Different Mechanisms for Social Transmission of Diet Preference in Rat Pups of Different Ages

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We examined the role of simple exposure to a diet in the development of preference for that diet in rat pups 21, 28, 38, and 45 days of age. We found: (1) that 21-day-old rat pups exhibited a preference for a diet to which they were simply exposed for 30 min; (2) that 28-, 38-, and 45-day-old pups failed to exhibit simple-exposure induced preference for a diet; and (3) that pups at all ages examined, exposed for 30 min to an anesthetized conspecific whose face had been dusted with a diet, subsequently exhibited a preference for that diet. We interpreted these data as indicating that socially-induced diet preference in 21-day-old pups can be explained by effects of simple exposure, while socially-induced diet preference in older rats cannot. Pups older than 21 days of age appear more sensitive to the social context in which diet-identifying olfactory cues are experienced than do 21-day-old pups.

During social interaction between rats, olfactory cues can pass from a recently fed rat (a demonstrator) to a naive conspecific (an observer) influencing the observer's subsequent diet selection. A naive rat that interacts with a demonstrator will, when subsequently given a choice between diets, exhibit a substantially enhanced preference for the diet its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984). Recent data from our laboratory indicate that, in the juvenile (42-day-old) rats we have studied, demonstrator influence on observer diet preference was not the result of simple exposure of naive observers to diet-related cues emitted by demonstrators during interaction of demonstrator and observer. Forty-two-day-old rats exposed for 30 min to an anesthetized demonstrator powdered with a diet subsequently exhibited a preference for that diet; 42-day-old rats exposed for 30 min to a rat-sized piece of

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cotton batting powdered with the same diet did not show a subsequent preference for that diet (Galef, Kennett, & Stein, 1985; Galef & Stein, 1985). We interpreted these findings as suggesting that, in 42-day-old rats, demonstrator influence on observer diet preference depends on observers experiencing diet-identifying odors within an as yet undefined context provided by the presence of a demonstrator, not on simple exposure of observers to diet-identifying cues emitted by demonstrators (Galef, in press; Galef et al., 1985).

It is well established in the literature that rat pups of pre-weanling age show an enhanced preference for odors to which they have been simply exposed (Alberts, 1981; Cornwell-Jones, 1979; Galef, 1981; Galef & Kaner, 1980; Marr & Lilliston, 1969). Further, there is some evidence that older rats fail to exhibit subsequent preference for odors to which they are simply exposed (Cornwell-Jones, 1979; Galef, 1982; Galef & Kaner, 1980). Thus, the literature suggests that young rats respond to simple exposure to an odor with enhanced preference for that odor, while older rats may not do so. Further, Leon, Galef, and Behse (1977) and Bronstein and Crockett (1976) have reported that simple exposure of preweanling rats to an odor in the general environment enhances preference at weaning for diets adulterated with that odor. Neither paper, however, examined the sufficiency of simple exposure to an odor to enhance preference for odor-scented food during the postweanling period.

In the present experiment, we examined the diet selection of rats of various ages that had either been simply exposed to a food odor or exposed to a food odor within the stimulus context provided by the presence of a conspecific demonstrator. We sought to determine the effects of age on sufficiency of the two types of olfactory experience (simple exposure or exposure in the presence of a conspecific) to alter diet preference. It was our expectation that rat pups of preweanling age would be affected in their subsequent food choice by simple exposure to an odorant, while older rats would not.

Method

Subjects

Observers in the main experiment were 156 Long-Evans rat pups born in the McMaster colony to females acquired from Blue Spruce Farms (Altamont, NY). Observers were weaned at 18 days of age, either directly to the experimental apparatus (observers that interacted with demonstrators at 21 days of age) or (all other observers) to 30 × 30 × 15 cm polypropylene cages containing four or five littermates, where they were maintained on ad lib Purina Laboratory Rodent chow and water until initiation of their participation in the experiment. Seventy-eight 56- to 90-day-old Long-Evans rats that had served as observers in previous experiments served as demonstrators in the main experiment.

An additional 48 observers and 24 demonstrators (treated identically to those observers and demonstrators described above) served in a partial replicate of the main experiment.

Apparatus

During most of the experiment, subjects were housed as demonstrator–observer pairs in 47.5 × 24 × 27.5 cm wire-mesh hanging cages (Washmann Co.,

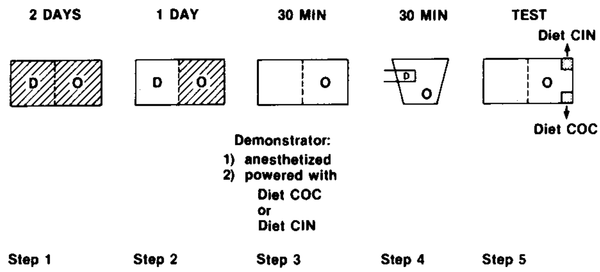

Fig. 1. Schematic diagram of procedure. O = observer, D = demonstrator, hatching indicates presence of Purina Laboratory Rodent chow.

Baltimore, MD). Each hanging cage was divided into two equal parts by a 1.25-cm (½-in.) screen partition (24 × 27.5 cm) attached to the midpoints of each cage's 42.5-cm sides.

During the period of interaction between demonstrator and observer (See Step 4 of Figure 1 and Procedure), observer and demonstrator were placed in an apparatus (illustrated in Figure 2) constructed from a 2.45-L (15.2-cm-high, 19.0-cm-top-diam., 14.0-cm-bottom-diam) cardboard bucket (Lily-Tulip Inc., Toledo, OH) of the type commonly used by fast-food franchises. A circular opening (5-cm diam.) was cut in the bucket wall 12 cm above its floor. Through this hole was inserted, for half its length, a 16-cm-long, 5-cm-diam. tube constructed of .63-cm (½-in.) screen. The end of this tube inside the bucket was closed with a disk of screen; the end outside the bucket was left open. A tight-fitting cardboard lid served to prevent observers from leaving the bucket.

Procedure

Demonstrator Groups. Treatment of subjects interacting with anesthetized demonstrators during Step 4 of the experiment was as follows (see Figure 1):

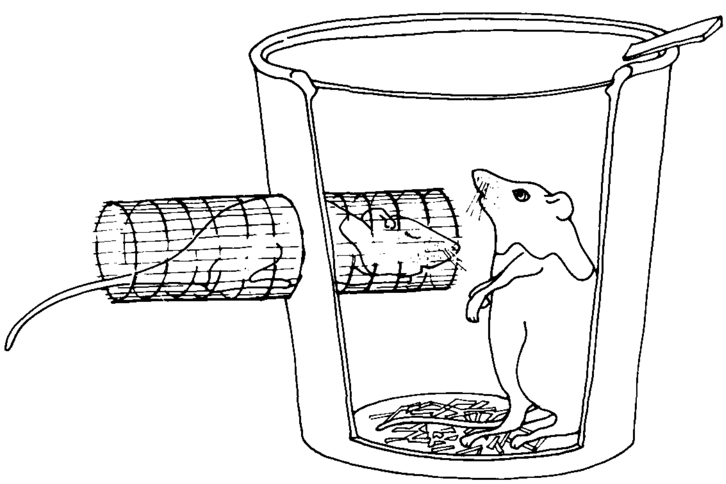

Fig. 2. Apparatus used during interaction of demonstrator and observer (see Step 4 of Figure 1 and Procedure).

(1) Demonstrator and observer were maintained on opposite sides of the screen partition with ad-lib access to Purina Laboratory Rodent chow pellets for a 2-day period of familiarization with both apparatus and cagemate.

(2) Each demonstrator was food-deprived for 24 hr to maximize survival under anesthesia.

(3) Chow was removed from each observer's side of the cage in preparation for testing and each demonstrator was removed to a separate room, anesthetized (intraperitoneal injection of 50 mg/kg sodium-pentobarbital), and its face rolled either in cocoa-flavored diet (powdered Purina Laboratory Rodent chow adulterated with 2% by weight Hershey's cocoa) or in cinnamon-flavored diet (powdered Purina Laboratory Rodent Chow adulterated with 1% by weight McCormick's pure ground cinnamon).

(4) Each demonstrator was then placed in the screen tube of the apparatus illustrated in Figure 2 and its observer was confined in the bucket. Observers were then left free to interact with their respective anesthetized demonstrators for 30 min.

(5) At the end of the 30-min period of demonstrator–observer interaction, demonstrators were removed from the experiment and each observer was returned to its cage and offered for 24 hr, two weighed food cups, one containing cinnamon-flavored diet and one containing cocoa-flavored diet.

Surrogate groups. Observers in Surrogate Groups were treated identically to those in Demonstrator Groups except that during Step 4 of the procedure each observer in Surrogate Groups interacted with a rat-size surrogate demonstrator. This surrogate was constructed of cotton batting stuffed into a piece of seamless tubular gauze (Size 12 Tubegauz, Scholl Canada Inc., Toronto, Ont.) that had been stapled closed at one end. The closed end of the surrogate was rolled in either cinnamon- or cocoa-flavored diet, and the surrogate was introduced into the tubular portion of the apparatus illustrated in Figure 2 with the diet-coated end inside the bucket.

Age of observers. In the main experiment subjects interacted with demonstrator or surrogate when either 21 (n = 48), 28 (n = 36), 38 (n = 36) or 45 (n = 36) days of age. Because, during testing in the main experiment, observers interacting with surrogates at 21 days of age behaved differently from observers in the other three age groups interacting with surrogates, we replicated both Demonstrator (n = 24) and Surrogate (n = 24) Groups at 21 days of age.

Data were discarded from any 21-day-old subject eating less than 2.0 g or older subject eating less than 5.0 g during the 22-hr test period.

Results

The main results of the present experiment are presented in Figure 3, which shows the amount of cocoa-flavored diet eaten, as a percentage of total amount ingested, by 21-, 28-, 38-, and 45-day-old observers interacting with cinnamon- or cocoa-dusted demonstrators or surrogates during Step 4 of the procedure. Also shown in Figure 3 are: (1) the mean total amounts eaten by observers in each condition and age group and (2) the results of statistical tests (Mann-Whitney U tests) of the significance of differences in the percentage of cocoa-flavored diet eaten by observers of various ages interacting with cocoa-diet- or cinnamon-diet-dusted demonstrators or surrogates during Step 4 of the experiment.

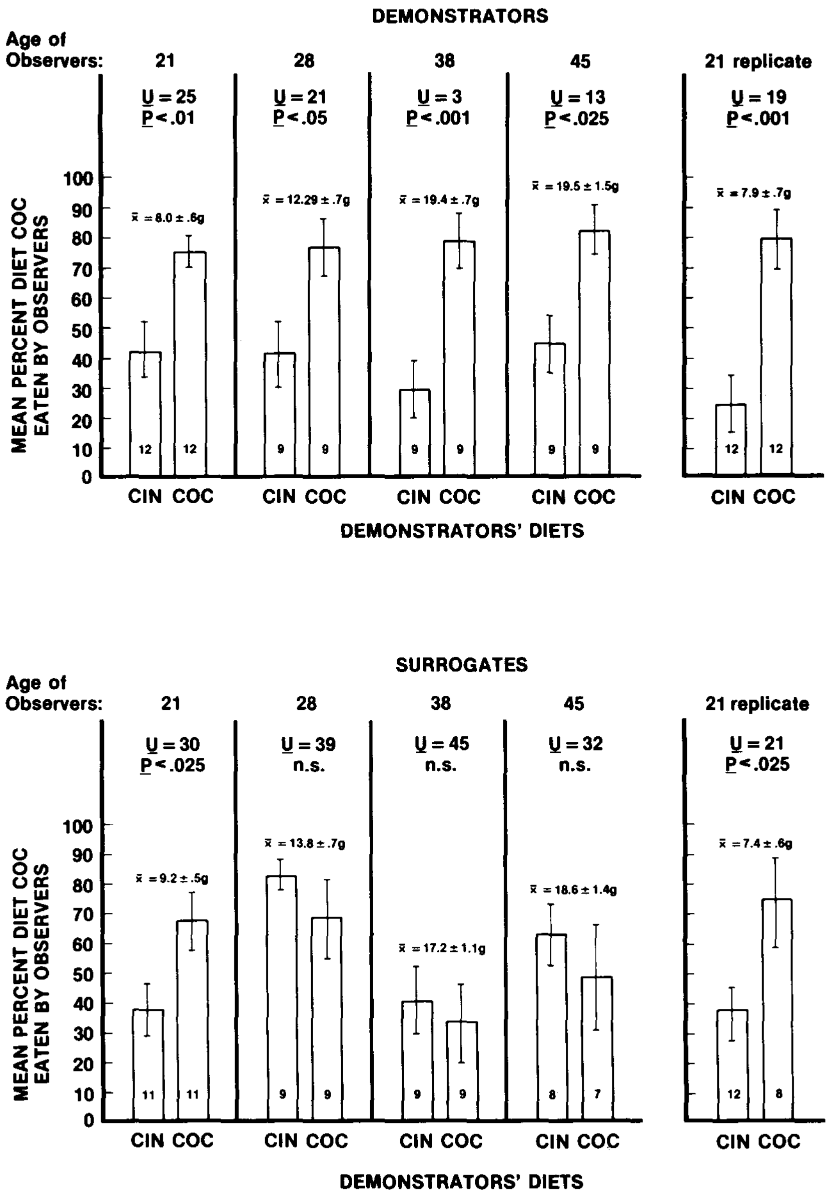

Fig. 3. Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by 21-, 28-, 38-, and 45-day-old observers exposed to either cocoa-flavored or cinnamon-flavored diet. Upper panel: observers exposed to anesthetized, diet-dusted demonstrators. Lower panel: observers exposed to diet-dusted surrogates. The number within each bar indicates the *n* for that group. The mean ± SEM above each pair of bars indicates the mean total amount eaten by subjects in that condition. Cin = cinnamon-flavored diet, Coc = cocoa-flavored diet.

As can be seen in the upper panel of Figure 3, observers of every age interacting with cocoa-diet-dusted demonstrators exhibited a significantly greater preference for cocoa-flavored diet than did observers interacting with cinnamon-diet-dusted demonstrators. Inspection of the lower panel of Figure 3 reveals that although 21-day-old observers interacting with a cocoa-diet-dusted surrogate exhibited a greater preference for cocoa-flavored diet than 21-day-old observers interacting with a cinnamon-diet-dusted surrogate, the flavor of diet placed on surrogates did not affect the diet preference of 28-, 38-, or 45-day-old observers. In sum, although the presence of a diet on a rat demonstrator influenced the subsequent diet preference of observers at all ages examined, the presence of diet on a surrogate influenced the subsequent diet preference only of 21-day-old pups.

One might expect, given that the demonstrators in the present experiment were unconscious and, hence, obviously "unwell," that each observer might have learned an aversion to its demonstrator's diet rather than a preference for it. However, in previous studies, my coworkers and I have found that rats acquire preferences for, rather than aversions to, the diets of demonstrators made ill by LiCl injection (Galef, Wigmore, & Kennett, 1983). Thus the present finding of observer preference for the diet eaten by an "ill" demonstrator are consistent with our earlier results (See Galef, 1985 for further discussion).

Discussion

The results of the present experiment suggest that transmission of diet preference from demonstrators to observers is the result of different behavioral processes in rats 21 days of age and those 28 days of age or older. A brief, simple exposure to diet identifying cues was sufficient to alter diet preference of pups 21 days of age, but not of pups 28, 35, or 45 days of age.

It cannot be inferred that the two different types of odor exposure had identical effects even in 21-day-old pups. It might, for example, be the case that extinction of simple exposure induced preference would be more rapid than extinction of a preference induced by exposure to diet odors in the presence of a conspecific. However, it does seem clear that brief simple exposures are sufficient to account for the diet preference alterations we observed in 21-day-old subjects in contact with demonstrators, while alterations in diet preference observed in older subjects following brief contact with a demonstrator cannot be explained in terms of simple exposure. Taken together with other reports in the literature briefly discussed in the introduction, the results of the present study indicate that preweaning rats may be more responsive to simple exposures to olfactory stimuli than postweaning rats. Conversely, our data indicate that post-weaning rats are more sensitive to the context within which olfactory stimuli are experienced than are their younger fellows.

Although the results of the present experiment may prove specific to olfactants or to rat pups (though not to the use of an ingestive measure of the effects of simple exposure to an olfactant [Galef (1982) and Galef and Kaner (1980) have demonstrated similar effects using a direct measure of olfactory preference]), the more interesting, if untested, possibility is that effects of simple exposure on subsequent behavior are, in general, greater early in life than later in development. There is some evidence consistent with such a view. For example, Baptista and Petrinovich (1984) have recently reported that although white-crowned sparrows less than 50 days of age will learn a song dialect played via a loudspeaker, those greater than 50 days of age will learn that dialect only if it is performed by a live tutor. Baptista and Petrinovich's result is analogous to that described in the present paper in suggesting greater sensitivity in older sparrows to the context in which auditory stimuli are experienced and greater response to simple exposure to auditory stimuli in younger sparrows.

Deficiencies in associative capacities of young animals have been the subject of much attention (See Spear & Campbell, 1979, for reviews). The present result suggests that young animals may compensate for such deficiencies in associative learning by enhanced dependence on stimulus familiarity in the development of their behavioral repertoires.

Notes

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