

Interaction With Demonstrator Rats Changes Observer Rats' Affective Responses to Flavors

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The authors examined whether exposing naive rats (observers) to recently fed conspecific demonstrator rats changed the observers' later affective responses to foods their demonstrators ate. In Experiment 1, observers learned an aversion to a flavored fluid, then interacted with demonstrators that had drunk that fluid. These observers, but not those interacting with demonstrators that had drunk water, increased their intake of the averted fluid and exhibited fewer negative responses when the averted fluid was infused into their mouths. Rats in Experiment 2 entered the arm of a T maze known to lead to banana-flavored pellets more frequently after interacting with demonstrators fed banana-flavored pellets than after interacting with demonstrators fed chow-flavored pellets. Results of both experiments indicated that interaction with demonstrator rats changed observer rats' affective responses to flavors.

In dozens of experiments conducted in our laboratory during the past decade, "observer" rats (*Rattus norvegicus*) interacted with conspecific "demonstrator" rats shortly after the demonstrators had eaten a food unfamiliar to their observers. Each observer then chose between two foods: one the food eaten by its demonstrator and the other a totally unfamiliar food. The results of such experiments are unequivocal; during the choice test, observer rats exhibit substantial enhancement of their relative intake of whatever food their respective demonstrators ate. Such socially induced increase in observers' intake of the diet fed to their respective demonstrators has been found even when the diet demonstrators ate was inherently unpalatable (Galef, 1989) or, more relevant to Experiment 1 of this article, was avoided by observer rats because they had learned an aversion to it as a result of its previous association with a toxin (Galef, 1986; Galef, McQuoid, & Whiskin 1990).

Although effects of demonstrator rats on the food choices of their observers are well established (Galef & Wigmore, 1983), little is known about how interaction with demonstrator rats modifies subsequent diet selection by their observers. We undertook the present series of experiments to examine the possibility that socially induced changes in the food choices of observer rats reflect changes in their

affective responses to flavors experienced in association with demonstrators: In Experiment 1, we used the taste-reactivity test developed by Grill and Norgren (1978) to ask whether effects of demonstrator rats on the food choices of their observers reflected changes in observers' perceptions of the "palatability" of foods (Berridge, 1991; Grill & Berridge, 1985). In Experiment 2, we used methods proposed by Irwin (1958) to determine whether social interaction caused an increase in observers' motivation to seek out foods that their demonstrators ate.

Experiment 1

In Grill and Norgren's (1978) taste-reactivity test, a flavored fluid is introduced directly into the oral cavity of a freely moving rat through a chronic cannula, and the subject's orofacial and general motoric responses to the infusion are videotaped for later frame-by-frame analysis. When flavored solutions that rats prefer to water in a two-bottle preference test (e.g., sugar solutions or dilute sodium-chloride solutions) are infused into rats' mouths, the rats respond with tongue protrusions, lateral tongue protrusions, and paw licking, all considered to be positive responses. On the other hand, when flavors that rats tend to drink less of than water in a two-bottle test are introduced into rats' mouths, they exhibit different responses. Gaping, passive dripping of fluid from the mouth, paw flailing, head shaking, and chin rubbing that are rarely seen in response to infusion of palatable fluids appear. (See Pelchat, Grill, Rozin, and Jacobs [1983] and Grill and Norgren [1978] for more detailed descriptions of responses to infusions of flavored solutions.) These negative responses become more frequent as the aversiveness of an infused fluid increases (Schwartz & Grill, 1984).

Berridge (1991) showed that the frequency of occurrence of positive responses of rats to infused sucrose solutions is increased by caloric deprivation and reduced by both satiety and sensory-specific satiety. Both Berridge and others have found that positive responses to infusions of sweet solutions

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are replaced by negative responses after ingestion of sweet taste has been paired with toxicosis (Berridge, Grill, & Norgren, 1981; Grill & Norgren, 1978; Parker & Jensen, 1991). Using such evidence, together with reports by human participants of affective responses to flavors when hungry and satiated, Berridge (1995) argued cogently, first, that reactions to flavors in the taste-reactivity test reflect assessments of palatability and, second, that changes in responses to a flavor in the taste-reactivity test reflect changes in the affect which taste elicits.

Berridge (1995) also provided a thorough examination of the complex question of whether increases in positive and decreases in negative responses to flavors in the taste-reactivity test reflect a single underlying process or orthogonal positive and negative hedonic processes. Because our results provide no information bearing on the mechanisms that underlie changes in response in the taste-reactivity test, in interpreting the present experiment, we made the parsimonious assumption that positive and negative responses in the taste-reactivity test reflect opposite ends of a single dimension of response (see Berridge, 1995, for further discussion).

As noted in the introduction, we have shown previously that most observer rats that have learned an aversion to a palatable food will resume eating that food after interacting with a conspecific demonstrator that has eaten it (Galef, 1986; Galef et al., 1990). If reversal of a learned aversion following interaction with a demonstrator rat is the result of a change in observer rats' perception of the palatability of the food to which it learned an aversion, and if, as Berridge and others proposed, the taste-reactivity test measures changes in affective response to flavors (Berridge, 1995; Berridge & Grill, 1983; Grill & Berridge, 1985), then socially induced increase in intake of flavors to which an aversion has been learned should be accompanied by decreased negative or increased positive responses to that flavor in the taste-reactivity test.

We implanted observer rats assigned to both experimental and control groups with chronic intraoral cannulas and then habituated them to fluid infusions. We next allowed these observers to drink water flavored with cocoa and sweetened with sugar (Fluid CoS) and, immediately afterward, injected them intraperitoneally with a lithium-chloride solution to produce an aversion to Fluid CoS. Then, we allowed each observer rat that we had assigned to the experimental group to interact with a demonstrator rat that had drunk Fluid CoS. At the same time, we allowed observer rats we had assigned to the control group to interact with demonstrator rats that had drunk water. Next, we measured each observer rat's responses to an infusion of Fluid CoS. Finally, we offered each observer rat a choice, for 22 hr, between Fluid CoS and a solution flavored with almond and sweetened with sugar (Fluid AIS) that we had previously determined was roughly equipalatable with Fluid CoS.

Method

Subjects

Thirty-five experimentally naive, female Long-Evans rats born in the vivarium of the McMaster University Psychology Depart-

ment (Hamilton, Ontario, Canada) to breeding stock acquired from Charles River (St. Constant, Quebec, Canada) served as observers. To facilitate surgical procedures, we ensured that each observer rat weighed more than 200 g at the start of the experiment. We used an additional 35 adult female rats (that had been subjects in other experiments) as demonstrators.

Apparatus

Throughout the experiment, observer and demonstrator rats were housed individually in wire-mesh hanging cages measuring $32 \times 20 \times 20$ cm.

During the taste-reactivity test, we placed each observer rat in a 30-cm diameter, circular Plexiglas test chamber (25 cm high) with a glass floor (Grill & Norgren, 1978). A Panasonic (WV-CL110) color video camera focused on a mirror held at a 45° angle in relation to the floor of the test chamber permitted unimpeded views of a subject's ventral surface during the taste-reactivity test. The video image of each rat first passed through a time-date generator (Panasonic WJ-810) and was then recorded on a Panasonic videocassette recorder (AG-1240). We viewed tapes on a Panasonic (CT-1331-YC) color television monitor.

Test Fluids

We prepared two distinctively flavored fluids for use in the experiment. We made Fluid CoS by mixing 20 g of unsweetened cocoa (Hershey's Pure Cocoa, Hershey Canada, Etobicoke, Ontario, Canada) and 50 g of sugar in 1 L of tap water and Fluid AIS by mixing 20 ml of almond extract (Club House Pure Almond Extract, McCormick Canada Inc., London, Ontario, Canada) and 70 g sugar in 1 L of tap water. In pilot tests, we had found that Fluid CoS and Fluid AIS were roughly equipalatable (9 experimentally naive female Long-Evans rats that were offered a choice between Fluid CoS and Fluid AIS for 24 hr drank an average of $54\% \pm 8\%$ Fluid AIS), and both fluids were clearly preferred to tap water by rats. (Six experimentally naive rats offered a choice for 24 hr, first between Fluid AIS and water, then between Fluid CoS and water, drank an average of $80\% \pm 8\%$ flavored fluids.)

Procedure

Day 1: Implanting oral cannulas. Using methods similar to those described in Grill and Norgren (1978), we placed all 35 observer rats under deep sodium pentobarbitol anesthesia (50 mg/kg) and implanted each with a chronic intraoral cannula.

Days 2 and 3: Recovery from surgery. We left the 35 observer rats undisturbed to recover from surgery for 2 days.

Day 4: Habituation to test apparatus and start of water deprivation. Two days after surgery, we placed each observer rat in the test apparatus and left it there undisturbed for 10 min.

Following each observer rat's 10-min period of habituation, we placed both observer rats and their demonstrators on water deprivation schedules. We deprived observer rats of water for 23 hr/day for the next 3 days so that we could teach them an aversion to Fluid CoS on Day 8, and we deprived demonstrator rats of water for 23.5 hr/day for the next 4 days so that they would drink promptly when offered fluid on Day 9, the day on which they were to act as demonstrators.

During daily 1-hr drinking periods, we gave water to each of the 19 demonstrator rats assigned to interact on Day 9 with observer rats in the control group and Fluid CoS to each of the 16 demonstrator rats assigned to interact on Day 9 with observer rats in the experimental group.

Days 5–7: Habituation of observer rats to the test procedure. Before each observer rat's daily 1-hr drinking session on Days 5, 6, and 7, we placed it in the test chamber for 5 min and used a syringe pump (Harvard Apparatus, Model 2400006) to infuse tap water through its cannula and into its mouth at a rate of 1 ml/min.

Day 8: Aversion induction. On Day 8, we gave each observer rat Fluid CoS (instead of water) to drink for 1 hr and then injected it intraperitoneally with 1% of body weight, 1% weight/volume lithium-chloride solution. We then gave each observer rat ad libitum access to water for 24 hr.

Day 9: Demonstration, taste-reactivity testing, and flavor-preference testing. For 30 min, we offered the 19 demonstrator rats we had assigned to interact with observers in the control group a weighed cup of water and the 16 demonstrator rats assigned to interact with observers in the experimental group a weighed cup of Fluid CoS. At the end of the 30-min period of access to fluid, we transferred each demonstrator rat to the cage of an observer rat and left demonstrator and observer undisturbed to interact for 30 min.

At the end of the 30-min period of interaction between demonstrator and observer rats, we removed all demonstrators from observers' cages and gave each observer a taste-reactivity test. During the test, each observer rat received a 1-min infusion of water followed by a 2-min infusion of Fluid CoS (both at a rate of 1 ml/min) while we recorded its responses on videotape.

As soon as the test was finished, we returned each observer rat to its home cage and offered it a choice, for 22 hr, between two weighed cups: one containing Fluid CoS and the other Fluid AIS. At the end of this flavor-preference test, we weighed both cups and determined the percentage of each observer's total intake that was Fluid CoS.

We estimated evaporative water loss during the 22-hr choice test by placing weighed cups of Fluid CoS and Fluid AIS in empty cages in the cage rack in which all observer rats were maintained. We used this estimate to correct for evaporation when determining the observer rat's fluid intakes.

Scoring videotapes. An experimenter who was unaware of observer rats' group assignment scored the behavior of each observer during the first 30 s of infusion of Fluid CoS on Day 9. The experimenter recorded both any negative responses (gapes, head shakes, chin rubs, passive drips, and paw flails) and positive ones (tongue protrusion, lateral tongue protrusions, and paw licks) exhibited by each subject.

Results and Discussion

The main results of Experiment 1 are presented in Figures 1 and 2, which show, respectively, the mean percentage of Fluid CoS drunk by observers in experimental and control groups during the 22-hr test of flavor preference (see Figure 1) and the percentage of observers in experimental and control groups that exhibited both positive (tongue protrusions, lateral tongue protrusions, and paw licks) and negative (gapes, passive drips, paw flails, and head shakes) affective responses during the taste-reactivity test (see Figure 2).

As can be seen in Figure 1, observer rats assigned to the experimental group (those that interacted with a demonstrator rat that had drunk Fluid CoS) showed a significantly weaker aversion to Fluid CoS during the 22-hr choice test than did observer rats assigned to the control group (Mann-Whitney U test, $U = 78$, $p < .02$).

The data in Figure 2 reveal that, although observers in experimental and control groups were equally likely to exhibit positive responses (tongue protrusions, lateral tongue

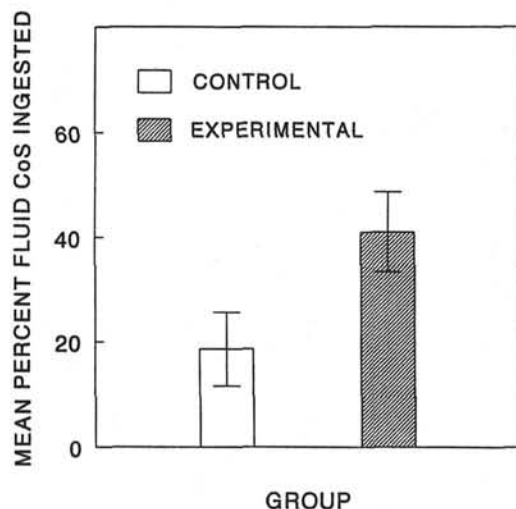


Figure 1. Amount of water flavored with cocoa and sweetened with sugar (Fluid CoS) ingested by control and experimental subjects in Experiment 1 during a 22-hr choice test, as a percentage of total amount drunk.

protrusions, and paw licks), observers assigned to the experimental group were significantly less likely than were observers assigned to the control group to exhibit the most common negative responses, gapes (Fisher's exact probability test, $p < .04$) and passive drips (Fisher's exact probability test, $p < .02$).

The results of the choice test repeat our previous finding that interaction of an observer rat that has learned an aversion to a substance with a demonstrator rat that has ingested that substance can induce the observer rat to increase its intake of the averted substance. The results of the taste-reactivity test provide evidence consistent with the view that the increased intake of the averted substance seen in the choice test is the result of an increase in its perceived palatability.

Experiment 2

In a stimulating, if seldom-referenced, article, Irwin (1958) described two possible causes of differential responses exhibited by animals when making a choice. According to Irwin, choice can be the result either of (a) a reflexive response to the stimuli present when the choice is made (e.g., a moth offered a choice between a flame and darkness will fly toward the flame, or a chick offered a choice between chips of two colors will peck more often at one than at the other) or (b) a motivated response that reflects an animal's expectancies regarding the outcomes of the behaviors it might exhibit (e.g., a hungry rat will turn left at the choice point in a T maze where it is not directly exposed to any food-related cues if it previously found food at the end of the left arm of the maze and not at the end of the right arm of the maze).

Irwin (1958) proposed that choices made in the presence of goal objects (like the approach of the moth to the flame or

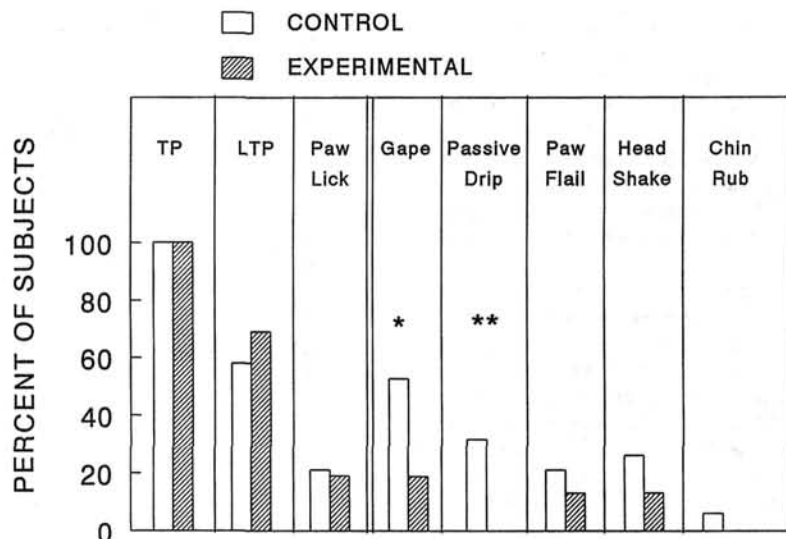


Figure 2. Percentage of subjects assigned to experimental and control groups exhibiting (left) positive responses: tongue protrusion (TP), lateral tongue protrusion (LTP), and paw licking, and (right) negative responses: gape, passive drip, paw flail, head shake, and chin rub during taste-reactivity testing in Experiment 1. * $p < .05$. ** $p < .02$.

the pecking of the chick exposed to colored chips) should be described as *biases* and that only differential responses made by an animal when it is not directly exposed to goal objects (e.g., the choices made by rats when at the choice point in a T maze) should be referred to as *preferences*. In Irwin's view, it is only in the latter case that an animal's behavior has been motivated by its expectancies as to the probable outcomes of its acts.

An observer rat faced with a choice between two foods after interacting with a demonstrator rat that had eaten one of them and exhibiting enhanced intake of whichever food its demonstrator ate might simply be biased by interaction with its demonstrator so that its ingestive responses were more strongly driven by whatever food it had experienced in contiguity with its demonstrator (Galef & Stein, 1985). Alternatively, after interacting with a conspecific demonstrator, the observer might be motivated to seek out and ingest the food that its demonstrator ate.

In Experiment 2, we first taught each of 8 rats that banana-flavored pellets were always to be found at the end of one arm of a T maze and that chow-flavored pellets were consistently available at the end of the other arm. Then, on 18 test days, before we tested each subject rat in the maze, we allowed it to interact with a demonstrator rat that had eaten either banana- or chow-flavored food. By comparing the frequency with which each observer rat entered the arm of the maze containing banana-flavored pellets on days when its demonstrator had eaten banana-flavored pellets with the frequency with which that observer entered the same arm of the maze on days when its demonstrator had eaten chow-flavored pellets, we could determine whether, in Irwin's (1958) sense, observers exhibited socially induced enhancement of their preferences for the foods that their demonstrators had eaten.

Method

Subjects

Eight, 42-day-old female Long-Evans rats, born and reared in the vivarium of the McMaster University Psychology Department, served as observers. An additional 8 rats from the same source that had served previously as subjects in other experiments served as demonstrators.

Apparatus

Observer and demonstrator rats were housed individually throughout the experiment in shoe-box cages kept in a temperature- and humidity-controlled colony room maintained on a 12-hr light-dark cycle.

The experiment was conducted in a T maze constructed of transparent Plexiglas with a grid floor of stainless steel rods. The start box of the maze measured 15 × 14 × 30 cm and opened, through a guillotine door, onto a 79-cm long alley leading to two arms, each 61 cm in length. A food cup was located on the wall at the end of each arm of the maze, and a line was drawn 5 cm inside the entrance to each arm of the maze. An observer rat was considered to have entered an arm of the maze when both of its forefeet crossed the line at the entrance to that arm.

To ensure that observer rats could not use the odor of pellets in the food cups at the ends of the maze arms when choosing which arm of the maze to enter, we placed 12 banana- and 12 chow-flavored pellets in a petri dish located under the grid floor of the maze at the point where the alley met the arms of the maze.

Procedure

Feeding demonstrators and observers. We generally fed both observer and demonstrator rats a nutritionally adequate, calorically dense diet (Normal Protein Test Diet [Rat], Catalog 170590, Harlan/Teklad, Madison, WI) for 1 hr/day. Demonstrators ate just

before training or testing of observers, and observers ate just after their daily sessions of training or testing.

The only exception to our normal feeding schedules occurred on Tuesday and Friday of each of the last 9 weeks of the experiment, when we fed demonstrators either banana-flavored (Bioserv, Frenchtown, NJ, Catalog F0059) or chow-flavored (P. J. Noyes Co., Lancaster, NH, Formula "A" [traditional]) pellets during their 1-hr feeding period.

Training observers. Using normal shaping procedures, we trained each observer rat to run from the start box of the maze to both goal boxes. For 4 of the observers, on every trial, the food cup in the left arm of the maze contained two 45-mg banana-flavored pellets and in the right arm of the maze two 45-mg chow-flavored pellets. For the other 4 observers, the locations of banana- and chow-flavored pellets were reversed. We had determined in a pilot study that, in a simple choice situation, rats ate substantially more banana-flavored than chow-flavored 45-mg pellets.

We conducted the experiment in two replications, each with 4 observers and 4 demonstrators. On each day, we tested 4 observer rats one after the other in the maze. Each trial for each observer required 30 to 60 s. Consequently, observers experienced intertrial intervals that ranged from approximately 90 to 180 s, depending on the latency of other observers to reach a food cup.

We ran each observer rat for 10 trials/day until all were consistently entering the arm of the maze that contained the banana-flavored food more frequently than they were entering the arm of the maze that contained chow-flavored pellets. We assumed that once an observer rat consistently preferred to enter the arm of the maze containing banana-flavored pellets (as all observer rats eventually came to do), it had learned where each type of pellet was to be found.

Testing subjects. Once training was complete, observer rats continued to be run in the maze 10 trials/day for 7 days/week. On Tuesday and Friday of each week, just before we ran observer rats for 10 trials in the apparatus, we allowed each observer to interact for 30 min in her home cage with a demonstrator rat that had just eaten either banana-flavored or chow-flavored pellets for 1 hr. The order in which demonstrator rats were fed banana- and chow-flavored pellets on Tuesday and Friday of each week was counter-balanced across weeks within subjects.

Subject testing proceeded exactly as had subject training. Each observer rat was given 10 trials/day in the T maze with banana- and chow-flavored pellets in their usual positions. On the remaining 5 days of each of the 9 weeks of the experiment, observers were run 10 trials/day in the maze as during training but did not interact with

a demonstrator. Comparing responses of observer rats on days they interacted with demonstrators fed banana- and chow-flavored pellets rather than comparing the behavior of observers on test and baseline days allowed us to control for any effects of simple interaction with a conspecific on a stable preference.

Results and Discussion

The main results of Experiment 2 are presented in Table 1. To examine the effect of demonstrator rats on the behavior of observer rats at the choice point in the maze, each week we subtracted the number of times (out of 10) that an observer rat entered the arm of the maze containing banana-flavored pellets on the day it interacted with a demonstrator rat fed chow-flavored pellets from the number of times (out of 10) that same observer rat entered the same arm of the maze after interacting with a demonstrator rat fed banana-flavored pellets.

Table 1 shows the differences that result from these subtractions for each of the 8 observer rats on each of the 9 weeks of the experiment. As can be seen in Table 1, sign tests revealed that, during testing, 6 of the 8 observer rats were significantly more likely to enter the arm of the maze containing banana-flavored pellets on those days when their demonstrators had eaten banana-flavored pellets than on those days when their demonstrators had eaten chow-flavored pellets. The effect of demonstrator rats on their observers' choice of an arm to enter, although relatively small, was reliable.

On Irwin's (1958) definition, the choices of observers in the T maze induced by interaction with demonstrators were due to changes in their preferences, not to changes in their biases.

General Discussion

The results of both experiments described in this article are consistent with the hypothesis that the change in food choice seen in observer rats after they interact with recently fed conspecific demonstrator rats is a result of a change in the affective responses of observers to the foods that their

Table 1
Difference in the Number of Entries Into the Arm of the Maze Containing Banana-Flavored Pellets by Subjects on Days in Each Week When Their Demonstrators Ate Banana- or Chow-Flavored Pellets

Subject	Week									% Pos
	1	2	3	4	5	6	7	8	9	
1	2	1	5	1	1	1	-1	1	1	89**
2	1	1	2	0	1	1	0	1	0	100***
3	1	-1	0	0	1	-1	-3	0	1	50
4	2	2	2	-2	1	1	1	0	4	87*
5	3	0	2	1	-1	1	2	2	1	87*
6	0	-1	-1	0	0	-2	1	2	0	40
7	1	1	-1	4	2	1	2	0	2	87*
8	3	2	1	1	1	4	-1	2	2	89**

Note. % Pos = percentage of positive and negative entries in each row that are positive.
* $p < .035$. ** $p < .020$. *** $p < .016$. All p values are one-tailed.

respective demonstrators ate. Social interaction affected observers' food choices by altering their motivation to find and ingest food their demonstrators had eaten (Experiment 2), and socially induced increased intake of a fluid to which an aversion had been learned changed observers' responses in the taste-reactivity test to the fluid ingested by their demonstrators (Experiment 1).

Understanding how socially acquired information changes rats' responses to foods requires more than analyses of the stimulus complex that controls social influences on food choice (Galef, Mason, Preti, & Bean, 1988; Galef & Stein, 1985; reviewed in Galef, 1988, 1996). There is also a need to explore the changes in affective or motivational state (Cabanac, 1976) that are induced by exposure to a food in a social context. The present experiments are a first step in that direction.

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