Stimulus Enhancement: Controls for Social Facilitation and Local Enhancement

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In two experiments, magazine-trained observer rats were given access to a pair of levers and allowed to make 50 reinforced responses immediately after the left or the right lever had been pressed 100 times for food reward by a conspecific demonstrator. In Experiment 1, where observers were rewarded for responses on either lever, those that had been able to see their demonstrators responding showed a response bias in favor of the demonstrator's lever, while rats that had been separated from their demonstrators by a metal screen did not. In Experiment 2, each observer saw a "viewed demonstrator" responding on one lever and was tested, with reinforcement for responses on the viewed demonstrator's lever or on the other manipulandum in a second chamber where a "box demonstrator" had just finished responding. Observers rewarded for responding on the same lever as the viewed demonstrator (Group SAME) showed better discrimination at the beginning of the test session than observers rewarded for responses on the other lever (Group DIF-FERENT). Within Group SAME, rats whose box demonstrator had responded on the reinforced lever showed better discrimination than those whose box demonstrator responded on the nonreinforced lever, but the reverse was true in Group DIFFER-ENT. Both experiments provide evidence of stimulus enhancement unconfounded by social facilitation and local enhancement, and the latter suggests that demonstrator-deposited scent cues can facilitate discrimination via local enhancement or on the basis of their sensory properties alone. © 2000 Academic Press

It is commonly believed that observation of a conspecific performing an action on an object can facilitate acquisition of the observed response via "stimulus enhancement" (e.g., Galef 1988, Whiten & Ham 1992, Zentall 1996). According to Spence (1937), who introduced the term, stimulus enhancement occurs when observation of an action leads the observer to increase the proportion of its behavior directed toward the location or object of the demonstrator's activity. It is assumed that this focusing of behavior increases the probability that the observer will contact the same contingencies as the demonstrator and thereby facilitates acquisition of the same response. Thus, to attribute behavioral matching to stimulus enhancement implies that the match is a product of two learning processes. The first process occurs during observation and somehow renders attractive the stimulus con-



tacted by the demonstrator. The second process is instrumental learning which occurs, with or without the presence of the demonstrator, when the observer gains access to the stimulus to which the demonstrator has been observed responding.

Although stimulus enhancement has been an established category of social learning for some 60 years, the phenomenon has never been clearly demonstrated. Early evidence was anecdotal, and putative cases in the more recent literature could be examples of social facilitation or local enhancement. According to Zajonc (1965), social facilitation occurs when the passive presence of another animal "energizes all responses made salient by the stimulus confronting the individual at the moment." Local enhancement, on the other hand, is used here to refer to cases in which an animal is attracted to a site or object by the current presence of a conspecific at the site or by residues of the demonstrator's activity at the site, e.g., odor cues. This usage of the term local enhancement is consistent with the practice of distinguishing local from stimulus enhancement in terms of whether the observer is attracted only to the object contacted by the demonstrator (local enhancement) or to all objects with the same physical appearance (stimulus enhancement) (e.g., Galef 1988, Thorpe 1963). If an animal were attracted to the demonstrator's manipulandum, and not to other objects of exactly the same physical appearance, it would imply that the attraction is mediated by the presence of the demonstrator or its residues (Heyes 1994).

Both social facilitation and local enhancement may be the products of learning, and each may give rise to learning, but neither constitutes a learning phenomenon in itself. For example, a rat may be attracted to odors deposited at a food site by a conspecific (Galef & Beck 1985) because these odors have been associated with reward, and as a result of consuming the food the rat may acquire a flavor preference. However, the rat's approach to the food site, the phenomenon of local enhancement itself, is a response to current stimulation, and not necessarily either a precursor or a product of learning.

Studies yielding the most ambiguous evidence of stimulus enhancement have allowed rats to observe a conspecific pressing a single lever for food reward, and then given the observers access to the same manipulandum on test. For example, Jacoby and Dawson (1969) found that rats given this treatment acquired lever pressing faster than rats that did not see the demonstrator's performance and were not tested on a lever recently manipulated by another animal. The observers in this experiment may have acquired the response faster because the sight of the demonstrator's action led them to concentrate their behavior on the lever (stimulus enhancement), but they may instead have been attracted to the lever by odor cues deposited there by the demonstrator (local enhancement).

"Duplicate cage" procedures, in which observers are simultaneously exposed to a lever pressing demonstrator and given access to a lever of their own, are likely to have excluded the possibility of local enhancement, but they have not isolated stimulus enhancement from social facilitation. Using

a duplicate cage procedure, Gardner and Engel (1971) found that, relative to no-observation controls, acquisition of lever pressing was facilitated equally by exposure to a demonstrator that was both pressing a lever and collecting food reward and to a demonstrator that was only collecting food pellets from the magazine. This result leaves open the possibilities that response acquisition was facilitated by the sight of the demonstrator contacting the lever (stimulus enhancement), the mere presence of a conspecific (social facilitation), or exposure to a feeding conspecific. In support of these alternative possibilities, other duplicate cage experiments (Zentall & Levine 1972, Levine & Zentall 1974) have confirmed that exposure to a demonstrator making consummatory responses can facilitate acquisition of lever pressing, and indicated that the mere presence of a conspecific can both facilitate and retard acquisition of lever pressing.

Other putative examples of stimulus enhancement have emerged from studies of pattern discrimination learning in a runway. For example, Kohn (1976) allowed rats to observe a demonstrator entering a goal box containing food through one of two doors, marked with horizontal and vertical stripes. The observers were subsequently transferred to the runway and given training involving the same pair of stimuli or one member of the pair combined with a novel stimulus. During this training period, observer rats learned faster than no-observation controls only when the discrimination problem involved approach to, rather than avoidance of, the stimulus that was positive for their demonstrator.

Kohn's (1976) discrimination procedure controlled effectively for social facilitation. Since observers of horizontal+/vertical- and horizontal-/vertical+ discrimination performance were exposed equally to conspecific presence, general activity, and consummatory behavior, the contrast between these groups could not have been due to any of these factors. However, the possibility of local enhancement, that the observers were attracted to the demonstrators' S+ panel by odor cues, was not satisfactorily eliminated. The response panels were said to have been "deodorized" (Kohn 1976) prior to the training of each rat, presumably by wiping with a cleansing agent, but the effectiveness of this procedure was not assessed. If the no-observation control rats had also been trained in the runway when it had been recently vacated by a demonstrator and "deodorized," then the contrast between their performance and that of the observers would suggest that the latter were not merely attracted to olfactory cues on the panel contacted by the demonstrator. However, it would appear that the control rats were instead trained on days when demonstrators were not run in the apparatus.

The primary purpose of the present experiments was to isolate stimulus enhancement from local enhancement and social facilitation in rats using a discriminative lever pressing procedure. This procedure was chosen because it combines the strength of a pattern discrimination procedure, which controls for social facilitation, with the advantages of an automated operant task. Magazine trained rats observed a conspecific pressing one of two levers for food reward before being given access to the same pair of levers (Experiment 1) or a similar pair (Experiment 2) on test. No attempt was made in either experiment to prevent the observer rats from being attracted to the demonstrator's lever on test by demonstrator-deposited scent cues for two reasons. First, odor cues can be more readily controlled than eliminated, and, second, the question of how scent and visual cues interact as social influences on behavior is of independent interest. Thus, instead of attempting to eliminate any odor-mediated local enhancement effects, the experiments were designed to compare the magnitude of any such effect with that of a stimulus enhancement effect, i.e., a bias in favor of the demonstrator's lever attributable to pretest observation of the demonstrator's lever pressing behavior.

EXPERIMENT 1

Each S in Experiment 1 was situated in the observation compartment of an operant chamber while a demonstrator pressed one of two levers, the left lever or the right lever, for food reward. Half of the subjects were able to observe their demonstrator's performance (Groups NO SCREEN–LEFT and NO SCREEN–RIGHT), while the other half had their view of the demonstration compartment blocked by an aluminum screen (Groups SCREEN–LEFT and SCREEN–RIGHT). When the demonstrators had completed 100 reinforced responses, they were removed from the apparatus and the subjects were transferred to the observation compartment and given a test session in which responses on either lever were reinforced.

It was anticipated that the rats in the NO SCREEN groups would show a bias in favor of the lever pressed by their demonstrators. Such a demonstrator-consistent bias could be due to stimulus enhancement or local enhancement, but not to social facilitation, because in this procedure observers of left and right responding are exposed equally to the presence, general activity, and consummatory responding of a demonstrator. Comparison between the NO SCREEN and SCREEN groups would indicate whether local enhancement was solely responsible for demonstrator-consistent responding in the former groups, or whether this response bias was due in some measure to stimulus enhancement. All groups are tested on the same pair of levers as their demonstrators and are therefore equally susceptible to the influence of scent cues deposited on or around the manipulanda by the demonstrators. Consequently, a stronger demonstrator-consistent bias in the NO SCREEN groups than in the SCREEN groups would suggest that, in the former case, observers are attracted to a lever to which they have observed a conspecific responding.

Method

Subjects

The subjects were 32 male hooded Lister rats, obtained from Harlan Olac Ltd. (Bicester, Oxon, UK), weighing 340–400 g at the beginning of the ex-

periment. All the animals had previously taken part in an appetitive observational learning procedure in which they learned to push a joystick for food reward. In the present experiment, 8 rats were randomly assigned the role of demonstrator, while the remaining 24 were observers. Each demonstrator was housed with its three observers. Water was available ad libitum and the rats were fed for 90 min following each daily training session.

Apparatus

The animals were trained and tested in four identical operant chambers. The walls and ceilings of the chambers were aluminum, and the floors consisted of stainless steel rods spaced 1 cm apart. Each chamber was divided into two compartments by a 1-cm-gauge wire mesh partition. During part of the experiment, the wire mesh was covered by a aluminum screen. The demonstration/test compartment measured $26 \times 25 \times 28$ cm and was illuminated by a 24-V, 2.6-W houselight in the center of the ceiling. The observation compartment measured $16 \times 25 \times 28$ cm and was featureless.

The demonstration/test compartment in each of the four chambers contained two Perspex levers in addition to the magazine tray on an operant panel parallel to the dividing wall between the observation and demonstration compartments. Thus, while responding, the demonstrators had their backs to the observers. The levers were 1 cm thick, 1 cm deep, and 4 cm wide. The levers were positioned 9 cm apart, 2 cm from the floor, on either side of the magazine tray. The magazine tray was situated at floor level in the middle of the operant panel. A 45-mg sucrose pellet was delivered to the food magazine immediately after each correct response (defined below).

A BBC Master computer running Spider on-line control language controlled the equipment and recorded the data.

Procedure

All sessions were initiated with illumination of the house light which was extinguished at the end of the session.

Demonstrator training. In 12 daily sessions, half of the demonstrators were trained on a continuous reinforcement schedule (CRF) to press the left lever, and half were trained to press the right lever. Sessions terminated when 100 food pellets had been delivered. To accustom the demonstrators to responding in the presence of a conspecific, a "dummy observer" was placed in the observation compartment for each of the last two demonstrator training sessions. These male rats, which were of approximately the same weight as the observers, played no other part in the experiment. At the end of training, all demonstrators showed perfect discrimination.

Observer training and testing. Observers received two daily sessions of magazine training in the demonstration/test compartment. In each session, 20 reinforcers were delivered on a RT60 schedule. The day after the second magazine training session, each observer was placed in the observation com-

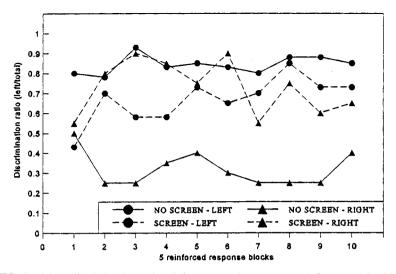


FIG. 1. Mean discrimination ratios (left responses/total responses) for successive blocks of five reinforced responses during the observers' test session in Experiment 1.

partment while its demonstrator made 100 reinforced responses on the right or the left lever in the demonstration/test compartment. Half of the observers could see their demonstrators responding, while the other half had their view of the demonstrator blocked by a screen. When the demonstrator had completed 100 reinforced responses, it was removed from the apparatus and the observer was immediately transferred to the demonstration/test compartment, where responses on either lever were reinforced. The test session ended when the observer had made a total of 50 reinforced responses.

Due to an error in implementation of the experimental design, there were eight observers in each of Groups NO SCREEN-LEFT and SCREEN-LEFT, and four observers in each of Groups NO SCREEN-RIGHT and SCREEN-RIGHT.

Results and Discussion

A discrimination ratio was calculated for each observer for each successive block of five responses by dividing the number of left lever presses by the total number of lever presses, i.e., five.

Figure 1 shows the mean discrimination ratios for each group. The overall bias in favoring of responding to the left lever, apparent in this graph, may have been due to the fact that the left lever was situated next to the door. In addition to this bias, Fig. 1 indicates that when the observers could see their demonstrators responding, those that observed left lever pressing made proportionately more left lever responses throughout the test session than those that observed right lever pressing. In contrast, when the observers'

view of the demonstrators' performance was blocked by a screen, those paired with a demonstrator pressing the left lever did not make more left responses than those paired with a right lever demonstrator. Three-way analysis of variance revealed a reliable screen (present vs absent) × side (left vs right) interaction ($F_{1,20} = 4.42$, p = .05). No other main effects or interactions were significant. Simple effects analysis confirmed that Group NO SCREEN–LEFT made proportionally more left responses than Group NO SCREEN–RIGHT ($F_{1,20} = 7$, p < .025), while Groups SCREEN–LEFT and SCREEN–RIGHT did not differ from one another (F < 1).

These results suggest that stimulus enhancement occurred among the rats that were able to observe their demonstrators' responses. These rats appear to have been attracted to their demonstrator's lever as a result of exposure to cues that arose from the demonstrators' action on the lever and were processed while that action was in progress. If attraction to the demonstrators' lever had been mediated solely by odor cues, i.e., local enhancement, the SCREEN and NO SCREEN groups would have shown an equally strong bias toward their demonstrators' manipulandum. In fact, no bias at all in favor of the demonstrators' lever was detected among animals that could not observe their demonstrators performance, and therefore these animals provided no evidence that demonstrator-deposited odor cues contributed to a response bias in this procedure.

It is noteworthy that the NO SCREEN observers' preference for their demonstrators' manipulandum persisted throughout the test session. This suggests that the stimulus enhancing effect of seeing a conspecific responding on one of the levers was strong enough to prevent the availability of reinforcement on the other lever from gaining control over behavior in the course of the test session.

EXPERIMENT 2

Experiment 1 detected a stimulus enhancement effect but no local enhancement effect; it provided evidence that rats are attracted to a lever on which they have observed a demonstrator responding, but provided no evidence that lever choice is affected by demonstrator-deposited scent cues. Since the NO SCREEN observers in Experiment 1 had access both to visual cues during observation and any demonstrator-deposited scent cues on test, and SCREEN observers had access to the latter only, these results are susceptible to two plausible interpretations. First, it is possible that the demonstrators did not deposit more scent cues on the lever to which they responded or that any such cues did not affect observers' performance in either the SCREEN or the NO SCREEN groups. Second, it is possible that in the discriminative lever pressing procedure used in Experiment 1, demonstratordeposited scent cues affect lever choice when they are augmented by compatible observation experience, but not when the subjects' view of the demonstrators' performance was blocked during the observation phase. Experiment 2 employed a "box-swapping" procedure, rather than a screening procedure, to replicate and extend the stimulus enhancement effect observed in Experiment 1. In the box-swapping procedure, every observer rat had the opportunity to observe a conspecific (the 'viewed demonstrator') responding on one of the two levers, and was then transferred for a test session to a second operant chamber where another conspecific (the 'box demonstrator') had just completed 100 responses on the same lever as the viewed demonstrator, or on the opposite lever. Thus, each subject had access to observation cues and to any scent cues, and for some groups these two kinds of cues were associated with the same lever, and for other groups they were associated with different levers. The purpose of Experiment 2 was to establish whether effects of observation (stimulus enhancement) and scent (local enhancement) on lever preferences could be detected under these conditions, and to examine their mode of interaction.

In addition to employing a new control procedure (box-swapping rather than screening), Experiment 2 used an alternative test procedure. Instead of being rewarded for responses on either lever on test, observers were rewarded for responses on just one lever. Use of this alternative test procedure provides an opportunity to assess the robustness of the stimulus enhancement effect observed in the previous experiment.

In summary, the design of Experiment 2 was as follows: Each rat observed its viewed demonstrator responding on one of two levers (left or right) and was then transferred to a second chamber for a test session in which responses on the lever pressed by the viewed demonstrator (Group SAME) or on the opposite lever (Group DIFFERENT) were reinforced. Half of the rats in each of these two groups were tested in a chamber where a box demonstrator had recently responded on the reinforced lever (Groups SAME+ and DIFFERENT+), while the other half were paired with box demonstrators that responded on the nonreinforced lever (Groups SAME- and DIFFER-ENT-). Thus, the SAME/DIFFERENT variable relates to the compatibility of the observed lever and the reinforced lever, while the +/- variable relates to the compatibility of the (hypothetically) scented lever and the reinforced lever. Within each of the four experimental groups, the location of the viewed demonstrator's lever, left or right, was counterbalanced. Taking as examples the half of the Ss whose viewed demonstrator responded on the left lever, Group SAME+ observed left responding and were rewarded for left responses in a chamber where the left lever was scented. Group SAME- observed left responding and were rewarded for left responses where the right lever was scented. Group DIFFERENT+ observed left responding and were rewarded for right responses where the right lever was scented, and Group DIFFERENT- observed left responding and were rewarded for right responses where the left lever was scented.

If lever preferences in this lever discrimination procedure are susceptible to both stimulus and local enhancement, i.e., if both observation and scent cues attract observer rats to the lever manipulated by a conspecific, and if these effects are additive, then one would expect observers rewarded for responding on their viewed demonstrator's lever to make more reinforced responses on test than those reinforced on the opposite lever (a main effect of SAME/DIFFERENT) and observers rewarded on their box demonstrator's lever to make more reinforced responses on test than those reinforced on the opposite lever (a main effect of +/-), but one would not expect any interaction between these variables.

Method

The method differed from that of Experiment 1 in the following respects.

Subjects

Forty-eight rats, weighing 270–340 g at the start of the experiment, served as observers. These animals had previously served in a Pavlovian conditioning experiment in which a light was paired with food reinforcement. The demonstrators and observers were housed separately throughout the experiment in groups of four.

Apparatus and Procedure

Each observer received four magazine training sessions, two in the demonstration/test compartment of the chamber in which it would observe demonstrator performance and two in the chamber in which it would be tested.

After observing its viewed demonstrator making 100 reinforced responses on the left or the right lever, each observer was immediately transferred to another chamber for the test session. This chamber had just been vacated by the target observer's box demonstrator (and the observer for which it functioned as the viewed demonstrator).

Results and Discussion

A discrimination ratio was calculated for each observer for each successive block of five reinforced responses by dividing the number of responses to the reinforced lever by the total number of responses.

One observer in Group SAME+ was excluded from the analysis because its discrimination ratio across all 50 reinforced responses was more than two standard deviations away from the mean for that group (Tukey 1977). A second rat, in Group DIFFERENT+, failed to respond on test. The resulting group sizes were SAME+, 11; SAME-, 12; DIFFERENT+, 11; DIFFER-ENT-, 12.

Mean discrimination ratios for each test block are given in Fig. 2, and for the first block of five responses only in Fig. 3. Inspection of these figures suggests that during the first test block, but not thereafter, observers produced a greater proportion of reinforced responses when they were rewarded for

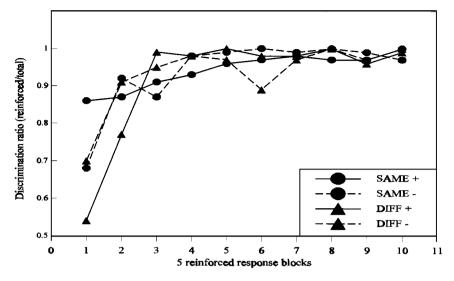


FIG. 2. Mean discrimination ratios (reinforced responses/total responses) for successive blocks of five reinforced responses during the observers' test session in Experiment 2.

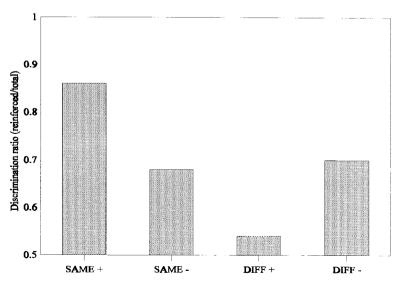


FIG. 3. Mean discrimination ratios (reinforced responses/total responses) for the first block of five reinforced responses in Experiment 2.

responses to the same lever as that pressed by the viewed demonstrator (Group SAME) than when responding to the other lever was reinforced (Group DIFFERENT). However, it would appear that while in Group SAME the ratio of reinforced responses was higher when the box demonstrator responded on the reinforced lever (Group SAME+) than when the box demonstrator responded on the nonreinforced lever (Group SAME-), the reverse was true in Group DIFFERENT. That is, when the viewed demonstrator responded on the nonreinforced lever, observers for whom the reinforced lever was scented (Group DIFFERENT+) had a *lower* discrimination ratio at the beginning of the session than those for whom the nonreinforced lever was scented (Group DIFFERENT-). As the test session progressed, group differences disappeared and all groups came to respond preferentially to the lever associated with food.

A preliminary four-way ANOVA of the whole data set indicated that there was no main effect of, or reliable interactions involving, the counterbalancing variable and therefore data from animals that observed left and right responding were pooled for further analysis. Three-way analysis indicated a significant main effect of block ($F_{9,378} = 29.33$, p < .0001) and significant interactions between block and treatment (SAME vs DIFFERENT) ($F_{9,378} = 3.23$, p = .001), and between block, scent, and treatment ($F_{9,378} = 3.56$, p = .0001). No other main effects or interactions were reliable.

The significant interactions involving the test block factor were explored by two-way analysis of the group differences which, according to the graph, were to be found during the first test block. The analysis used an error term comprising the weighted average of the between- and within-subjects error mean squares from the original three-way ANOVA and yielded a significant main effect of treatment (SAME vs DIFFERENT, $F_{1.42} = 19.38$, p = .0001) and a reliable treatment \times scent (+ vs -) interaction ($F_{1,42} = 26.92$, p =.00001). There was no main effect of scent (F < 1). Preplanned contrasts, evaluated against an alpha level of .01 to reduce family-wise error, explored the source of the group differences. As expected, when considered together, Groups SAME+ and SAME- made a greater proportion of their responses on the reinforced lever than groups DIFFERENT+ and DIFFERENT- $(F_{1,437} = 22.77, p < .01)$. Furthermore, Group SAME+ made proportionately more reinforced responses than Group SAME- ($F_{1,437} = 14.06$, p < .01), while Group DIFFERENT+ responded less on the reinforced lever than Group DIFFERENT- $(F_{1.437} = 12.80, p < .01)$.

These results suggest that at the beginning of the test session the observer rats in this experiment were influenced both by their observation of the viewed demonstrators' behavior and by odor cues deposited on the manipulanda by the box demonstrators. The former effect is relatively straightforward. The fact that the group which saw a demonstrator responding on the reinforced lever showed superior discrimination performance to those which saw a demonstrator responding on the nonreinforced lever implies that, at the beginning of the test session, the rats in one or both of these groups were attracted to the lever on which they had observed a conspecific responding. Thus, like those of Experiment 1, which used different control and test procedures, these results provide evidence of stimulus enhancement in rats unconfounded by possible effects of social facilitation and local enhancement.

In contrast, the effect of the box demonstrator is more surprising and apparently more complex. Assuming that the box demonstrators would deposit more scent cues on or around the lever to which they responded, that these cues would be attractive to observers, and that the attractive effects of scent and observation cues would be additive, we predicted that in both Group SAME and Group DIFFERENT rats whose box demonstrators responded on the reinforced lever would show better discrimination than those whose box demonstrator responded on the nonreinforced lever. In fact, this was found to be true of Group SAME, but the reverse was found in Group DIF-FERENT.

There are at least two possible interpretations of the reported effects, both of which assume that the box demonstrators deposited more scent cues on or near the lever to which they responded. The first possibility is that the rats were attracted to levers by observing them being pressed and by demonstrator-deposited odor cues, and that in both cases the levers acquired positive hedonic properties that could act as discriminative cues. Thus, it was easier for the observers to discriminate the reinforced and nonreinforced levers when both observation and scent cues were biased in favor of the same manipulandum (Groups SAME+ and DIFFERENT-) than when the observers saw responding on one lever and encountered a majority of scent cues on the other (Groups SAME- and DIFFERENT+). In the former case, the difference in attractiveness of the levers was greater; one lever was attractive on two counts and the other on none. In the latter case, one lever was attractive by virtue of the subject's observation experience, and the other was rendered attractive by scent cues.

The second possibility is that while observation made the viewed demonstrator's lever attractive, i.e., affected its hedonic properties, demonstratordeposited odors were neither attractive nor aversive to the observers in this experiment. Instead, the sensory, rather than the hedonic, properties of demonstrators' deposits functioned as distinctive cues facilitating learning about the relationship between responding and reinforcement on the scented lever. This facilitation effect was stronger when the deposits were on the viewed demonstrator's lever (Groups SAME+ and DIFFERENT-) than when they were on the other lever (Groups SAME- and DIFFERENT+), because in the former case the rats were attracted by their observation experience to the scent-bearing lever and therefore received more exposure to the scent cues.

Facilitation effects of this kind have been observed in potentiation experiments (e.g., Galef & Osborn 1978, Durlach & Rescorla 1980; see Lolordo & Droungas 1989 for review). For example, aversion learning to a flavor, A, is sometimes more pronounced when A is presented with a second flavor, B, prior to toxicosis, then when A alone is paired with the US. If a demonstratordeposited odor cue functioned as a potentiating stimulus, B, in the present experiment, it may have facilitated learning about the relationship between a lever and reward by focusing attention on the lever (Galef & Osborn 1978) or via second-order conditioning (Durlach & Rescorla 1980). To investigate this potentiation hypothesis it would be necessary to run control groups in which scent cues were eliminated.

GENERAL DISCUSSION

Both experiments provided evidence of stimulus enhancement by showing that observation of a conspecific responding on a lever results in focusing of the observer's behavior on that manipulandum. In Experiment 1, where observers were rewarded on test for responses on either lever, those that had been able to see their demonstrators responding showed a response bias in favor of the demonstrator's lever, while rats that had been separated from their demonstrators by a metal screen did not. In Experiment 2, with differential reinforcement on test, observers rewarded for responding on the same lever as the viewed demonstrator showed better discrimination at the beginning of the test session than observers rewarded for responses on the other lever.

In contrast with potential examples of stimulus enhancement provided by previous studies (e.g., Gardner & Engel 1971, Jacoby & Dawson 1969, Kohn 1976), these effects could not have been due to social facilitation because, regardless of the lever pressed by its demonstrator, each observer was exposed equally to the presence, activity, and consummatory behavior of a conspecific. Furthermore, these effects are not attributable to local enhancement because the demonstrators were not present during the test session, and the influence of any demonstrator residues was controlled using screening (Experiment 1) and box-swapping (Experiment 2) procedures.

In Experiment 1, when responses to both levers were reinforced on test, the social facilitation effect persisted throughout the test session, while in Experiment 2, when lever responses were differentially reinforced on test, the effect was reliable only during the first block of five test responses; subsequently all observers showed a consistent bias in favor of the rewarded lever. Like recent studies of social learning of mate choice (Dugatkin 1996) and food preferences (Galef and Whiskin 1998), this contrast confirms that so-cially induced response biases can be swiftly eliminated by direct exposure to contingencies of reinforcement.

The mechanism underlying the stimulus enhancement effects reported here could be single-stimulus, exposure learning or associative learning during observation. For example, observation of the demonstrator's activity may increase the observer's exposure to one of the levers and thereby promote habituation of neophobia to that lever or, on the other hand, give the observer the opportunity to learn about the contingent relationship between the lever stimulus and reinforcement. The term stimulus enhancement has been used to refer to phenomena thought to be mediated by both single-stimulus and associative learning (e.g., Beck 1976), but in the latter case it might be more appropriate to describe it as observational conditioning (Heyes 1994). Whatever the terminology applied, to establish whether the mechanism is associative, it would be necessary to vary or abolish the contingency between the demonstrator's responses and reinforcement.

In a recent study of food finding behavior in zebra finches, Coleman and Mellgren (1997) found evidence of local enhancement but not of stimulus enhancement. Birds foraging in pairs showed a tendency to approach a feeding site adjacent to that at which their partner was feeding, but did not bias their search in favor of sites of the same color as that to which the demonstrator was directing its behavior. The contrast between this result and those of present experiments may indicate that zebra finches are less susceptible to stimulus enhancement than rats, but a much more likely explanation is that the procedure used here was more sensitive to stimulus enhancement. In both the Coleman and Mellgren study and the present experiments, observers were tested simultaneously for the effects of local and stimulus enhancement, but in the former case the local enhancement cue was the presence of a conspecific, rather than of conspecific residues, at a given site. It is likely that a conspecific is a more potent cue than its products, and therefore any effects of stimulus enhancement may have been overwhelmed by those of local enhancement in the zebra finch experiment.

Although the principal purpose of the present experiments was to control the effects of demonstrator-deposited odor cues in order to isolate stimulus enhancement, the effects of the box demonstrators' behavior in Experiment 2, which are likely to have been mediated by scent cues, are of some interest in their own right. Scent cues may originate in traces of saliva, perhaps containing food particles, and/or secretions from the scent glands on the demonstrators' forepaws and snout being transferred to the lever during responding. The results of Experiment 2 raise the possibility that these cues do not merely attract or avert the observer to the object manipulated by the demonstrator (e.g., Galef & Beck 1985), but instead or in addition act as discriminative stimuli by virtue of either their hedonic or their sensory properties. If this is the case, then identical odor deposits would be expected to have different effects on the behavior of an observer rat depending on the stimulus context in which they are encountered. For example, when contact with only one of two similar objects is rewarded, as in Experiment 2, scent cues may promote a response bias against the scented object when that stimulus has become attractive through conspecific observation and in favor of the scented object when the observer has seen a conspecific manipulating another, similar object. Thus, local enhancement is likely to be just one of many potential effects of demonstrator-deposited scent cues, and these effects may interact in a variety of ways with those of conspecific observation, promoting both convergence and divergence of behavior between observers and demonstrators.

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HEYES ET AL.

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