

Are socially acquired behaviours irreversible?

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Abstract

Norway rat subjects were exposed for either 3 or 10 days to conspecific demonstrators eating a cinnamon-flavoured, protein-deficient diet. While in contact with their demonstrators, and for several days thereafter, subjects were offered a choice between the cinnamon-flavoured, protein-deficient diet that their demonstrators were eating and a less palatable, nutmeg-flavoured, protein-rich diet. While subjects were in contact with their respective demonstrators they ate little protein-rich diet; during the 7 days immediately following removal of demonstrators from the experiment, subjects learned to eat sufficient amounts of protein-rich diet to permit normal growth. The results indicate that effects of social influence on food choice are transitory. They suggest that the time scale on which animals learn individually to modify socially acquired behaviour is considerably shorter than usually considered in discussions of quantitative models of the evolution of social learning processes.

Keywords: Food preference; Social learning; Duration

1. Introduction

It is sometimes assumed in formal models of the diffusion of socially learned behaviours through animal populations that culturally transmitted traits, like their genetically transmitted analogues, are irreversible (Rogers, 1988; see also Dawkins, 1976). In discussion of other models in which socially learned behaviours can be altered by individual experience of the consequences of their expression, the time scale over which such adaptive modification of socially learned behaviour occurs is usually treated as though it took years or generations rather than days or weeks (Boyd and Richerson, 1988; Laland et al., 1993).

Models such as Rogers (1988) in which it is assumed that socially learned behaviours are immutable lead to the counter-intuitive prediction that animals in variable environments continue to exhibit socially learned behaviours even when those behaviours become maladaptive following environmental change (Galef, 1995). On the other hand, those models that are discussed assuming that

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environmentally induced alterations in socially learned behaviour are painfully slow may underestimate the ability of animals to track short term changes in their immediate environments.

Relatively few studies of the stability of socially learned behaviours have been described in the literature. Mason et al. (1984) compared the longevity of socially and individually acquired preferences and aversions of blackbirds and found socially learned behaviours no more stable than their individually learned counterparts. Galef (1989), on the other hand, found relatively permanent effects of social learning on flavour preferences of Norway rats. However, neither Mason et al. (1984) nor Galef's (1989) studies are entirely to the point. In both sets of experiments, the items that subjects learned socially either to approach or to avoid and their respective alternatives were of equal value. Consequently, in the experiments of both Galef and Mason et al., socially learned responses were not truly maladaptive; they were simply arbitrary.

Below we describe experiments examining the stability of a socially learned, maladaptive preference for a food lacking sufficient protein to support normal growth.

2. Experiment 1

2.1. *Materials and methods*

Selecting diets for the experiment

The success of the present studies depended critically on the relative palatabilities of the diets that we offered to subjects. If subjects found the protein-rich food more palatable than the protein-poor alternative available to them, there would be a confounding of high palatability and high nutritive value, so it could not be determined whether subjects were eating protein-rich diet because of its nutritive value or its pleasant taste. After some pilot testing we chose to work with two diets: protein-poor, cinnamon-flavored Diet Cin was composed of 50 g casein (Teklad Diets, Madison, WI; Catalogue number 160030), 800 g Protein-Free Basal Mix (Teklad Diets, Catalogue number TD 86146), 100 g corn starch, 50 g granulated sugar and 10 g bulk, ground cinnamon; and protein-rich, nutmeg-flavored Diet Nut, composed of 200 g casein, 800 g Protein-Free Basal Mix and 10 g of bulk, ground nutmeg.

When given a 24-h-long choice between bowls of Diet Cin and Diet Nut, 12 individually housed, 42-day-old female rats (taken from the same source that provided subjects for the experiments described below) took an average (± 1 S.E.M.) of only $16.6 \pm 3.7\%$ of their total intake from the bowl containing protein-rich Diet Nut. We were thus successful in finding two diets, one protein-rich, the other protein-poor, with the latter less palatable than the former.

Subjects

Sixteen 42-day-old, female Long-Evans rats that were born and reared in the vivarium of the McMaster University Psychology Department to breeding stock descended from animals acquired from Charles River Canada (St. Constant, Quebec) served as subjects in Experiment 1. An additional 16 49- to 56-day-old female rats that had served as subjects in other experiments served as demonstrators in the present experiment. We weaned both subjects and demonstrators at 21 days of age and maintained them in sibling groups of three or four on ad lib Purina Rodent Laboratory Chow

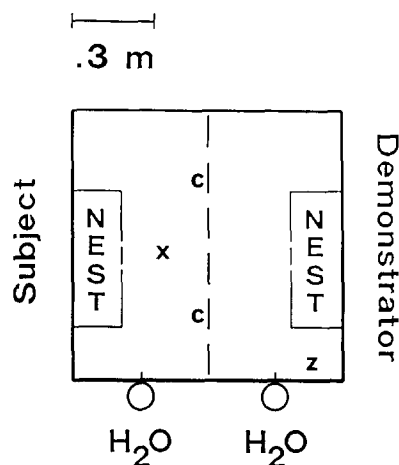


Fig. 1. Overhead schematic of enclosure. x = location of each subject's food-cup at the start of experiments. z = location of each demonstrator's food cup. c = locations of each subject's food cups during the choice phase of the experiment.

5001 and water in a temperature-and humidity-controlled colony room, until they were old enough to participate in experiments.

Apparatus

The experimental enclosure ($1 \times 1 \times 0.3$ m), constructed of hardware cloth and angle iron, with a floor of galvanized sheet metal covered with wood-chip bedding was divided into two compartments of equal size by a barrier of 1/2-in (1.3 cm) mesh hardware cloth (see Fig. 1). Each of the two compartments in an enclosure contained a wooden nest box and water bottle. Food bowls were placed in the enclosure as indicated in Fig. 1.

Procedure

To begin the experiment we introduced each of our 16 subjects individually into one compartment of an enclosure like that illustrated in Fig. 1. Each subject's compartment contained a food bowl filled with powdered Purina Rodent Laboratory Chow 5001, the subjects' familiar maintenance diet, in the position indicated in Fig. 1. At the same time that we introduced subjects into their compartments, we introduced a demonstrator rat into the demonstrator compartment of each enclosure and gave the demonstrator a food cup containing either cinnamon-flavoured, protein-deficient diet (Diet Cin) or nutmeg-flavoured, protein-rich diet (Diet Nut).

After introducing subjects and demonstrators into their respective compartments, we left them undisturbed for three days. We then removed demonstrators and all food cups from enclosures, weighed subjects, and placed two new weighed food cups, one containing Diet Cin and the other Diet Nut, in each subject's compartment in the positions indicated in Fig. 1. Each day, for the next 7 days, we weighed both subjects and food cups.

As can be seen in Fig. 2 and as expected: (a) on the first day of the experiment subjects that had interacted with demonstrators eating protein-rich Diet Nut ate significantly more protein-rich Diet Nut than did subjects that had interacted with demonstrators eating protein-poor Diet Cin ($t(14) = 7.35$, $P < 0.0001$); and (b) on average, during the first 5 days of choice between Diets Cin and Nut, the

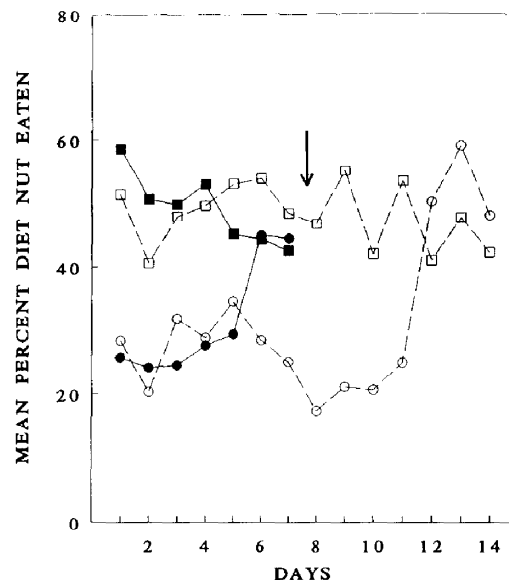


Fig. 2. Mean amount of protein-rich Diet Nut eaten, as a percentage of total amount ingested on successive days. (■) Experiment 1, demonstrators fed Diet Nut; (●) Experiment 1, demonstrators fed Diet Cin; (□) Experiment 2, demonstrators fed Diet Nut; (○) Experiment 2, demonstrators fed Diet Cin. Arrow indicates time of removal of demonstrators in Experiment 2.

eight subjects that had interacted with demonstrators eating Diet Cin gained significantly less weight ($\bar{X} \pm 1$ S.E.M. = 0.4 ± 3.5 g) than did the eight subjects that had interacted with demonstrators eating Diet Nut (10.3 ± 1.1 g; $t(14) = 2.70$, $P < 0.02$).

As can also be seen in Fig. 2, the effects of demonstrators' diets on subjects' food preferences lasted for 4 or 5 days after demonstrators were removed from the experiment (on each of Days 2–4 of the Experiment $t(14) > 2.95$, $P < 0.01$) and was no longer evident on the 6th day of subject testing ($t(14) = 0.1$, NS). Clearly, socially learned food preferences were not irreversible or particularly long lasting. Rather, rats appeared to detect the negative post-ingestive consequences of the socially induced preference for the relatively palatable, protein-poor Diet Cin and modified their behaviour accordingly (Galef, 1995), increasing their relative intake of the relatively unpalatable, protein-rich Diet Nut.

Although subjects never totally abandoned ingestion of the more palatable, protein-poor Diet Cin, they settled on a mixture of Diets Cin and Nut that contained an average 11.5% protein and permitted all 16 subjects to gain weight during the final 24 h of the experiment ($\bar{X} \pm 1$ S.E.M. = 4.1 ± 0.8 g). A 12% protein diet is considered adequate for young rats (Guide to the Care and Use of Experimental Animals, 1980, Canadian Council on Animal Care, Ottawa).

3. Experiment 2

It is possible that the transitory effect of social influence on food preference observed in Experiment 1 resulted from the brief time that we allowed subjects to interact with their respective

demonstrators. In Experiment 2, we allowed demonstrators and subjects to interact for 10 days before we removed demonstrators from the experiment and allowed subjects to choose between Diet Cin and Diet Nut in the absence of further social influence.

3.1. *Materials and methods*

Subjects

Twenty-eight 42-day-old, female Long-Evans rats from the vivarium of the McMaster University Psychology Department served as subjects in Experiment 2. A further 28 49-day-old rats from the same source served as demonstrators.

Apparatus

We used the same apparatus in Experiment 2 that we had used in Experiment 1.

Procedure

In Experiment 2, we used methods identical to those that we had used in Experiment 1 except that in Experiment 2, after we placed food cups containing Diets Cin and Nut in each subject's compartment, we left demonstrators eating either Diet Nut or Diet Cin to interact with their respective subjects for 7 more days.

After 10 days of interaction between subjects and demonstrators, we removed demonstrators and their food cups from enclosures and gave subjects 7 more days to choose between Diets Cin and Nut.

3.2. *Results and discussion*

Once again exposing subjects to demonstrators fed Diet Cin or Diet Nut affected subjects' food preferences. On each of Days 1 to 7 of choice (see Fig. 2), the 14 subjects interacting with demonstrators eating Diet Nut ate significantly more diet Nut than did the 14 subjects interacting with demonstrators eating Diet Cin (all $t(26)s > 2.39$, all P s < 0.02). Further, during the first 7 days of Experiment 2, when subjects were both interacting with demonstrators and choosing between Diets Cin and Nut, those subjects interacting with demonstrators eating Diet Cin gained significantly less weight ($\bar{X} \pm 1$ S.E.M. = 6.1 ± 1.1 g) than did those subjects interacting with demonstrators eating Diet Nut (16.4 ± 2.0 g; $t(26) = 4.51$, $P < 0.001$). However, as in Experiment 1, soon after subjects stopped interacting with their respective demonstrators, they abandoned their socially learned food preferences. In Experiment 2, as in Experiment 1, experience of the negative consequences of the socially learned preference soon reversed the effects of social learning in the absence of continuing social influence. Also as in Experiment 1, although subjects continued to eat both Diet Cin and Diet Nut, by the last day of the experiment subjects had arrived at a mixture of Diets Cin and Nut that would be expected to permit them to gain weight.

4. **General discussion**

In each of two experiments, animals that had been socially induced to ingest substantially more of a relatively palatable, protein-poor diet than of a relatively unpalatable protein-rich diet abandoned

their socially acquired preference as they experienced the negative physiological consequences of ingesting too little protein. In a matter of a few days, subjects learned to ingest a mixture of protein-rich and protein-poor foods that permitted both adequate protein intake and normal growth.

Our results indicate that quantitative models like that of Rogers (1988) incorporating the assumption that social learning is irreversible are not generally applicable. Our results also indicate that, in at least one case, appraisal of the consequences of engaging in a socially acquired behaviour and subsequent modification of that socially acquired behaviour is sufficiently rapid to allow individuals to track short-term changes in the environment.

The ability rapidly to adjust socially learned behaviours in response to day-to-day environmental variation has not been made explicit even in those models of interaction of social and individual learning (Boyd and Richerson, 1988) that do allow individual modification of socially learned behaviour over extended time scales. The present results suggest that the rate of individual modification of social learned behaviours may be considerably faster than discussions of such models generally indicate (Galef, 1995). Indeed, the present results suggest that an appropriate time scale for thinking about the interaction of social and individual learning in animals may be on the order of days or weeks rather than generations.

Acknowledgements

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