

Effects of Isolation Rearing and Mirror Exposure on Social and Asocial Discrimination Performance

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Four experiments examined the effects of rearing in isolation on rats performance on discrimination-based and social learning tasks. After demonstrating that the rearing procedures produced similar results in an open field task to those previously established (Experiment 1), rats were subjected to two discrimination tasks: an instrumental occasion setting procedure (Experiment 3) and a nonspatial win-stay/lose-shift versus win-shift/lose-stay procedure (Experiment 4). Deficits in acquisition of the necessary discriminations were noted in the rats raised in isolation, but there were no differences between isolation-reared and socially reared subjects in response acquisition per se. In Experiment 2, rats were presented with an observational learning task using the bidirectional control procedure. Socially reared rats had a tendency to imitate the behavior they had observed, but rats raised in isolation performed the opposite behavior to that observed, indicating a failure to use a conspecific as a reference point in the task. The presence of a mirror during rearing in isolation was also investigated, but was found to have little effect in attenuating the above deficits in behavior. © 1996 Academic Press, Inc.

Investigations of the effects of rearing in isolation have led to the view that there is a critical period, from birth to 50 days old, in which isolation will produce relatively persistent alterations in behavior (e.g., Morgan, 1973). Isolation after 50 days of age does produce behavioral changes, but these are short-term and reversible (Einson, 1980). The effects of early isolation are wide-ranging and include hyperactivity (Morgan, 1973), lack of inhibition (Latane, Cappell, & Joy, 1970), slower habituation in the open field (Einson, Morgan, & Sahakian, 1975), retarded extinction (Morgan, Einson, & Morris, 1977), and impairments in radial maze performance (Einson, 1980).

As well as having effects on the rat's behavior, early social isolation has been shown to affect how the animal reacts in the presence of a conspecific (Latane *et al.*, 1970, 1972). Latane *et al.* (1970) demonstrated that long-

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term isolation produced a significant increase in gregariousness and social interaction, which could be reduced by very small intervals of social contact during the isolation period. Since social isolation produces differences in social behavior, the performance of isolation-reared rats may differ from that of socially reared rats on tasks that require interaction with a conspecific. One important feature of social development is thought to be learning through the observation of conspecifics, and in particular, through imitation (see Heyes & Dawson, 1990). The present study aimed to document whether isolation would impair the ability of rats to learn through observation.

In some respects the social learning procedure in which one animal responds based on the cues provided by another suggests an analogy with instrumental discrimination performance. In fact, such a parallel is the basis for several explanations of imitation learning and modeling (see Heyes, 1994a; Reed, 1994; Skinner, 1969). If isolation rearing impairs socially mediated learning by influencing the extent to which animals reared in isolation can perform discrimination tasks, this rearing treatment would be expected to impair performance on a range of asocial discrimination tasks. In fact, an impairment in a simultaneous discrimination task due to social isolation has been noted by Jones, Marsden, and Robbins (1991). The present report sought to extend this investigation by examining the performance of rats reared in social isolation on two tasks: occasion setting, in which responses are only reinforced in the presence of a particular stimulus, and win-shift lose-stay/win-stay lose-shift tasks, in which reward is only obtained for specific responses depending on the outcome of previous responses.

The second aim of the present series of experiments was to examine whether the presence of mirrors during rearing in isolation would attenuate the effects of isolation-rearing on behavior. Many studies have been carried out to investigate the reaction of animals to their mirror image. It has been claimed that some species, such as the orangutan and chimpanzee, have a capacity for self-recognition (e.g., Gallup, 1970; Suarez & Gallup, 1981; but see Heyes, 1994b), but mostly the subjects tested have responded to the mirror image as if it were a conspecific. For example, monkeys typically treat a mirror image as another monkey and show social behavior toward it (Anderson, 1984, see also Tinbergen, 1951; Smythe, 1962, for similar observations using other species). These latter findings have prompted the use of mirrors in attempting to reduce stress in isolated animals. Parrott, Houpt, and Misson (1988) held sheep in an isolation pen in the presence and absence of mirrors. Using a number of behavioral (e.g., bleats) and physiological (e.g., cortisol and prolactin levels) measures of stress, it was noted that isolation produced a significant increase in stress, and that this effect was ameliorated by the presence of a mirror during isolation rearing. Similarly, Anderson (1981) noted that the behavioral deficits produced in isolation-reared macaques could

be attenuated by the presence of a mirror. Although there is evidence that mirrors may attenuate behavioral deficits produced through isolation in some species, there is no evidence relating to rodents.

EXPERIMENT 1

The first experiment sought to demonstrate that the present rearing procedures were effective in producing previously established differences between socially and isolation-reared rats. The open field test has previously been used to assess the level of activity (Einon *et al.*, 1975) and fear (Salmon & Stanford, 1989) of laboratory rodents. An animal is placed in an enclosure that contains no objects, but which has been marked into equally sized areas. The number of times the areas are entered in a specific time period is then recorded. In typical studies involving isolation-reared rats, the subjects are exposed to the open field twice. Generally, there is a reduction in activity between the trials for the socially reared rats, but not for the isolates, suggesting that fear has declined to a lesser extent in the isolates. In the present experiment, the amount of activity in the center of the maze and in the periphery was also used to assess the level of fear exhibited by the subject. The level of fear is defined as activity at the edges of the field compared to the center (see Salmon & Stanford, 1989). The level of activity in the regions of the open field is to be preferred to a time-based measure, since it is possible that a rat may freeze in the center of the field, which on a time-based measure would suggest little fear, whereas, in fact, this conclusion would not be warranted.

In addition to the comparison of socially reared and isolate rats, the effect of the presence of a mirror on performance was also assessed in the present experiment. If the mirror serves to ameliorate deficits produced by isolation rearing, then it might be expected that the behavior of rats reared in isolation with a mirror present would be more like that of socially reared rats than would the behavior of rats reared in isolation without a mirror.

Method

Subjects. Fifty-two Lister Hooded rats were bred and reared in the laboratory. All were born over a period of 5 days. The rats were weaned at 21 days and rehoused in one of four rearing conditions: Social plus mirror, in which the subjects were housed in same-sex pairs, with an unbreakable, acrylic mirror along the entire length of one wall of the cage ($n = 14$); Social-no mirror, in which the subjects were housed in same-sex pairs ($n = 14$); Isolation with mirror, housed singly with a mirror as in the social plus mirror group ($n = 11$); Isolation-no mirror, housed singly with no mirror ($n = 13$). All the cages used for the housing were molded white plastic with metal grid tops. The cages measured $42 \times 20 \times 24$ cm.

At 50 days old, the rats were all placed in same-sex pairs, in which the two rats in each pair belonged to the same experimental group. Throughout the rearing period, and between experiments, the rats had food and water

TABLE 1

Mean Number of Areas Entered in the Three Parts of the Open Field (Center, Middle, and Periphery) by the Four Groups on Trial 1 and Trial 2 of Experiment 1

	Trial 1			Trial 2		
	Cen	Mid	Per	Cen	Mid	Per
Social/mirror	7.0	18.4	30.9	9.9	18.4	21.0
Social/no mirr	6.5	14.9	34.9	8.3	16.4	22.0
Isolate/mirror	7.3	19.5	39.5	8.4	19.3	26.1
Isolate/no mirr	8.2	19.4	41.5	7.6	19.7	30.1

freely available in the home cage. During experiments the rats were reduced to 85% of their free-feeding body weight, but still had constant access to water in the home cage. They were maintained on a 12/12-h light/dark cycle, with lights on at 0800. Testing took place in the light portion of the cycle.

Apparatus. A circular enclosure (circumference = 245 cm, diameter = 78 cm) with a painted black-matt acrylic floor and metal walls with a dull nonreflective surface was used. The floor was marked into 27 equal areas with indelible ink, as shown in Fig. 1. The three areas in the center of the field were referred to as the "center," the next ring of areas as the "middle," and the outer ring as the "periphery."

The field was illuminated from one side by a 60-W bulb attached to the top of the wall of the field. Testing was carried out in a quiet darkened room, with the experimenter positioned behind the light source.

Procedure. Each rat was given two 3-min trials, with an intertrial interval (ITI) of 1 min. For each trial, the rat was placed in one of the central areas and released. The number of times the rat's back legs entered each of the areas was then noted. Scoring was achieved by tally-marking area entries on a plan of the open field. During the ITI, the rat was removed from the open field and placed in a holding cage. The field was wiped clean of feces with a dry cloth between each trial and between successively tested rats.

The running order of rats was random with respect to sex and experimental group to reduce any effects that time of day may have on activity levels of the rats. The rats were also run in an order that ensured that each animal was not run directly before or after its cagemate. Several rats not involved with this experiment were placed in the open field before the experimental groups, so that all the rats were exposed to the smells of other animals in the enclosure.

The same observer carried out all the trials, and at the time of scoring the observer did not know the rearing condition of the subjects.

Results and Discussion

Table 1 displays, for all groups, the mean number of times areas in the center, middle, and periphery were entered, during each trial. Inspection of

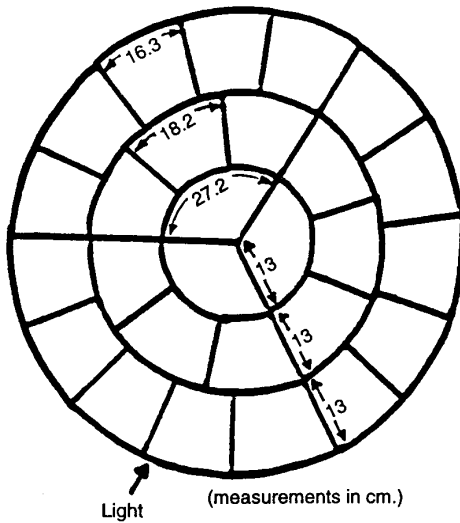


FIG. 1. Schematic representation of the open field apparatus used in Experiment 1.

these data reveals that, in both trials, the rats entered more areas around the periphery than in the middle of the field and entered more areas in the middle of the field than in the center. In general, fewer areas were entered on trial 2 than on trial 1. This reduction consisted largely of the subjects entering fewer areas in the periphery on the second trial. The isolation-reared rats entered more areas than the socially reared rats on both trial 1 and trial 2. This difference consisted largely of the isolate animals entering a greater number of areas in the periphery than the socially reared rats. There was little difference between the rats reared with and without mirrors between trials, or between areas during a trial.

These data were subjected to a four-factor analysis of variance (ANOVA) with Rearing (social versus isolation), Mirror (present versus absent), Trial (first versus second), and Area (center versus middle versus periphery) as factors. A rejection criterion of $p < .05$ was adopted for this and all subsequent studies. This analysis revealed statistically significant main effects of Rearing, $F(1,48) = 4.59$, Trial, $F(1,48) = 31.58$, and Area, $F(2,96) = 90.72$. None of the interactions, except that between Trial and Area, $F(2,96) = 45.85$, proved to be statistically reliable.

To allow further comparison between the groups, the percentage of entries that were made to areas in the center and in the periphery of the field were calculated for trial 1 and trial 2. The means for these scores are displayed in Table 2 for each of the four groups of subjects. Inspection of the data reveals little difference in the percentage of areas entered in either the center or the periphery between any of the groups on trial 1. However, during trial 2 there

TABLE 2

Mean Percentage Areas Entered in the Center and Periphery of the Open Field, by the Four Groups on Trial 1 and Trial 2 of Experiment 1

	Trial 1		Trial 2	
	Cen	Per	Cen	Per
Social/mirror	13.1	53.6	22.0	39.5
Social/no mirr	11.6	62.0	18.6	47.7
Isolate/mirror	11.3	58.2	15.9	48.1
Isolate/no mirr	12.0	59.6	13.1	53.1

was a marked increase in the percentage of times areas in the center were entered by both of the socially reared groups. There was a decrease in the number of areas entered in the periphery in these two groups. Both groups of isolation-reared animals showed little change on trial 2 from their performance on trial 1.

These data were subjected to a four-factor ANOVA (Rearing \times Mirror \times Trial \times Area) which revealed significant main effects of Trial, $F(1,48) = 14.51$, and Area, $F(1,48) = 145.51$, and significant interactions between Trial and Area, $F(1,48) = 43.62$, and a three-way interaction among Rearing, Trial, and Area, $F(1,48) = 4.74$. Subsequent analysis of the difference in entries to areas the central region between trial 1 and trial 2, revealed a significant difference between these trials for the socially reared rats (collapsed across mirror factor), $F(1,44) = 86.92$, but there was no statistically significant change for the isolation-reared animals, $p > 0.05$.

That the socially reared rats entered more areas in the central region of the field on trial 2 than on trial 1 suggests that during the second trial, the rats were familiar with the field and consequently less afraid. The isolation-reared animals, however, showed no reliable difference in the number of areas entered in the center between trial 1 and trial 2. These findings are consistent with those of Eimon *et al.* (1975), who demonstrated that isolation-reared rats behaved in both trials like socially reared animals placed in a novel field. Thus, these results suggest that the present rearing procedures produced results similar to those reported in previous studies. The presence of a mirror in the present study had no reliable effect on the rats' behavior.

EXPERIMENT 2

Heyes and Dawson (1990; see also Heyes, Dawson, & Nokes, 1992) have provided evidence of observational learning in socially reared rats. In these experiments, a rat which had observed a demonstrator pushing a joystick in one of two directions pushed the joystick in the same direction as the demonstrator when initially exposed to the joystick. In the present experiment, the

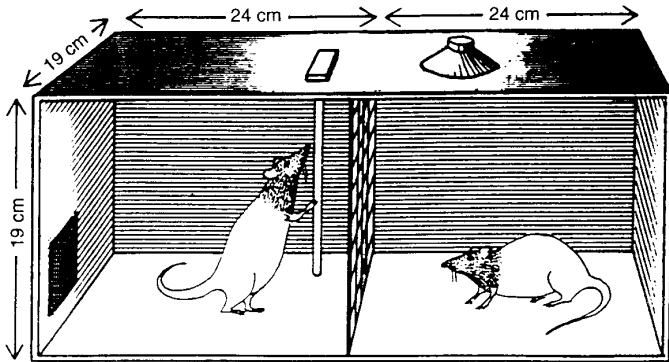


FIG. 2. Schematic representation of the apparatus used in Experiment 2.

observational learning of isolates and socially reared rats was compared using the bidirectional-control procedure developed by Heyes and Dawson (1990). It was hoped that this task would detect any effects of differential rearing on the ability to learn a simple response-reinforcer contingency by observation. Again, this study tested whether the presence of a mirror during rearing in isolation would attenuate any deficit noted in those animals.

Method

Subjects and apparatus. The same subjects as employed in Experiment 1 were used. However, the subjects were now housed in same-sex groups of two or four, with another adult animal which had previously been trained to push the joystick in one of two directions. The apparatus was that employed by Heyes and Dawson (1990) and is displayed in Fig. 2.

Procedure. Sixteen joystick demonstrator rats (8 male and 8 female) were trained to push a joystick either to the left or to the right. The demonstrator animals were initially given three sessions of magazine training. During each session, reinforcement (one 45-mg Noyes pellet) was delivered on a random time (RT) 45-s schedule. Thirty pellets were delivered per session. The delivery of a pellet was accompanied by a tone and brief illumination of the food tray. Following magazine training, the demonstrators were trained to push a joystick. A small deflection of the joystick (approximately 2 cm) in the allotted direction was reinforced by the delivery of a food pellet. Each session lasted until 50 reinforcers had been obtained. Once the demonstrator had acquired a fairly high response rate and was pushing in the reinforced direction only, the deflection required to obtain a reinforcer was increased in gradual stages to approximately 7 cm, and training continued until the animal was achieving a reasonable response rate and accuracy. The final stage of training involved running the demonstrator with a dummy observer in the other side of the chamber. This procedure was followed in order to habituate the demonstrator

TABLE 3
 Mean Discrimination Ratios (Left Responses/Left + Right Responses) for Subjects Observing
 Left-Hand Right-Pushing Demonstrators in the Four Groups in Experiment 2

Demonstrator	Left	Right
Social/mirror	0.52	0.49
Social/no mirr	0.60	0.48
Isolate/mirror	0.46	0.66
Isolate/no mirr	0.32	0.60

to the presence of other rats. Each demonstrator was then housed with two or four of the experimental subjects.

Training of the experimental subjects consisted of four sessions of magazine training (as described for the demonstrator subjects), followed by the test session. The test session commenced with the demonstrator animal being placed in the side of the chamber with the joystick. The experimental animal observed the demonstrator pushing the joystick in the allotted direction. Each time the demonstrator pushed the joystick, it received a food pellet. Following 50 reinforcements, the demonstrator was removed from the box and the observer placed in the compartment containing the joystick with a minimum of delay. Pushes of the joystick in either direction were reinforced for the experimental subjects. The required deflection for the experimental subjects was reduced to 2 cm.

Results and Discussion

Response rates were obtained for the subjects that observed left-pushing demonstrators and for those that observed right-pushing demonstrators. There were no pronounced differences between the rates of response in any of the eight subgroups. A three-factor ANOVA (Rearing \times Mirror \times Observation condition) revealed no statistically significant main effects or interactions, all $ps > .10$.

Table 3 displays the mean discrimination ratio for each of the four groups. The discrimination ratio was calculated for each rat by dividing the number of reinforced left responses made by the total number of reinforced responses (left plus right = 50). Inspection of these data suggests that socially reared rats that had observed left-pushing and right-pushing differed marginally in their directional preferences. Subjects that had observed a left-pushing demonstrator tended to push to the left (indexed by a discrimination ratio greater than 0.50), and subjects that had observed a right-pushing demonstrator tended to push to the right (indexed by a discrimination ratio lower than 0.50). In contrast, isolation-reared rats that had observed left-pushing made more responses to the right, and isolation-reared animals that had observed right-pushing demonstrators made more responses to the left.

These data were subject to a three-factor ANOVA (Rearing \times Mirror \times Direction) which revealed a significant interaction between Direction and Rearing, $F(1,44) = 6.18$. No other main effect nor interactions were significant. Analysis of the simple main effect of observation for the socially reared rats (collapsed across mirror factor) revealed no statistically significant difference between the rats that observed a left- and a right-pushing demonstrator, $p > .10$. However, there was a statistically significant difference between the isolate rats (collapsed across mirror factor) that witnessed a left- and a right-pushing demonstrator, $F(1,44) = 47.40$.

Thus, although not statistically significant, the numerical difference that existed in the socially reared group was consistent with previous demonstrations of observational learning in socially reared subjects; socially reared rats tended to push the joystick in the same direction relative to their own bodies as had their demonstrators (see Heyes & Dawson, 1990). However, the striking finding from the present experiment was that the isolation-reared rats showed the reverse pattern of results from that typically noted with socially reared subjects. Instead of pushing the joystick in the same direction as their demonstrators, the isolation-reared rats pushed in the opposite direction. This suggests that the isolated rats did not use the conspecific as a reference point when encoding the joystick movement, as is thought to be the case with socially reared subjects (Heyes & Dawson, 1990). Instead, they may have responded to the movement of the joystick across their own visual field. The presence of a mirror, again, had no effect on behavior in the joystick test.

EXPERIMENT 3

The third experiment examined the effect of the social isolation and mirror manipulations upon performance of instrumental responding when under the control of an occasion setter. The subjects were presented with a task in which a response to an illuminated lever would result in food, but responses to a darkened lever would not result in food. In addition to extending the empirical documentation of the effects of isolation rearing, and the possible ameliorative effects of mirror-rearing, this task allows assessment of the degree to which discrimination performance per se is impaired. This experiment also enables a partial replication of the results reported by Jones *et al.* (1991), who noted poor simultaneous light/dark discrimination in isolation-reared rats.

Method

Subjects. Thirty-two of the subjects were selected for this experiment. These subjects were selected randomly from the original set of 52 with the following constraints. There were 16 socially reared and 16 isolation-reared rats. Within each of these sets, 8 had been exposed to mirrors and 8 had not. Of each of these sets of eight subjects, half were male and half were female. The animals were housed in same-sex, same-group pairs.

Apparatus. Four identical operant conditioning chambers (Campden Instruments Ltd.) were used. Each chamber was housed in a light- and sound-attenuating case, and ventilated by a fan that provided background masking noise (65 dB(A)). Each chamber had two levers, both of which were permanently inserted into the chamber. Each lever was made of transparent Perspex, and had a light bulb mounted behind the lever, outside the chamber, which could be used to illuminate the lever. The illumination or darkening of the response lever served as the stimulus in the present experiment. A jeweled houselight was located on the ceiling of the chamber and this could be used to provide an additional stimulus. This light was not employed in the present experiment. Reinforcement (which consisted of one 45-mg food pellet) was delivered to a centrally located, recessed, food tray that was covered by a clear Perspex, hinged flap. Apart from the visual signal, the chamber was not illuminated during the course of the experiment.

Procedure. Subjects were initially magazine trained in two 20-min sessions, during which food was delivered according to an RT 45-s schedule. For the first session, the magazine flap was taped open to allow easy access to the food pellets. During the second session, and for all future sessions, the flap was lowered to its standard resting position. Following magazine training subjects were taught to lever-press in one session, during which every response to each of the two levers was reinforced (i.e., a concurrent continuous reinforcement (CRF) schedule was in operation).

The critical phase of training commenced immediately after the above pretraining. In this phase all subjects were given the same treatment. At the start of a session one of the two response levers would be illuminated and the other would be darkened. For half the subjects in each of the conditions the darkening of the lever served as the S+, and for the other half the illumination of the lever served as the S+. Responses to the lever associated with the S+ could produce food according to a variable ratio (VR) 3 schedule (range 1–5). Responses to the lever associated with the S– did not produce food. These contingencies lasted for 3 min. After this period, the illuminated lever was darkened, and the previously darkened lever was illuminated. This lasted for a further 3 min, during which responses to the S+ lever were reinforced according to a VR-3 schedule, and responses to the S– lever were never reinforced. During the course of a session, each lever was illuminated three times, each for a 3 min duration. Thus, the session was 18 min long. Subjects received six sessions of such training.

Results and Discussion

The rates of response emitted to the levers in the presence of the stimulus, and in its absence, were calculated for all four groups. A four-factor ANOVA (Housing, group versus isolate, \times Mirror, presence versus absence, \times Stimulus, presence versus absence, \times Session) conducted on these data revealed no main effects or interactions except Session, $F(5,140) = 3.10$, reflecting

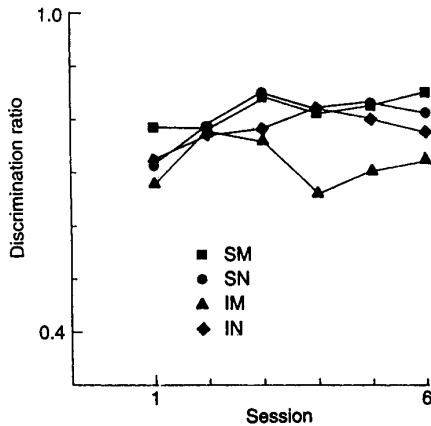


FIG. 3. Group-mean discrimination ratios for all groups over the six sessions of Experiment 3. SM, socially reared with a mirror; SN, socially reared with no mirror; IM, isolation-reared with a mirror; IN, isolation-reared with no mirror.

acquisition of the leverpress response; Stimulus, $F(1,28) = 132.25$, reflecting a greater response rate in the presence of the stimulus; and the Session by Stimulus interaction, $F(5,140) = 4.80$, indicating acquisition of control over responding by the S+ over the course of training.

Figure 3 displays the mean discrimination ratios for the four groups of subjects in each session. This score was calculated by dividing the total number of responses to the S+ lever by the total number of responses to both levers (S+ and S-). Inspection of these data shows that there was little difference at any point in training between the two groups reared socially. Both of these groups had higher discrimination ratios than the groups reared in isolation. A three-factor ANOVA (Housing \times Mirror \times Session) revealed significant main effects of Session, $F(5,140) = 2.48$, and of Rearing, $F(1,28) = 3.54$. No other main effect or interaction was significant.

The results obtained using discrimination ratios demonstrate that socially reared subjects performed the task better than those raised in isolation. These results corroborate those of Jones *et al.* (1991) and support the view that isolation rearing impairs subsequent ability to perform discrimination tasks. Moreover, the fact that a deficit was found in the rats reared in social isolation provides evidence that, even after extended periods of social housing (over 2 weeks), the effects of isolation rearing were still pronounced. As in the previous experiments, the deficit produced by social isolation was not ameliorated by the presence of a mirror.

EXPERIMENT 4

To examine further the effect of isolation rearing and mirror-rearing on discrimination performance, the subjects' ability on either a win-stay/lose-

shift or a win-shift/lose-stay contingency was examined. This task represents a form of discrimination in which reinforcement is presented upon the emission of one of two responses depending upon the outcome of the previously emitted response. Specifically, the rats were trained in a two-lever conditioning chamber. One group of rats obtained reinforcement according to a win-stay/lose-shift contingency and the other according to a win-shift/lose-stay contingency. For both of these contingencies, the outcome of the first half of a trial, in conjunction with the contingency in operation, would determine the response to be reinforced in the second half of the trial.

Method

Subjects and apparatus. The same subjects and apparatus as described in the previous experiment served in the present study.

Procedure. The subjects continued to experience the discrimination training outlined in Experiment 3 until there were no differences between the groups; all were responding in the presence of the S+ to a far greater degree than in the presence of the S-.

Following this training, the subjects were divided into two groups ($n = 16$). One group experienced the win-stay/lose-shift contingency (Group Win-stay), and the other experienced the win-shift/lose-stay contingency (Group Win-shift). In each of these groups, there were eight socially reared and eight isolation-reared subjects, four of which had experienced mirrors and four which had not, and there were two males and two females in each of the mirror-experience subgroups.

Subjects in the two main groups of interest (Win-stay and Win-shift) were treated identically except for the rule that governed reinforcement. Each trial in this training consisted of two elements; an information stage and a choice stage. The houselight was illuminated throughout each trial. The intertrial interval was 30 s, and during this period the chamber was in darkness.

Information stage. One lever was randomly selected and the S+ (illumination or darkening of the lever) was presented on this lever. If the rat completed the response requirement within the specified time on this lever, the S+ was terminated, and the trial continued. The response requirement was one response for Sessions 1 and 2, two responses for Sessions 3 and 4, and three responses for the remainder of the experiment. Completion of the response requirement sometimes led to the delivery of a food pellet (i.e., a win trial) and sometimes did not (i.e., a lose trial). If the rat did not fulfil the response requirement, the S+ was terminated, the trial was abandoned, and an ITI of 30 s commenced.

Choice stage. The choice stage commenced 1 s after completion of the information stage of the trial. During this part of the trial, the S+ was presented on both levers. The identity of the correct lever (i.e., the lever to be reinforced) during the choice stage was determined by a combination of the identity of the lever associated with the S+ in the information stage, and the

TABLE 4
 Mean Percentage Trials Correct for the Individual Rules of the Two Contingencies in the Four Groups in Experiment 4

	Win-stay/lose-shift		Win-shift/lose-stay	
	Win	Lose	Win	Lose
Social/mirror	88.0	53.0	68.3	54.3
Social/no mirr	85.2	47.2	67.4	60.5
Isolate/mirror	90.0	56.8	56.6	55.8
Isolate/no mirr	74.5	51.7	56.5	53.7

outcome of the response. During the choice stage, rats in the win-shift/lose-stay group were required to press the lever that was not associated with the S+ in the information trial if reward had been given in the information stage, but were required to press the lever that had been associated with the S+ in the information stage if no reward had been given. Rats in the win-stay/lose-shift group were required to press the lever that had been associated with the S+ in the information stage if reward had been delivered in the information stage, but were required to respond to the lever that had not been associated with the S+ in the information stage if no reward had been delivered.

The choice stage was complete when the rat had made the required number of leverpresses on one of the levers. The response requirement was identical to that in operation during the information stage. If the rat had chosen correctly, the levers were darkened, and a food pellet was delivered after which the ITI began. If the rat did not fulfil the response requirement, the S+ was terminated, the trial was abandoned, and an ITI of 30 s commenced.

Sessions lasted until the rat had completed 40 trials, or until 40 min had elapsed. There were 15 sessions of critical experimental training, but due to machine failure in recording data, only data from the final five sessions of training were available for analysis.

Results and Discussion

The group-mean response accuracy for each of the four rules governing reinforcement delivery is displayed in Table 4. Data for the socially reared and isolation-reared groups are presented separately. Response accuracy was calculated by summing the number of trials in the last five sessions on which the animal correctly performed the rule and dividing this by the total number of times the rat correctly performed the rule plus the number of times that the rat performed incorrectly in relation to the rule. Trials on which the response criterion was not satisfied were excluded from this analysis. Examination of these data shows that the win-based rule was performed better than the lose-based rule in the win-stay/lose-shift contingency, but there was little

difference between the win-shift and lose-stay rules in the alternative contingency. Moreover, rats reared socially appeared to perform the win-based rules better than the lose-based rules. The mean for the performance of all the socially reared animals on the two win-based rules was 77.2, and this score was 67.2 for the rats reared in isolation. There was little difference in the performance of the lose-based rules.

A four-factor ANOVA (Rearing \times Mirror \times Contingency, win-shift/lose-stay versus win-stay/lose-shift \times Rule, win versus lose) conducted on these data revealed significant main effects of Contingency, $F(1,24) = 9.22$, and Rule, $F(1,24) = 93.64$. There were also significant interactions between Contingency and Rule, $F(1,24) = 42.36$, and between Rearing and Rule $F(1,24) = 4.41$. Subsequent analysis of the interaction involving the rearing condition revealed that there was a significant difference between the socially and isolation-reared groups (collapsed across mirror and contingency factors) on the win trials, $F(1,24) = 26.00$, but there was no difference between these groups on the lose trials, $F < 1$.

These data show that rearing in isolation produces an effect on win-stay/lose-shift and win-shift/lose-stay performance. Rats reared in isolation appear to perform poorly on a win-based rules compared to socially reared animals.

GENERAL DISCUSSION

The present set of experiments demonstrated a set of effects of social isolation on behavior. Experiment 1 replicated an effect of isolation in the open field task noted previously (e.g., Einon *et al.*, 1975). These results suggest that the present rearing conditions did produce similar deficits to those noted in previous studies. Rats reared in isolation performed a discrimination/occasion setting task less well than socially reared subjects. In Experiment 4, isolation-reared rats appeared to have a general deficit in acquiring win-stay/lose-shift and win-shift/lose-stay contingencies compared to socially reared rats. In Experiment 2, it was noted that the rats reared in isolation failed to show imitation and in fact appeared to do the opposite to that normally found with rats reared in social conditions. It should be noted, however, that the standard imitation effect, found elsewhere to be reliable (e.g., Heyes *et al.*, 1992), was not noted in the present experiment.

From the results of experiments reported here, it would appear that the presence of mirrors was ineffective in preventing the detrimental effects of rearing rats in isolation. It is difficult, of course, to interpret null results, and there are a number of possibly trivial explanations for this lack of an effect. For example, the mirror's lack of effectiveness could have been due to inappropriate positioning in the rats' cages, so that the mirror image was not perceived as a conspecific. Possibly, the rat initially perceived the image as a conspecific but then habituated to the stimulus since no behavioral feedback was provided.

Returning to the performance of the socially reared versus the isolation-

reared animals, it is possible to rule out a number of explanations for the differences noted in behavior. The deficits in isolation-reared rats are unlikely to be due purely to hyperactivity. Isolation-reared animals displayed some hyperactivity in the open field (entered more areas than the socially reared animals), and therefore it might have been expected that they would be more active in the apparatus in Experiments 2, 3, and 4, resulting in a lack of attention to the relevant cues (the demonstrator in Experiment 2, and the discriminative stimulus in Experiment 3). However, since the response rates of socially and isolation-reared rats were comparable in Experiments 2, 3, and 4, there is no evidence to support this hypothesis. The isolates could have been more fearful of novel situations, as suggested by the open field task, but this similarly would not explain the fact that response rates were similar in the two groups in Experiments 2 and 3. Given this, it appears that more specific deficits in learning ability needs to be postulated to explain the behavior of the isolates.

Of particular interest is the tendency, noted in Experiment 2, of isolation-reared rats to push a joystick in the opposite direction to that in which they have seen it being pushed by a conspecific. This finding suggests that the isolation-reared animals learned through observation, but that they did not learn the same thing as typically noted in socially reared animals (e.g., Heyes & Dawson, 1990; Heyes *et al.*, 1992). Rats reared in groups apparently equate the demonstrator's responses with their own and learn by observation a relationship between directional responding and reinforcement. In contrast, the behavior of the isolates in the present Experiment 2 may have been due to learning by observation about a stimulus-reinforcer relationship, specifically that movement of the joystick in a particular direction within the observer's visual field signals food-related cues.

Prior to offering any explanation of these effects, it should be noted that use of the same subjects in a series of experiments might have compromised the level at which significance was tested by each analysis of variance. For example, if significant differences between any two groups were caused initially by a type 1 error (e.g., assignment of generally less active/mobile animals to the socially deprived condition), then this type 1 error will pervade statistical comparisons when the same animals are compared on the same performance measures employed in later experiments. Although initially the subjects were randomly assigned to groups and the same set of animals was not consistently used in all experiments (only a subset of the animals was employed in Experiments 3 and 4), this possibility may limit the generality of the present claims.

Explanations of isolate performance are usually given in terms of a general impairment in learning (e.g., Eimon, 1980). The present data from Experiments 3 and 4 support the notion of impaired learning in isolates by extending the range of tasks over which an impairment is noted to discrimination-based tasks. One reason for this impairment might be that the isolate animals, due

to a lack of contingent feedback on their behavior, develop an impairment in learning similar to that noted after exposure to a learned helplessness procedure. Although there is some evidence to support such a view (Einon *et al.*, 1982), it would be unwise to do more than note the possibility at this time.

REFERENCES

- Anderson, J. R. (1981). *Mirror image stimulation and behavioral development in stump-tail macaques*. Ph.D. thesis, University of Stirling, Stirling.
- Anderson, J. R. (1984). Monkeys with mirrors: Some questions for primate psychology. *International Journal of Primatology*, **5**, 81–98.
- Daly, M. (1973). Early stimulation of rodents: A critical review of present interpretations. *British Journal of Psychology*, **64**, 435–460.
- Davidson, T. L., & Jarrard, L. E. (1989). Retention of concurrent conditional discriminations in rats with ibotenate lesions of hippocampus. *Psychobiology*, **17**, 49–60.
- Dawkins, M. S. (1990). From an animals point of view: Motivation, fitness, and animal welfare. *Behavioural and Brain Sciences*, **13**, 1–61.
- Einon, D. F. (1980). Spatial memory and response strategies in rats: Age, sex, and rearing differences in performance. *Quarterly Journal of Experimental Psychology*, **32**, 473–489.
- Einon, D. F., Morgan, M. J., & Sahakian, B. J. (1975). The development of inter-session habituation and emergence in socially-reared and isolated rats. *Developmental Psychobiology*, **8**, 553–559.
- Einon, D. F., Will, B. E., & Morgan, M. J. (1982). Effects of postoperative environment on recovery from dorsal hippocampal lesions in young rats. *Quarterly Journal of Experimental Psychology*, **32**, 121–134.
- Gallup, G. G. (1970). Chimpanzees self-recognition. *Science*, **167**, 86–87.
- Heyes, C. M. (1994a). Social learning in animals: Categories and mechanisms. *Biological Review*, **69**, 207–231.
- Heyes, C. M. (1994b). Reflections on self-recognition in primates. *Animal Behavior*, **47**, 909–919.
- Heyes, C. M., & Dawson, G. R. (1990). A demonstration of observational learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology*, **42B**, 59–71.
- Heyes, C. M., Dawson, G. R., & Nokes, T. (1992). Imitation in rats: initial responding and transfer evidence. *Quarterly Journal of Experimental Psychology*, **45B**, 229–240.
- Jones, G. H., Marsden, C. A., & Robbins, T. W. (1991). Behavioral rigidity and rule-learning deficits following isolation rearing in the rat: Neurochemical correlates. *Behavioural Brain Research*, **43**, 35–50.
- Latane, B., Cappell, H., & Joy, V. (1970). Social deprivation, housing density, and gregariousness in rats. *Journal of Comparative and Physiological Psychology*, **70**, 221–227.
- Latane, B., Nesbitt, P., Eckman, J., & Rodin, J. (1972). Long- and short-term social deprivation and sociability in rats. *Journal of Comparative and Physiological Psychology*, **81**, 69–75.
- Morgan, M. J. (1973). Effects of post-weaning environment on learning in the rat. *Animal Behaviour*, **21**, 429–442.
- Morgan, M. J., Einon, D. F., & Morris, R. G. M. (1977). Inhibition and isolation rearing in the rat: extinction and satiation. *Physiology and Behaviour*, **18**, 1–6.
- Pacteau, C., Einon, D. F., & Sinden, J. D. (1989). Early rearing environment and dorsal hippocampal ibotanic acid lesions: long term influences on spatial learning and alternation in the rat. *Behavioral and Brain Research*, **34**, 79–96.
- Parrot, R. F., Houpt, K. A., & Misson, B. H. (1988). Modification of the responses of sheep to isolation stress by the use of mirror panels. *Applied Animal Behavior Science*, **12**, 3–13.
- Reed, P. (1994). Learning theory: The determinants of conditioned responding. In D. Tantam & M. Birchwood (Eds.), *Psychology and the Social Sciences* (pp. 22–41). Glasgow: Gaskell.

- Salmon, P., & Stanford, S. C. (1989). Beta-adrenoceptor binding correlates with behaviour of rats in the open field. *Psychopharmacology*, **98**, 412–416.
- Skinner, B. F. (1969). *Contingencies of reinforcement: A theoretical analysis*. New York: Appleton Century Crofts.
- Smythe, R. H. (1962). *Animal habits: The things animals do*. Springfield, IL: Thomas.
- Suarez, S. D., & Gallup, G. G. (1981). Self-recognition on chimpanzees and orangutans, but not gorillas. *Journal of Human Evolution*, **10**, 175–188.
- Tinbergen, N. (1951). *The study of instinct*. London: Oxford University Press.

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