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Effectiveness of familiar kin and unfamiliar nonkin demonstrator rats in altering food choices of their observers

BENNETT G. GALEF & ELAINE E. WHISKIN
Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton

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In a series of three experiments, we examined the prediction from formal theories of the evolution of social learning that, all else being equal, animals should be more likely to learn socially from familiar individuals or kin than from unfamiliar individuals or nonkin. In all three experiments, contrary to prediction, naïve Norway rats, *Rattus norvegicus*, were marginally more likely to learn to prefer a food eaten by an unfamiliar than by a familiar conspecific demonstrator. The finding that, when given a choice, naïve rats spent more time near unfamiliar than near familiar demonstrators offers a possible explanation for the observed greater influence of the former compared to the latter on the food choices of their observers.

Keywords: familiarity; food choice; kinship; Norway rat; *Rattus norvegicus*; social learning

Although copying the behaviour of others has the potential to reduce costs associated with individual trial-and-error learning, such copying does not invariably enhance fitness. Only when social learning has a greater positive effect on fitness than individual trial-and-error learning is learning from the behaviour of others a superior strategy (Boyd & Richerson 1985, 1995; Rogers 1988; Giraldeau et al. 2002; Laland 2004; Kendal et al. 2005).

Mathematical analyses of the evolution of social learning indicate that both the circumstances under which an individual copies the behaviour of others and the characteristics of the individuals chosen as models can affect the fitness value of engaging in social rather than individual learning (for reviews see Laland 2004; Kendal et al. 2005). We investigated two predictions from formal models of the evolution of social learning as to the type of individual one should copy, predictions that Laland (2004, page 5) has labelled 'copy kin' and 'copy friends'.

In moderately variable environments, copying either kin or friends should prove a superior strategy to copying unrelated or unfamiliar individuals for several reasons (see Laland 2004 for review). For example, because kin or friends are more likely than nonkin or strangers to share, respectively, genes or environments with a focal individual, kin or friends are more likely to engage in behaviours that, if copied, would increase a focal individual's fitness.

For several decades, our laboratory has been engaged in studies of the role of social learning in the development of food preferences of Norway rats, *Rattus norvegicus*. In our basic experiment (e.g. Galef & Wigmore 1983), we first fed a 'demonstrator' rat one of two foods, both of which were unfamiliar to a rat that served as its 'observer'. We then allowed the demonstrator and the observer to interact in a location other than that where the demonstrator ate before offering the observer a choice between two unfamiliar foods, one of which was the food that its demonstrator had previously eaten (Galef 2002). We have found repeatedly that observer rats show an enhanced preference for the diet that their respective demonstrators ate (for review see Galef 1996).

Such social influence on rats' food preferences has been used previously in our laboratory to explore the effects of several variables that formal theory predicts should influence either the extent to which animals should rely on socially acquired information when making decisions (e.g. environmental predictability, Galef & Whiskin 2004, and the cost and success of individual learning, Galef & Whiskin 2006, 2008) or from whom they should learn socially (e.g. the age of a demonstrator relative to its observer, Galef et al. 1984, Galef & Whiskin 2004, and the relative success of a potential demonstrator, Galef et al. 1983, 1991). Results of such investigations have sometimes

Correspondence: B. G. Galef, Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, Ontario, Canada L8S 4K1 (email: galef@mcmaster.ca).

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provided evidence consistent with theoretical predictions, and sometimes not (see Galef 2006 for preliminary review). Here, we examined effects of both familiarity and kinship on the influence of demonstrator rats on observers' food choices.

Each of the first two experiments reported below consists of two studies, with each study providing a different way of comparing the effectiveness of familiar and unfamiliar demonstrators in altering their observers' food choices. In the first study in each of experiments 1 and 2, we first allowed some observers to interact with a familiar demonstrator and other observers to interact with an unfamiliar demonstrator and then compared the effects of interacting with familiar and unfamiliar demonstrators on the observers' subsequent preferences for the foods that their respective demonstrators had eaten. In the second study in each of experiments 1 and 2, we allowed observers to choose between two foods after interacting simultaneously with two demonstrators, one familiar and one unfamiliar, each fed one of the two foods between which the observer subsequently chose.

Although the need to restrict exposure of observers to diets fed to their demonstrators before the observers interacted with them complicated our procedures, the basic experimental design was straightforward: in study 1 of experiments 1 and 2 an observer rat interacted with either a familiar or an unfamiliar conspecific demonstrator and then chose between two diets, one of which was the diet its demonstrator had eaten, or, in study 2 of experiments 1 and 2 and in experiment 3, an observer rat interacted simultaneously with both a familiar and an unfamiliar conspecific demonstrator and then chose between two diets, the diet that its familiar demonstrator had eaten and the diet that its unfamiliar demonstrator had eaten.

EXPERIMENT 1: FAMILIAR KIN VERSUS UNFAMILIAR NONKIN

In an important paper on the relationship between social dynamics and social learning, Coussi-Korbel & Fragaszy (1995) described potential effects of the identity and characteristics of interacting individuals on the probability that social learning would occur. As Coussi-Korbel & Fragaszy (1995) indicate, field studies of social learning frequently reveal that individuals are more likely to adopt the behaviour of kin than that of nonkin. Although such bias in social learning may simply reflect a tendency of the young of innumerable species to spend more time interacting with kin than with nonkin, theoretical analyses suggest that a bias towards copying the behaviour of either familiar individuals or kin might have been favoured by selection. Such bias might evolve because: (1) social learning is useful only when models and their copiers are exposed to similar environments and experience similar outcomes as a result of engaging in similar behaviours and (2) kin and familiar individuals are more likely to share environments and experience similar outcomes as a result of similar actions than are nonkin or unfamiliar individuals (Boyd & Richerson 1985, 1988; Laland 2004).

Previous experiments in our laboratory have shown that the food choices of observer rats can be influenced by interaction with unfamiliar demonstrators and unrelated demonstrators as well as with familiar demonstrators or related demonstrators (Galef & Wigmore 1983; Galef et al. 1984, 1998). Here, we compared directly the relative effectiveness on observer rats' food choices of demonstrators that were either familiar kin or unfamiliar nonkin.

Methods (Study 1: Single Demonstrators)

Subjects

Fifty-one female rat pups born to eight female Long-Evans rats purchased late in gestation from Charles River Canada (St. Constant, Quebec, Canada) served as subjects when 8 to 9 weeks of age. We randomly assigned three members of each litter to serve in the experiment as: (1) a demonstrator, (2) a familiar kin observer or (3) an unfamiliar nonkin observer. When we weaned the pups at 21–24 days of age, we marked each pup's tail with coloured ink to indicate its future role in the experiment and placed a trio of littermates (one demonstrator, one familiar kin observer and one unfamiliar nonkin observer) together in one of 17 shoebox cages, measuring $46 \times 25 \times 22$ cm, and provided them with ad libitum access to food (pellets of Teklad Laboratory Rodent Diet 8640; diet 8640). We kept all subjects from arrival in the laboratory to completion of the experiment in a temperature- and humidity-controlled colony room illuminated for 12 h/day. After completion of the experiment the subjects served in other studies of social learning before being euthanized by exposure to CO_2.

Apparatus

Experiments took place in stainless-steel hanging cages, measuring $20 \times 20 \times 34$ cm, with grid floors that permitted easy monitoring of spillage by inspection of the trays beneath the cages (no spillage was ever detected). We presented food to all subjects, while they were in the hanging cages, in semicircular food dishes, 10 cm in diameter and 5 cm deep, which we filled to a depth of 2.5 cm or less to prevent spillage. While in the shoebox cages, subjects fed from 8-cm-diameter Pyrex bowls, 4 cm deep.

Diets

We composed two diets by mixing either 10 g of McCormick's pure ground cinnamon (diet cin) with 990 g of powdered Teklad Laboratory Rodent Diet 8640 or 20 g of Hershey's cocoa (diet coc) with 980 g of diet 8640.

Procedure

Before starting the experiment proper, we left subjects undisturbed for 6 days in trios in shoebox cages to become familiar with their cagemates. At the end of the 6 days of familiarization, we removed all food from the shoebox cages and placed all subjects on a feeding schedule, eating powdered diet 8640 for 1 h/day. We fed the member of each trio designated as a demonstrator in a hanging cage before returning them to their respective home cages. Whilst trio members designated as demonstrators were eating in hanging cages, we fed the two members of