. Soc. Open Sci. 5, 172391. https://doi.org/10.1098/rsos.172391.

Balcombe, J.P., Barnard, N.D., Sandusky, C., 2004. Laboratory routines cause animal stress. J. Am. Assoc. Lab. Anim. Sci. 43, 42–51.

Bean, N.J., Galef, B.G., Mason, J.R., 1988. The effect of carbon disulfide on food consumption by house mice. J. Wildl. Manage. 52, 502–507. https://doi.org/10.2307/3801599.

Boyd, R., Richerson, P.J., 1985. Culture and the Evolutionary Process. University of Chicago Press, Chicago.

Burne, T.H.J., Johnston, A.N.B., Wilkinson, L.S., Kendrick, K.M., 2009. Effects of anesthetic agents on socially transmitted olfactory memories in mice. Neurobiol. Learn. Mem. 93, 268–274. https://doi.org/10.1016/j.nlm.2009.10.007.

Chaperon, F., Soubrié, P., Puech, A.J., Thiébot, M.-H., 1998. Involvement of central cannabinoid (CB 1) receptors in the establishment of place conditioning in rats. Psychopharmacology (Berl.) 135, 324–332. https://doi.org/10.1007/s002130050518.

Choleris, E., Guo, C., Liu, H., Mainardi, M., Valsecchi, P., 1997. The effect of demonstrator age and number on duration of socially-induced food preferences in house mouse

Mus domesticus. Behav. Processes 41, 69–77. https://doi.org/10.1016/S0376-6357(97)00029-6.
Choleris, E., Ogawa, S., Kavaliers, M., Gustafsson, J.-Å., Korach, K.S., Muglia, L.J., Pfaff, D.W., 2006. Involvement of estrogen receptor α, β and oxytocin in social discrimination: a detailed behavioral analysis with knockout female mice. Genes Brain Behav. 5, 528–539. https://doi.org/10.1111/j.1601-183X.2006.00203.x.
Choleris, E., Clipperton-Allen, A.E., Gray, D.G., Diaz-Gonzalez, S., Welsman, R.G., 2011. Differential effects of dopamine receptor D1-type and D2-type antagonists and phase of the estrous cycle on social learning of food preferences, feeding, and social interactions in mice. Neuropsychopharmacology 36, 1689–1702. https://doi.org/10.1038/npp.2011.50.
Clipperton, A.E., Spinato, J.M., Chernets, C., Pfaff, D.W., Choleris, E., 2008. Differential effects of estrogen receptor alpha and beta specific agonists on social learning of food preferences in female mice. Neuropsychopharmacology 33, 2362–2375. https://doi.org/10.1038/sj.npp.1301625.
Coelho, C.G., Falótico, T., Izar, P., Mannu, M., Resende, B.D., Siqueira, J.O., Ottoni, E.B., 2015. Social learning strategies for nut-cracking by tufted capuchin monkeys (Sapajus spp.). Anim. Cogn. 18, 911–919. https://doi.org/10.1007/s10071-015-0861-5.
Coria-Avila, G.A., 2012. The role of conditioning on heterosexual and homosexual partner preferences in rats. Socioaffect. Neurosci. Psychol 2. https://doi.org/10.3402/snp.v2i0.17340.
Coria-Avila, G.A., Ouimet, A.J., Pacheco, P., Manzo, J., Pfaus, J.G., 2005. Olfactory conditioned partner preference in the female rat. Behav. Neurosci. 119, 716–725. https://doi.org/10.1037/0735-7044.119.3.716.
Coussi-Korbel, S., Fragaszy, D.M., 1995. On the relation between social dynamics and social learning. Anim. Behav. 50, 1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8.
Crusio, W.E., 2001. Genetic dissection of mouse exploratory behaviour. Behav. Brain Res. 125, 127–132. https://doi.org/10.1016/S0166-4328(01)00280-7.
De Houwer, J., 2011. Evaluative conditioning: a review of functional knowledge and mental process theories. In: Reilly, T.R., Schachtman, S.S. (Eds.), Associative Learning and Conditioning Theory: Human and Non-Human Applications. Oxford Scholarship Online Associative. https://doi.org/10.1093/acprof.
Dhand, N.K., Khatkar, M.S., 2014. Statulator: an Online Statistical Calculator. Sample Size Calculator for Comparing Two Paired Means (Accessed 28 April 2019). http://statulator.com/SampleSize/ss2PM.html.
Dugatkin, L.A., Sih, A., 1995. Essay on contemporary issues in ethology behavioral ecology and the study of partner choice. Ethology 99, 265–277. https://doi.org/10.1111/j.1439-0310.1995.tb00901.x.
Ervin, K.S.J., Mulvale, E., Gallagher, N., Roussel, V., Choleris, E., 2015. Activation of the G protein-coupled estrogen receptor, but not estrogen receptor α or β, rapidly enhances social learning. Psychoneuroendocrinology 58, 51–66. https://doi.org/10.1016/j.psyneuen.2015.04.002.
Forestier, T., Féron, C., Gouat, P., 2018. Transmission of food preference between unfamiliar house mice (Mus musculus domesticus) is dependent on social context. J. Comp. Psychol. 132, 268–279. https://doi.org/10.1037/com0000101.
Galef, B.G., 1983. Utilization by norway rats (R. norvegicus) of multiple messages concerning distant foods. J. Comp. Psychol. 97, 364–371. https://doi.org/10.1037/0735-7036.97.4.364.
Galef, B.G., 1996. Social enhancement of food preferences in norway rats: a brief review. In: Heyes, C.M., Galef, B.G.J. (Eds.), Social Learning and Imitation: The Roots of Culture. Academic Press, New York, New York, pp. 49–64. https://doi.org/10.1016/B978-012273965-1/50004-2.
Galef, B.G., 2009. Strategies for social learning: testing predictions from formal theory. Advances in the Study of Behavior. Elsevier Inc., pp. 117–151. https://doi.org/10.1016/S0065-3454(09)39004-X.
Galef, B.G., Whiskin, E.E., 1998. Determinants of the longevity of socially learned food preferences of Norway rats. Anim. Behav. 55, 967–975.
Galef, B.G., Whiskin, E.E., 2000. Demonstration of a socially transmitted flavor aversion in rats? Kuan and Colwill (1997) revisited. Psychon. Bull. Rev. 7, 631–635. https://doi.org/10.3758/BF03213000.
Galef, B.G., Whiskin, E.E., 2004. Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. Anim. Behav. 68, 897–902. https://doi.org/10.1016/j.anbehav.2003.10.029.
Galef, B.G., Whiskin, E.E., 2008. Effectiveness of familiar kin and unfamiliar nonkin demonstrator rats in altering food choices of their observers. Anim. Behav. 76, 1381–1388. https://doi.org/10.1016/j.anbehav.2008.07.004.
Galef, B.G., Wigmore, S.W., 1983. Transfer of information concerning distant foods: a laboratory investigation of the "information-centre" hypothesis. Anim. Behav. 31, 748–758. https://doi.org/10.1016/S0003-3472(83)80232-2.
Galef, B.G., Wigmore, S.W., Kennett, D.J., 1983. A failure to find socially mediated taste aversion learning in norway rats (R. norveticus). J. Comp. Psychol. 97, 358–363. https://doi.org/10.1037/0735-7036.97.4.358.
Galef, B.G., Kennett, D.J., Wigmore, S.W., 1984. Transfer of information concerning distant foods in rats: a robust phenomenon. Anim. Learn. Behav. 12, 292–296. https://doi.org/10.3758/BF03199970.
Galef, B.G., Mason, J.R., Preti, G., Bean, N.J., 1988. Carbon disulfide: a semiochemical mediating socially-induced diet choice in rats. Physiol. Behav. 42, 119–124. https://doi.org/10.1016/0031-9384(88)90285-5.
Galef, B.G., Attenborough, K.S., Whiskin, E.E., 1990a. Responses of observer rats (Rattus norvegicus) to complex, diet-related signals emitted by demonstrator rats. J. Comp. Psychol. 104, 11–19. https://doi.org/10.1037/0735-7036.104.1.11.
Galef, B.G., McQuoid, L.M., Whiskin, E.E., 1990b. Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. Anim. Learn. Behav. 18, 199–205. https://doi.org/10.3758/BF03205259.
Galef, B.G., Rudolf, B., Whiskin, E.E., 1998. Familiarity and relatedness: effects on social learning about foods by Norway rats and Mongolian gerbils. Anim. Learn. Behav. 26, 448–454.
Galef, B.G., Whiskin, E.E., Horn, C.S., 1999. What observer rats don't learn about foods from demonstrator rats. Anim. Learn. Behav. 27, 316–322. https://doi.org/10.3758/BF03199730.
Giraldeau, A., 1984. Group foraging: the skill pool effect and frequency-dependent learning. Am. Nat. 124, 72–79. https://doi.org/10.1086/284252.
Giraldeau, L.A., Valone, T.J., Templeton, J.J., 2002. Potential disadvantages of using socially acquired information. Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci. 357, 1559–1566. https://doi.org/10.1098/rstb.2002.1065.
Harper, L., Choleris, E., Ervin, K., Fureix, C., Reynolds, K., Walker, M., Mason, G., 2015. Stereotypic mice are aggressed by their cage-mates, and tend to be poor demonstrators in social learning tasks. Anim. Welf. 24, 463–473. https://doi.org/10.7120/09627286.24.4.463.
Harrison, N., Lopes, P.C., Konig, B., 2016. Oxytocin and social preference in female house mice (Mus musculus domesticus). Ethology 122, 571–581. https://doi.org/10.1111/eth.12505.
Harten, L., Matalon, Y., Galli, N., Navon, H., Dor, R., Yovel, Y., 2018. Persistent producer-scrounger relationships in bats. Sci. Adv. 4, e1603293. https://doi.org/10.1126/sciadv.1603293.
Herrera, V.L.M., Decano, J.L., Bagamasbad, P., Kufahl, T., Steffen, M., Ruiz-Opazo, N., 2008. Sex-specific hippocampus-dependent cognitive deficits and increased neuronal autophagy in DEspR haploinsufficiency in mice. Physiol. Genomics 35, 316–329. https://doi.org/10.1152/physiolgenomics.00044.2008.
Heyes, C.M., 1994. Social learning in animals: categories and mechanisms. Biol. Rev. 69, 207–231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x.
Heyes, C.M., 2016. Who knows? Metacognitive social learning strategies. Trends Cogn. Sci. 20, 204–213. https://doi.org/10.1016/j.tics.2015.12.007.
Heyes, C.M., Pearce, J.M., 2015. Not-so-social learning strategies. Dokl. Biol. Sci. 282. https://doi.org/10.1098/rspb.2014.1709.
Hishimura, Y., 2000. Enhancement of food aversion by exposure to a poisoned conspecific in Norway rats (Rattus norvegicus). Psychol. Res. 42, 183–187. https://doi.org/10.1111/1468-5884.00144.
Holmes, W.G., 1988. Kinship and the development of social preferences. In: In: Blass, E. (Ed.), The Handbook of Behavioral Neurobiology 9. Plenum, New York, New York, pp. 389–414.
Hoppitt, W., Laland, K.N., 2008. Social processes influencing learning in animals: a review of the evidence. Advances in the Study of Behavior. Academic Press, New York, New York, pp. 105–165. https://doi.org/10.1016/S0065-3454(08)00003-X.
Howard, A., Mainali, K., Fagan, W.F., Visalberghi, E., Izar, P., Jones, C., Fragaszy, D., 2018. Foraging and inter-individual distances of bearded capuchin monkeys. Am. J. Primatol. 80, 1–11. https://doi.org/10.1002/ajp.22900.
Kareem, A.M., 1983. Effect of increasing periods of familiarity on social interactions between male sibling mice. Anim. Behav. 31, 919–926. https://doi.org/10.1016/S0003-3472(83)80247-4.
Kendal, R.L., Coolen, I., Van Bergen, Y., Laland, K.N., 2005. Trade-offs in the adaptive use of social and asocial learning. Adv. Study Behav. 35, 333–379. https://doi.org/10.1016/S0065-3454(05)35008-X.
Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J., Hoppitt, W., 2015. Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. Evol. Hum. Behav. 36, 65–72. https://doi.org/10.1016/j.evolhumbehav.2014.09.002.
Kendal, R.L., Boogert, N.J., Rendell, L., Laland, K.N., Webster, M., Jones, P.L., 2018. Social learning strategies: bridge-building between fields. Trends Cogn. Sci. 22, 651–665. https://doi.org/10.1016/j.tics.2018.04.003.
Kent, K., Arientyl, V., Khachatryan, M.M., Wood, R.I., Wood, R.I., 2013. Oxytocin induces a conditioned social preference in female mice. J. Neuroendocrinol. 25, 803–810. https://doi.org/10.1111/jne.12075.
Kent, K., Butler, K., Wood, R.I., 2014. Ethanol induces conditioned social preference in male mice. Alcohol. Clin. Exp. Res. 38, 1184–1192. https://doi.org/10.1111/acer.12342.
Koops, M.A., 2004. Reliability and the value of information. Anim. Behav. 67, 103–111. https://doi.org/10.1016/j.anbehav.2003.02.008.
Kosaki, Y., Watanabe, S., 2016. Conditioned social preference, but not place preference, produced by intranasal oxytocin in female mice. Behav. Neurosci. 130, 182–195. https://doi.org/10.1037/bne0000139.
Kuan, L.-A., Colwill, R.M., 1997. Demonstration of a socially transmitted taste aversion in the rat. Psychon. Bull. Rev. 4, 374–377. https://doi.org/10.3758/BF03210795.
Lachlan, R.F., Crooks, L., Laland, K.N., 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. Anim. Behav. 56, 181–190. https://doi.org/10.1006/anbe.1998.0760.
Laland, K.N., 2004. Social learning strategies. Learn. Behav. 32, 4–14.
Lister, R.G., Hilakivi, L.A., 1988. The effects of novelty, isolation, light and ethanol on the social behavior of mice. Psychopharmacology (Berl.) 96, 181–187.
Maes, J.H.R., Vossen, J.M.H., 1993. Context conditioning: positive reinforcing effects of various food-related stimuli. Physiol. Behav. 53, 1227–1229. https://doi.org/10.1016/0031-9384(93)90385-S.
Mesoudi, A., 2008. An experimental simulation of the "copy-successful-individuals" cultural learning strategy: adaptive landscapes, producer–scrounger dynamics, and informational access costs. Evol. Hum. Behav. 29, 350–363. https://doi.org/10.1016/j.evolhumbehav.2008.04.005.
Nagy, Z.M., 1965. Effect of early environment upon later social preference in two species of mice. J. Comp. Psychol. 60, 98–101. https://doi.org/10.1037/h0022317.
Nicol, C.J., 1995. The social transmission of information and behaviour. Appl. Anim. Behav. Sci. 44, 79–98. https://doi.org/10.1016/0168-1591(95)00607-T.

Nicol, A.U., Sanchez-Andrade, G., Collado, P., Segonds-Pichon, A., Kendrick, K.M., 2014. Olfactory bulb encoding during learning under anesthesia. Front. Behav. Neurosci. 8, 193. https://doi.org/10.3389/fnbeh.2014.00193.

Ottoni, E.B., Briseida, ·, De Resende, D., Izar, P., 2005. Watching the best nutcrackers: what capuchin monkeys (Cebus apella) know about others' tool-using skills. Anim. Cogn. 24, 215–219. https://doi.org/10.1007/s10071-004-0245-8.

Perks, S.M., Clifton, P.G., 1997. Reinforcer revaluation and conditioned place preference. Psychol. Behav. 61, 1–5. https://doi.org/10.1016/S0031-9384(96)00243-0.

Phan, A., Lancaster, K.E., Armstrong, J.N., MacLusky, N.J., Choleris, E., 2011. Rapid effects of estrogen receptor and selective agonists on learning and dendritic spines in female mice. Endocrinology 152, 1492–1502. https://doi.org/10.1210/en.2010-1273.

Phan, A., Gabor, C.S., Favaro, K.J., Kaschack, S., Armstrong, J.N., MacLusky, N.J., Choleris, E., 2012. Low doses of 17β-estradiol rapidly improve learning and increase hippocampal dendritic spines. Neuropsychopharmacology 37, 2299–2309. https://doi.org/10.1038/npp.2012.82.

Seyfarth, R.M., Cheney, D.L., 2012. The evolutionary origins of friendship. Annu. Rev. Psychol. 63, 153–178. https://doi.org/10.1146/annurev-psych-120710-100337.

Strupp, B.J., Bunsey, M., Bertsche, B., Levitsky, D.A., Kesler, M., 1990. Enhancement and impairment of memory retrieval by a vasopressin metabolite: an interaction with the accessibility of the memory. Behav. Neurosci. 104, 268–276. https://doi.org/10.1037/0735-7044.104.2.268.

Tan, A.W.Y., Hemelrijk, C.K., Malaivijitnond, S., Gumert, M.D., 2018. Young macaques (Macaca fascicularis) preferentially bias attention towards closer, older, and better tool users. Anim. Cogn. 21, 551–563. https://doi.org/10.1007/s10071-018-1188-9.

Tecamachaltzi-Silvaran, M.B., Barradas-Moctezuma, M., Herrera-Covarrubias, D., Carrillo, P., Corona-Morales, A.A., Perez, C.A., García, L.I., Manzo, J., Coria-Avila, G.A., 2017. Olfactory conditioned same-sex partner preference in female rats: role of ovarian hormones. Horm. Behav. 96, 13–20. https://doi.org/10.1016/j.yhbeh.2017.08.006.

Terranova, M.L., Laviola, G., Alleva, E., 1963. Ontogeny of amicable social behavior in the mouse: gender differences and ongoing isolation outcomes. Dev. Psychobiol. 26, 267–481. https://doi.org/10.1002/dev.420260805.

Terranova, M.L., Loggi, G., Chiarotti, F., Laviola, G., 2000. Attractivity and social preferences in mice (Mus musculus domesticus): the role of prepubertal sexual segregation and of precocious weaning. J. Comp. Psychol. 114, 325–334. https://doi.org/10.1037//0735-7036.114.4.32S.

Vale-Martõ Ânez, A., Baxter, M.G., Eichenbaum, H., 2002. Selective lesions of basal forebrain cholinergic neurons produce anterograde and retrograde deficits in a social transmission of food preference task in rats. Eur. J. Neurosci. 16, 983–998. https://doi.org/10.1046/j.1460-9568.2002.02153.x.

Valone, T.J., 1989. Group foraging, public information, and patch estimation. Nord. Soc. Oikos 56, 357–363. https://doi.org/10.2307/3565621.

Valsecchi, P., Galef, B.G., 1989. Social influences on the food preferences of house mice (Mus musculus). Int. J. Comp. Psychol. 2, 245–256.

Valsecchi, P., Choleris, E., Moles, A., Guo, C., Mainardi, M., 1996. Kinship and familiarity as factors affecting social transfer of food preferences in adult Mongolian gerbils (Meriones unguiculatus). J. Comp. Psychol. 110, 243–251. https://doi.org/10.1037/0735-7036.110.3.243.

van de Waal, E., Renevey, N., Favre, C.M., Bshary, R., 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proceedings: Biological Sciences 277 (1691), 2105–2111. https://doi.org/10.1098/rspb.2009.2260.

Ward, P., Zahavi, A., 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. Ibis (Lond. 1859) 115, 517–534. https://doi.org/10.1111/j.1474-919X.1973.tb01990.x.

Weidt, A., Hoffman, S.E., Konig, B., 2008. Not only mate choice matters: fitness consequences of social partner choice in female house mice. Anim. Behav. 75, 801–808. https://doi.org/10.1016/j.anbehav.2007.06.017.

Weidt, A., Lindholm, A.K., König, B., 2014. Communal nursing in wild house mice is not a by-product of group living: females choose. Naturwissenschaften 101, 73–76. https://doi.org/10.1007/s00114-013-1130-6.

Wood, R.I., Knoll, A.T., Levitt, P., 2015. Social housing conditions and oxytocin and vasopressin receptors contribute to ethanol conditioned social preference in female mice. Physiol. Behav. 151, 469–477. https://doi.org/10.1016/j.physbeh.2015.08.018.