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EFFECTS OF DIFFERENTIALLY REINFORCED PRE-EXPOSURE ON SIMULTANEOUS ODOUR DISCRIMINATION LEARNING IN THE ALBINO AND PIGMENTED RAT (*Rattus norvegicus*)

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ABSTRACT: Pigmented dark agouti and albino Wistar rats were compared for the effect of differentially reinforced pre-exposure to peppermint as a positive and vanilla as a negative odour cue. Both types of rat showed significantly enhanced performance on the simultaneous odour discrimination task with the same cues, when compared to control groups not pre-exposed to the odour cues. However, the pigmented rats had steeper learning curves than the albinos, with the albino controls performing significantly worse than the other groups. The results are discussed in terms of task components of cue significance and response regulation. It appeared that the response component was more difficult for the albino rats compared to the pigmented rats.

In this experiment pigmented and albino rats were compared for the efficacy of differentially reinforced pre-exposure to odour cues, in enhancing subsequent learning of a simultaneous odour discrimination task. In earlier studies we showed that differentially reinforced pre-exposure to three dimensional shapes (a triangle and a circle), in which one of the two cues was associated with food, significantly enhanced performance in a subsequent simultaneous discrimination learning task with the same or similar cues (Bell & Livesey, 1977, 1981). Pigmented (dark agouti) rats showed significantly greater transfer from the visual-tactual prior exposure than did albino rats even though there was no significant difference between them in the control condition (where no prior exposure had occurred). We demonstrated that the albino rats did not learn as much about the shape cue during prior exposure as did the pigmented rats and we attributed this to a difference in salience of the exposure stimuli for albino and pigmented animals in this situation (Bell & Livesey, 1981).

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Lubow, Rifkin, and Alek (1976) suggested that pre-exposure may be more effective with odour cues since it employs a more dominant sensory modality for the rat. The rat has a complex nasal cavity with intricate convolutions and large sorptive surface area, ideally suited to analysis of odorants. Behaviourally, a sniffing strategy is used which appears to be applied for effective detection, discrimination and recognition of odours (Youngentob, Mozell, Sheehe, & Hornung, 1987). Rats have been shown to attend to odour cues in preference to auditory or visual cues (Nigrosh, Slotnick, & Nevin, 1975); to show rapid learning of a go/no go discrimination with odour cues (Eichenbaum, Shedlack, & Eckmann, 1980) and learning-set performance with odour cues far superior to that with visual cues (Jennings & Keefer, 1969; Slotnick & Katz, 1974). According to Jennings & Keefer (1969), variety of rat (pigmented vs. albino) was not a significant factor in learning various odour discriminations which included peppermint and vanilla cues.

Most studies of odour pre-exposure have used nonreinforced exposure, exploring the effects of preference for odour (Cornwell, 1976) or adaptation to odours (Laing & Panhuber, 1980). No study previous to the present one has examined the effect of reinforced prior exposure to odour cues on subsequent discrimination performance. Lubow, et al.'s (1976) experiment investigated the effect of 14 days of nonreinforced pre-exposure to odour cues on discrimination performance with the same or other cues. In that study pre-exposure was for 2 hours daily, either to lemon versus water cues (presented at two outlets in the cage), or wintergreen versus water. The discrimination task was in a Y-maze with approach to the strong odour (lemon or wintergreen) reinforced with a food pellet and approach to water nonreinforced. Findings from the experiment included enhancement of discrimination learning with the same cues if pre-exposure was given in a different environment to the test environment. If, however, the pre-exposure and test environments were the same, discrimination learning appeared to be retarded. These findings are similar to our results from pre-exposure to non-differentially reinforced shape cues, where discrimination learning was enhanced only if pre-exposure and discrimination tasks were presented in different environments. However, with differentially reinforced pre-exposure, we found that discrimination learning was enhanced only if the pre-exposure and test environments were similar (Bell & Livesey, 1981).

In order to compare our odour discrimination results with those from the earlier shape discrimination experiments we used essentially the same apparatus and procedures as those employed in our earlier studies, rather than those that have been employed in other studies of odour discrimination learning. Previous tasks involved a simple approach response to the positive stimulus (Braun & Marcus, 1969; Eichenbaum et al., 1980; Kimble & Zack, 1967; Lubow et al., 1976; O'Grady & Jennings, 1972; Ruddy, 1980; Slotnick & Nigrosh, 1974; Staubli, Fraser, Farraday, & Lynch, 1987). For our odour task the discriminanda were presented in a Grice-type manual apparatus with the stimuli mounted side by side on two panels, as described in Bell & Livesey (1981, 1988) for the visual/tactual tasks.

For presentation of the odour cues a gauze pad (5 × 5 cm) was taped to the middle of each stimulus panel and the odours were instilled into these pads. The rat had to push open the positive stimulus panel to retrieve the food reward, a small pellet of dog food presented from behind it. Since this apparatus and procedure had not previously been used for odour discrimination, preliminary studies were used to determine appropriate odour stimuli. Initially, lemon and water odours as used by Lubow et al. (1976) were investigated. However, these proved to be unsatisfactory in the discrimination apparatus. Both albino and pigmented rats showed an aversion for the lemon stimulus (not noted in previous reports), and performance was erratic in some animals. An alternative discrimination task, between peppermint and vanilla was tried, as this had been used previously with no reported problems or indication of possible preference or aversion for either odour (Jennings & Keefer, 1969; Kimble & Zack, 1967). Two groups of 6 brown rats each, were employed, one group trained with vanilla as the positive and peppermint as the negative stimuli and the other group with peppermint positive and vanilla negative.

This experiment revealed a clear preference for the vanilla positive condition evidenced by a significantly better performance by the vanilla positive group at all stages of acquisition. This effect was probably due to some aversion to the peppermint since the six drops of this essence used, produced a pungent and powerful odour. The need for the animal to approach close to the source of the odour in order to push the panel could have enhanced this aversion. It was also noted that the performance of individual rats was less erratic than in the lemon/water task. With such a pronounced preference for the vanilla cue, reinforced pre-exposure could have little additional effect on the performance of this task. We, therefore, decided that a peppermint-positive/vanilla-negative task would be suitable for the pre-exposure experiment, provided the strength of the vanilla and peppermint cues was reduced to reduce the aversion to peppermint.

Thus, with odour cues, pre-exposure was expected to be more effective for the albino rats since this involves a more dominant sense. We, therefore, decided to investigate the effect of differentially reinforced pre-exposure to odour cues on learning of an odour discrimination task presented in the same environment and comparing albino and pigmented rats. We predicted that an effective enhancement of discrimination learning would follow differentially reinforced pre-exposure in the albino group as well as in the pigmented group.

METHOD

The design of the experiment was a two by two factorial: Preexposure Condition (Control vs. Differentially Reinforced) by rat type (Brown vs. Albino). Planned comparisons, to test whether each of the two differentially reinforced (DR) groups performed significantly better than their respective control groups, were made using one-tailed t tests for the measure of number of trials to criterion. An unweighted means analysis of variance (because of uneven group numbers) was used to compare the rat types on this measure (Kirk, 1968). Rate of acquisition in terms of mean correct responses per day was examined by a Rat Types × Conditions × Days analysis of variance.

Animals

Eighteen male agouti rats (*Rattus norvegicus*, DA strain) from the colony bred within the Psychology Department and 18 male albino (Wistar strain) rats from the Biological Sciences Breeding unit, University of Western Australia were employed in the study. Animals were aged between 65-75 days at the beginning of the experiment. Housing consisted of racked cages (36 × 26 × 20 cm) with wire mesh back and front and solid metal sides. Rats were housed two or three from the same group per cage. The housing room was air conditioned (constant 22°C) with a 12 hr light/dark cycle.

Apparatus

This was essentially the same as that used in our shape discrimination experiments (Bell & Livesey, 1981).

Exposure Apparatus. There were six units, each consisting of a small mesh cage (36 × 26 × 20 cm) joined along one of the longer sides to a wooden compartment (25 × 26 × 20 cm) painted flat grey. The compartments could be separated by a metal slide. A clear Plexiglas lid was hinged over each compartment. In the end of the wooden compartment opposite the cage section, were two openings, 9 × 9 cm and 4.5 cm apart. Behind the openings was a 9 cm projecting ledge on which two food containers could be placed so that one was behind each opening. Each container had a small tray at the bottom that was the only access to the food. The front of each container, including the food tray, was covered by an aluminium panel (14 × 7.5 cm) that rats pushed inwards to reach the food. The food was a minced, concentrated dog food, preferred by the rats to the standard laboratory pellets. Cod liver oil was mixed with the food to provide a vitamin supplement. For the presentation of the odour cues the food container panels were covered with white opaque plastic. A dark gauze pad, 5 × 5 cm, was taped to the middle of the panel with the bottom of the pad 2 cm from the bottom. For the control groups two drops of water were placed on the food container panels, for the DR groups in pre-exposure the container without food had two drops of vanilla essence placed on the gauze pad. The container with the food in it had two drops of peppermint essence placed on the pad. The essences used were pure Fauldings food essences.

Test Apparatus. The two compartments were identical to those of the exposure apparatus but, instead of food containers, there were two small food wells behind the openings in the discrimination apparatus. Aluminium panels (16 × 10 cm) covered with white plastic were hung on a metal rod behind the openings. A gauze pad was taped to each panel. Two drops of vanilla essence were placed on one pad and two drops of peppermint were placed on the other. The panels were held closed against the back of the opening by magnetic tape. A gray wooden shield could be lowered in front of the stimuli. Reinforcement was obtained by pushing the entire stimulus panel backward exposing the food well. The incorrect response panel was held shut by a small wooden block placed behind it. When the incorrect panel was pushed partially open a microswitch on the block was closed and this activated a light outside the compartment signalling an error to the experimenter.

Procedure

Pre-exposure. Rats were handled by being placed on a tray, stroked and picked up for 20-min each day, placed on 22 hour food deprivation and introduced to dog food for 4-5 days prior to starting pre-exposure. All rats were given two 40-min feeding periods in the exposure apparatus, one in the morning and the other in the afternoon. During the 15 days of pre-exposure this was their only access to food. Water was available ad lib. The animals were fed singly in the exposure apparatus. At the beginning of the exposure period the rat was placed in the cage section, then the dividing shield was raised to allow access to the whole apparatus. To counteract association of food with a particular position, positions of the food containers were altered twice each period according to Fellows' (1967) revised Gellerman sequence. These changes were made at the beginning of the session and again halfway through. At that stage the rat was returned to the cage section with the slide inserted. It was then allowed re-entry when the container positions had been adjusted according to the sequence. Between exposure periods the food containers were removed and the air exhausted. For the first two days the panels on the food containers were taped open to accustom the rats to feeding from the containers.

For the 9 rats in each control group (Wistar and DA) pre-exposure was to containers (one with food, one empty) with no distinctive odour (water). For the 9 rats in each differentially reinforced (DR-Wistar and DR-DA) group, pre-exposure was to the peppermint scented panel on the container with food and the vanilla scented panel on the empty container. All animals were trained on the discrimination task with peppermint as the positive and vanilla as the negative cue.

On completion of the 15 days pre-exposure the rats were maintained on the 22 hour food deprivation schedule and discrimination training commenced. Pre-exposure was discontinued when testing began.

Discrimination Training. All rats were given 10 trials per day on the peppermint/vanilla discrimination. A noncorrection procedure was used. A response (push) to the negative stimulus panel signalled the end of the trial, the shield was lowered and the rat returned to the starting compartment. For a response to the positive stimulus panel, the rat pushed the panel fully open. The food pellet, made from the minced dog food was then presented to the animal on the end of a rod by the experimenter, so that the smell of the food did not interact with the odor stimuli. The food pellets were stored well away from the apparatus.

The positions of the two stimuli were determined for each trial by the Fellows sequence. The criterion for learning of the discrimination was 90% correct responses on three consecutive days. Rats had to complete the criterion trials with both stimulus panels unblocked to ensure that they were not using any extraneous cues that might have been provided by the block, e.g., pressure cues. Testing was conducted by the two experimenters. Between the end of the test session for one rat and the beginning for the next the stimulus panels were removed from the apparatus and the air exhausted for several minutes.

RESULTS

Results were considered for two measures: trials to criterion, that is, a broad measure of ability to learn the task; and rate of acquisition, measured by number of correct responses out of the 10 attempted each day.

Trials to Criterion

Using this measure, the principle hypothesis that differentially reinforced pre-exposure to the cues would result in significant improvement in acquisition of the discrimination task was tested using

TABLE 1
Mean Number of Trials to Criterion, with Standard Errors for Each Group

	CDA	*CW*	*DRDA*	*DRW*
Mean	82.2	117.5	67.7	80
Standard Error	4.93	13.72	4.93	8.65

Note: CDA = Control Dark Agouti. CW = Control Wistar. DRDA = Differentially Reinforced Dark Agouti. DRW = Differentially Reinforced Wistar.

the planned comparisons. Two animals, one from each of the albino groups, failed to reach criterion. These two animals, therefore, could not be included in the criterion analyses as they did not have trials to criterion measures. Mean trials to criterion for all the other rats in the four groups are shown in Table 1.

For both the albino Wistar and pigmented DA rats, performance of the DR group was significantly superior to the C group as assessed by one-tailed t tests (CDA VS DRDA, $t(16)=2.16$, $p = .025$; CW VS. DRW, $t(16)=2.24$, $p < .025$). Analysis of variance was by unweighted means because of loss of the two albino rats that did not reach criterion. This revealed that differences in both Rat Type ($F(1,30) = 9.6$, $p<.01$) and Condition ($F(1,30) = 8.06$, $p < .01$) were significant with a nonsignificant interaction. This analysis confirmed that for both W and DA rats, the differentially reinforced exposure significantly enhanced learning (nonsignificant interaction). Overall, the pigmented DA rats reached criterion in significantly fewer trials than the albino (W) rats, as shown in Table 1.

Rate of Acquisition

Figure 1 shows performance for each of the four groups in terms of mean correct responses per day. All 9 animals from each group were included in this analysis as failure to reach criterion did not affect this measure. All 18 of the brown rats and 10 of the 18 albinos had reached criterion by 10 days so this was taken as a cut off point for this analysis. Animals that had reached criterion before 10 days were given a score "10" for each subsequent day to Day 10.

These data were examined by a Rat Type (Wistar vs. DA) × Condition (control vs. exposure) × Days analysis of variance for the first 10 days of acquisition. In overall acquisition over the 10-day period the pigmented animals did not differ significantly from the albinos ($F(1,32) = 2.49$, $p > .05$), however both groups given differentially reinforced prior exposure performed significantly better than the control groups ($F(1, 32) = 16.38$, $p < .01$). The interaction between Rat

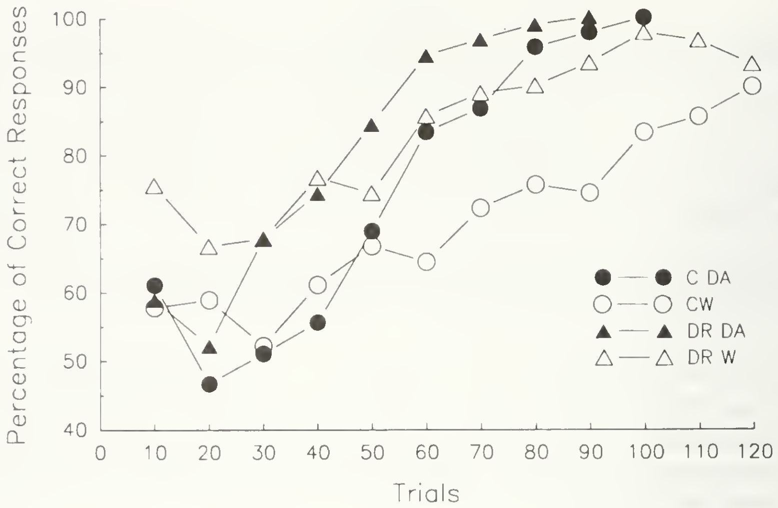

FIGURE 1. Mean percent correct responses for blocks of 10 discrimination trials for the four groups in the experiment (Control Dark Agouti, Control Wistar, Differentially Reinforced Dark Agouti and Differentialy Reinforced Wistar).

Type and Condition was not significant. The days effect was significant (*F*(9, 288) = 4.92, *p* < .01). The Days × Rat Type interaction was significant (*F*(9, 288) = 4.92, *p* < .01), because of the flatter learning curves of the albino groups, compared to the steeper curves of the DA groups (Figure 1). The Days × Condition and the Days × Condition × Rat Type interactions were not significant. An epsilon factors for degrees of freedom adjustment was made for the days analysis. Thus, on this measure, although W and DA rats did not differ significantly in total number of correct responses, they did differ in rate of change of correct responses over the first 100 trials.

DISCUSSION

Both the pigmented DA and albino Wistar differentially reinforced prior exposure groups showed a significant enhancement of learning despite the fact that the negative cue (vanilla) had previously been found in the pilot study to be preferred to the positive (peppermint) cue.

Caza and Spear (1984) have commented that the effect of pairing an odour cue with positive reinforcement may simply reduce neophobia by making the odour less aversive in comparison to a novel odour. When a preference test is used to examine the effect of pre-exposure to a single odour, a control condition (e.g., exposure to the odour without reinforcement) is necessary to account for the neophobia reducing effect. As we used a discrimination task rather than a preference test we did not include such a control condition. Any neophobic reaction in our control groups would only be present at the earliest stage of training. However, as is evident in Figure 1, on the first 20 trials one of the differentially reinforced groups (DRW) performed better than its control group and one (DRDA) did not perform any better than its control group. Superiority of each DR group over its control became more obvious as trials increased, when neophobia would no longer be present.

The enhancement effect of odour pre-exposure for the albino rats in this experiment was much stronger than that observed in the earlier visual-tactual exposure to shapes where a significant effect was evident only in the early stages of learning. In that study, brown rats given shape pre-exposure performed significantly better than their albino counterparts. On the odour task there was no such simple relationship. The extent of facilitation from DR exposure was the same for DA and Wistar rats, on both trials to criterion and correct response measures (neither Rat Type × Condition interaction was significant). However on the correct response measure, there was a significant Days × Rat Type interaction because of both Wistar groups' rates of acquisition being slower than that of the DA groups.

As the shape of learning curves was similar for the C and DR groups within each variety of rat, as evidenced by the absence of any interaction effect between Days and Conditions, the differences between the rat varieties appear to be related to aspects of the discrimination task which were common to both the control and experimental conditions. The pigmented rats made more errors in the early stages of learning and this showed particularly as an absence of enhancement of odour test performance on the first 20 trials for the brown DR group. This may well have been due to the brown rats showing a strong reaction when first introduced into the test apparatus even though it was very similar to the exposure apparatus. They were very reluctant to respond on the first two or three days of testing. They displayed freezing responses often refusing to leave the holding section of the discrimination apparatus for the stimulus area for several minutes. Even when DRDA rats were forced to stay in the stimulus compartment by lowering the dividing shield, they were reluctant to make a response and appeared to respond without attending to the odours. They would immediately return to the holding area often without retrieving the food reward, suggesting that they initially found the different test apparatus aversive. On the other hand, the albino rats appeared unaffected by the transfer to the test situation and responded readily, taking many fewer minutes to complete 10 trials. Differences in neophobic or exploratory behaviour have been reported among various strains of rats (Harrington, 1971).

The slower rates of acquisition by the albinos over the later stages of learning led to the differences in trials to criterion between the two types of rat. It is unlikely that there are physiological differences related to odour detection in the two strains to account for the generally slower rate of acquisition by the albinos. Moulton and Beidler (1967) found no differences in nasal mucosae between albino and pigmented rats, and albino rats had a slightly lower threshold for odour detection. Beidler found no evidence that albino rats were more adversely affected by respiratory infection with corresponding partial anosmia. None of the subjects in our study displayed overt symptoms of respiratory infection. It should also be noted that the Wistars were more variable on trials to criterion measure (as shown by respective standard errors in Table 1).

The different performance patterns of albino and pigmented rats found with the odour task had also been evident in a two dimensional (visual) shape discrimination task and a tactual reduced visual task (Bell & Livesey, 1988). It appears that once the pigmented rats had adapted to the apparatus, they were better able to maintain discrimination performance with respect to the relevant cues. In the later stages of learning it was noted that, in both the odour and the visual tasks some of the albino rats, although performing at between 70-90 percent correct responses on one day, were not able to maintain criterion performance level (90%) over the required number of days. On some trials these animals appeared to be using irrelevant cues. In particular, the motor response involved (panel push) seemed to lead some of the albino rats to attempt to select the correct panel on the basis of the pressure required to open it. Two experimenters independently observed rats surreptitiously and gently pushing at the corner of one or both panels. If the panel gave easily, the rat would push it completely open. The same strategy had been observed in a previous study in tasks with reduced visual cues (Bell & Livesey, 1988). However, this tactic was irrelevant to the task as the pressure required to open the panels did not differ systematically and was certainly not related to which was the positive or negative odour stimulus. The strategy resulted only in the albino rats continuing to make errors. This kind of behaviour and accompanying erratic performance was much less evident in the brown rats.

This response strategy in the albinos appeared to be reduced by the effect of the differentially reinforced pre-exposure, which made the odour cues prepotent in the task. We, therefore, suspect that for the albino controls, the odour cues were not as potent and that the nature of the panel push response predisposed them on some occasions to test the panels for ease of opening. In an experiment by Jennings and Keffer (1969), with a different type of response (running into the alley with the correct odour cue), albino and hooded rats did not differ in the learning of odour discriminations. Thus, it appears that albino rats may compensate for reduced visual capability by the use of other sensory information. In the context such as our discrimination task where it was assumed that the odour cues would be quite potent, to some animals, kinesthetic cues offered a conflicting source of possible (but incorrect) information.

With this experiment we have extended our reinforced pre-exposure paradigm to learning with odour cues. Differentially reinforced pre-exposure to odours significantly enhanced discrimination learning for both pigmented and albino rats when the exposure and test environments were very similar. This can be contrasted with the Lubow et al. (1976) finding that prior exposure to nonreinforced odour cues did not enhance discrimination performance when the environments were the same, but was facilitatory when the environments were quite different. We have previously explained these effects in terms of two different learning processes (Bell & Livesey, 1981). One involves learning of stimulus properties whereby particular properties defining a stimulus within the total stimulus input are isolated (Gibson, Walk, and Tighe, 1959). This is exemplified in Lubow et al.'s study and in our non-differentially reinforced prior exposure studies. The other process in which stimuli (cues) without relevance for an animal may acquire significance when associated with events that are of importance for its survival, e.g., food, we have described as learning of cue significance. It appears from a number of experiments that stimulus property learning transfers across different environments but that cue significance does not transfer in this way (Bell & Livesey, 1981). Our concept of cue-significance learning is related to other postulations involving sign tracking (e.g., Jenkins, Barrera, Ireland, & Woodside, 1978), and transfer of control (e.g., Thomas, 1985; Bolles, 1975).

We had expected that pre-exposure to odour cues would be more effective than that with the shape cues used previously. This was certainly the case for albino rats, who did not learn a great deal from the pre-exposure to the shape cues but did benefit considerably from the learning situation with the olfactory cues. The comparable albino DR group on the shape task took a mean of 146 trials to reach criterion (66 trials more than the odour DR group), while the control group took 154 trials (36.5 trials more than the odour group). For the brown rats, the DR group on the shape task reached criterion in 124 trials (56.3 more than the odour DR group), and the C group in 146 trials

(63.8 more than the odour C group). The magnitude of the facilitatory effect from DR pre-exposure for the pigmented rats thus appeared similar for the shape and odour pre-exposure.

While the odour task appeared to be learned more rapidly than the shape task, we had anticipated that the odour task with clearly distinct vanilla and peppermint cues would have been learnt more quickly than was the case in this experiment. However, the particular method that we used placed some constraints on the rate of learning. Furthermore, it is difficult to compare our results with other studies because often the authors did not give a trials-to-criterion measure or relevant procedural details such as the learning criterion. Experiments using the maze-learning procedure often yielded very rapid learning; with various odour cues, criterion was reached in 30-60 trials (Jennings & Keefer, 1969); in Ruddy (1980), with lemon/lime, vinegar/alcohol, clove/cinnamon cues, 30-40 trials to criterion but with the not very stringent criterion of 8/10 correct responses. In Kimble and Zack's (1967) study control animals learnt an anise/peppermint task in a mean of 8l trials.

While the present task was not learnt as quickly as some of the others reported, we did use a very stringent criterion of 9/10 correct responses over three consecutive days. Also the response component of our task (pushing open the positive cue panel) was probably more difficult than the maze type tasks and this appeared to be particularly so for the albino rats. According to Mackintosh (1983), most simultaneous discrimination tasks require only approach to or contact with the positive stimulus for the correct response, (e.g., maze tasks). Such responses may be largely a product of a classical contingency between the positive stimulus and reinforcement, similar to an autoshaped response. In our task the response involved appears to be more difficult. In none of our pre-exposed experiments was there perfect transfer from differentially reinforced exposure to the discrimination task (Bell & Livesey, 1977, 1981). The panel push response (with non-correction) required further learning before criterion level of performance was reached. For some of the albino rats, the response provided a particular difficulty as it appeared to lead to attention to an irrevelant cue—the pressure required to open the panel.

The albino rats were shown to learn more from odour pre-exposure than they had from pre-exposure to shape (visual/tactual) cues. This is in line with findings from other studies comparing learning with olfactory and visual or auditory cues (Nigrosh et al., 1975). However, the slower acquisition rate of the albinos compared with the pigmented animals has suggested that the response component of the task provided a particular difficulty. This again emphasizes that the relationship between discriminative cues and the motor requirement of a particular response for a particular subject must always be taken into consideration when assessing the rate of learning (Bell & Livesey, 1985, 1988).

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