The poisoned partner effect in rats: Some parametric considerations

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Five experiments are reported establishing the poisoned partner effect (PPE) in rats as a robust phenomenon and indicating some of the factors that control its occurrence. Experiment 1 was a replication of Lavin, Freise, and Coombes (1980) and demonstrated that the PPE could be obtained under the conditions they described. Experiment 2 established that the PPE was not due to sensitization. Experiment 3 indicated that the nonpoisoned partner (NPP) had to be familiar with its poisoned partner in order for the PPE to be observed. Experiment 4 established that, under the conditions employed here, the NPP and its sick partner had to be paired together for at least 30 min following poisoning of the latter for the PPE to occur. Finally, Experiment 5 demonstrated that the NPP and its poisoned partner had to be paired together immediately following the poisoning episode. If 40 min or more was allowed to elapse following poisoning before the two were placed together, the PPE was attenuated. Taken together, these results indicate that the time course of the PPE is similar to that of the effects of the poisoning agent and suggest that some stimulus secreted by the poisoned rat and associated with the administration of the poison is the causative factor in the PPE.

As omnivores, rats appear to have developed a number of strategies for determining the positive or negative value of the foods they encounter. Numerous studies have shown that they can associate novel flavors with illness and avoid such flavors, even under conditions in which there is a considerable temporal delay between presentation of the flavor and the onset of illness (Barker, Best, & Domjan, 1977). Similarly, they are adept at learning to cope with deficiencies in their diet and to modify their preferences when presented with an adequate diet (Rozin & Kalat, 1971). Finally, recent studies have indicated that rats are able to associate flavors with the caloric value of a diet, learning to prefer flavors associated with rich diets (Bolles, Hayward, & Crandall, 1981). All of these abilities are individual, and yet the rat is a social creature living in colonial groups. It is no surprise, then, to discover that a number of social factors augment the abilities outlined above. These factors have been explicated by Galef (e.g., 1977), who demonstrated that weanling rat pups learn about "safe" foods from a variety of sources. First, they appear to pick up the flavor of the food that their mother consumes while she is lactating. Second, during the weaning period they appear to find adult rats extremely attractive and follow them to the food caches where the adults eat. As a result, they tend to consume the foods that the adults are consuming. Both of these factors mean that the young are weaned onto

"safe" foods and, as a result of their propensity to stick to familiar foods, weaning is far less dangerous than it otherwise might be.

If social factors are exploited to help the young rat get through the weaning period, it would be surprising if this were the only occasion on which social influences prevailed. Recently, Lavin, Freise, and Coombes (1980) reported a series of experiments that seemed to indicate that adult rats could also benefit from social influences during feeding. They found that rats would avoid consuming a novel flavor that was experienced prior to exposure to a sick rat. This phenomenon has come to be known as the poisoned partner effect, or PPE (Coombes, Revusky, & Lett, 1980; Lavin et al., 1980). Since these original studies, the PPE has been found to occur whether the nonpoisoned (NPP) rat consumes the novel flavor in the presence of or prior to exposure to the sick rat. Indeed, the NPP can consume the flavor up to 6 h before being placed with a sick partner, a delay gradient similar to that observed in the normal flavor-aversion paradigm (Coombes et al., 1980; Lavin et al., 1980). The aversion obtained is not a transferred aversion, since it occurs whether the poisoned rat has an aversion to the test flavor or not, although it is directly related to the amount of poison administered to the sick rat (Revusky, Coombes, & Pohl, 1982). Preexposure of the sick rat to the poison prior to its being paired with the NPP attenuates the PPE, probably because the poisoned rat is not as sick. Similarly, preexposure of the NPP to a number of poisoned rats prior to its receiving the pairing of the test flavor with a sick rat attenuates the aversion (Revusky et al., 1982). The PPE has also

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been observed with an odor CS (Bond, 1982). Finally, Stierhoff and Lavin (1982) have provided some evidence that the putative UCS is olfactory in nature in that the PPE is not observed in rats that have been made anosmic by the nasal administration of zinc sulfate.

However, although these early reports of the PPE were positive, Revusky, Coombes, and Pohl (1981) reported a failure to observe the PPE in guinea pigs and also noted that other investigators had failed to obtain the effect in rats. The present author has been similarly informed of failures to replicate in rats (Westbrook, personal communication). A problem of many failures to replicate an experiment is that the investigator often alters seemingly minor but important parameters, and then does not obtain the previous result. The present experiments sought to replicate the PPE in rats and then examined some of the factors that might influence it.

EXPERIMENT 1

The first study was designed to replicate as closely as possible the experimental design of Lavin et al. (1980) in order to establish a robust PPE.

Method

Subjects and Apparatus. Thirty male Wistar albino rats were used. They weighed approximately 355 to 432 g and were housed individually in wire-mesh cages (15 × 24 × 20 cm) located in an air-conditioned temperature-controlled room on a 12-h light/dark cycle with lights on at 7 a.m. The experimental procedures always took place during the light portion of the cycle. Food in the form of laboratory chow was available at all times, but access to water was provided only as indicated below.

Procedure. The exact details of the experimental procedure may be found in Lavin et al. (1980). Briefly, on the first 4 days (Days 1-4), the rats were divided into 15 pairs and allowed to drink from glass Richter tubes in the host rat's cage for 30 min daily. On Day 5, all rats were given individual access to 15 min of water in their home cages. At the end of the 15-min period, the water consumption was recorded and the bottles were placed back on the cages until conditioning. (Lavin et al. found that the PPE was not obtained if the animals were deprived of fluid just prior to conditioning.)

Conditioning took place on Day 6. The host rat and visitor rat in each pair were weighed and then placed together in the host's cage, where they were allowed access to a .6% saccharin sodium solution (w/v) for 2 h. Both rats from each pair were then removed and weighed, and their consumption of the saccharin solution was noted. Subsequently, the visitor from each of 12 pairs received an intraperitoneal injection of 10 ml/kg of .3 M LiCl. Both the hosts, which will be referred to as the nonpoisoned partners (NPP), and the visitors, which will be referred to as the conditioning group (COND), were then returned to the NPP's cage for a further 2-h access to the saccharin. The remaining three pairs of rats were returned to the host's cage following weighing; neither host nor visitor was injected. These animals formed the control group (CONT). At the end of the 2-h period, all rats were weighed, and the consumption of saccharin was again noted.

Day 7 served as the test day, each animal being given access to the saccharin solution in its home cage for a 15-min period. Amount consumed was taken as an index of strength of aversion.

Results and Discussion

The animals drank a mean of 12.1 ± 4.8 ml of the saccharin solution and gained 1.4 ± 1.7 g of weight during the first 2-h period on the conditioning day. They lost 1.7 ± 2.6 g of weight and drank 3.9 ± 3.2 ml during the second 2-h period. Importantly, and in contrast to the findings of Lavin et al. (1980), there were no differences between the three groups—that is, NPP, COND, and CONT—in weight change at either period, or between the paired NPP and COND animals and the CONT group in saccharin consumption at either period.

The result of most interest is the amount of the saccharin consumed on the test day. This is illustrated for each group in Figure 1. (In this and subsequent experiments, the data for the COND animals, that is, the animals actually injected with the LiCl, are included in the figure for comparative purposes. However, since the major interest concerns the nonpoisoned animals, only they are included in the statistical analyses.)

As illustrated in Figure 1 and confirmed by a *t* test, the NPP animals consumed less of the saccharin than

Figure 1. Mean consumption of the saccharin solution on the test day for each of the three groups in Experiment 1. PP stands for poisoned partner, NPP for nonpoisoned partner, and CONT for control. Vertical lines denote standard deviations.

the CONT animals [$t(16) = 3.3$, $p < .005$]. This finding replicates that of Lavin et al. (1980). They suggested that the decrease in saccharin consumption displayed by Group NPP occurred because the NPP animals associated the saccharin flavor with the presence of the COND rat on the conditioning day. However, because there was no unpaired control group, one could interpret the reduced saccharin consumption of Group NPP as evidence of sensitization.

EXPERIMENT 2

One could argue that the results obtained in Experiment 1 and previously by Lavin et al. (1980) were due to sensitization in that there was no unpaired control group employed. Lavin et al. (1980) ran a study designed to take account of this factor by using one group that was exposed to a poisoned partner and one that was not, both in the absence of fluid. However, establishing that the PPE was not due to sensitization depended upon a null result, which was inappropriate, given the numbers of subjects in each group ($n = 6$, in each case). The findings of Coombes et al. (1980) that the PPE is attenuated as the interval between consumption of the flavor and the presentation of the sick rat is increased points to an associative account of the phenomenon. However, to establish that the effects reported here were due to associative learning rather than to sensitization, the present experiment employed a group in which an NPP was paired with a sick rat but in the absence of the flavor.

Method

Subjects and Apparatus. Thirty male Wistar albino rats weighing 410–574 g were used. They were housed, trained, and tested under conditions similar to those described for Experiment 1.

Procedure. The rats were divided into 15 pairs, and the procedure for the first 5 days was the same as that described for Experiment 1. Day 6 served as the conditioning day. The seven pairs of rats in the conditioning group were weighed, and then the host and visitor rats were placed together in the host's cage, where they were allowed access to the saccharin solution for 2 h. Both rats from each group were then removed and weighed, and their consumption of the saccharin solution was noted. Subsequently, the visitor from each pair received an injection of 10 ml/kg of .3 M LiCl. Both the hosts, which were the NPPs, and the visitors, which were the conditioning group (COND), were then returned to the NPP's cage for a further 2 h of access to saccharin. At the end of the 2-h period, all rats were weighed and the consumption of saccharin was again noted. The procedure for the remaining eight pairs of animals was identical except that they received water, not saccharin, on the conditioning day. These two groups of animals were included to control for sensitization, so, for expository purposes, they are called NPP-S and SENS, respectively. Day 7 served as the test day, each animal being given access to the saccharin solution in its home cage for a 15-min period. Amount consumed was taken as an index of strength of aversion.

Results and Discussion

The animals exposed to the saccharin on the conditioning day drank a mean of 19.8 ± 6.7 ml of the

saccharin solution and gained 5.1 ± 2.1 g of weight during the first 2-h period on the conditioning day. They drank 9.1 ± 4.0 ml during the second 2-h period. The animals receiving water drank a mean of 11.7 ± 2.4 ml during the first 2-h period and gained 3.9 ± 1.8 g of weight. During the second 2-h period, they drank 5.6 ± 1.2 ml. The animals that received the LiCl injections lost 1.53 g during the second 2-h period, following the injection. In contrast, the unpoisoned rats gained 2.8 g during the same period. This difference was significant [$t(28) = 3.5$, $p < .01$]. The differences in consumption between the rats receiving the saccharin and those receiving water were significant during both periods [$t(13) > 2.4$, $p < .05$, in both cases].

The result of greatest interest is the saccharin consumption on the test day. This is illustrated for each group in Figure 2. An analysis of variance on these data was significant [$F(2,22) = 19.8$, $p < .001$]. Newman-Keuls tests indicated that there were significant differences between Group NPP-S and both Group NPP and Group SENS ($p < .05$). These results indicate that the PPE observed in Experiment 1 was probably not due to sensitization. If the PPE was due to sensitization, one would expect groups NPP and NPP-S to evidence similar levels of consumption of the saccharin on the test day, since both were exposed to poisoned partners on the conditioning day. The fact that Group NPP consumed less fluid on test

Figure 2. Mean consumption of the saccharin solution on the test day in Experiment 2. COND denotes the group that received the saccharin together with an injection of LiCl on the training day. NPP stands for their nonpoisoned partners. SENS denotes the group that received water together with an injection of LiCl on the training day. NPP-S stands for their nonpoisoned partners. Vertical lines denote standard deviations.

than Group NPP-S indicates that an association between the saccharin and the PP is a necessary condition for the PPE to be observed. It might be objected that Group NPP-S had not received the saccharin prior to the test and thus was not an unpaired control group. This was so, but note that, as a result, Group NPP-S is a more conservative control, since its consumption may be reduced by both sensitization and neophobia.

It is interesting to note that the PPE appeared to be similar in strength to the enhanced neophobia to saccharin observed following the injection of LiCl in Group SENS. A similar finding was obtained when a novel odor predicted the presence of a poisoned rat (Bond, 1982). Certainly, the present results, together with those of Bond (1982) and Coombes et al. (1980), indicate that the PPE is probably due to the NPP animals' associating the flavor or odor CS with the presence of the poisoned partner.

EXPERIMENT 3

In the studies described by Coombes et al. (1980) and Lavin et al. (1980) and in Experiments 1 and 2, the NPP was familiar with the sick rat placed in its cage during the conditioning procedure; both animals had received access to water together for 4-5 days previously. Interestingly, in their reported failure to obtain the PPE in guinea pigs, Revusky et al. (1981) do not appear to have used this pretraining procedure. The possibility arises therefore that the PPE will be observed only when the NPP is familiar with the sick rat that is to function as the putative UCS. Experiment 3 examined this question.

Method

Subjects and Apparatus. Seventy-eight male Wistar albino rats weighing 340-570 g were used. They were housed, trained, and tested under conditions similar to those described for Experiment 1.

Procedure. The procedure for the first 5 days for all 39 pairs of rats was identical to that described for Experiment 1. Day 6 served as the conditioning day. Eighteen pairs of rats were allocated to the familiar-partner group. They were exposed to the .6% saccharin solution together for 2 h. At the end of this period, they were removed and weighed and the visitor was injected with 10 ml/kg of .3 M LiCl. At the same time, the saccharin was removed and the amount consumed noted. Subsequently, the host and the visitor were returned to the host's cage for a further 2 h with no fluid present. The nonpoisoned partners in this group will be referred to as Group FAM. [Note that the NPP experienced the sick rat after consuming the novel saccharin solution. This procedure has been shown by Coombes et al. (1980) to be as effective in producing the PPE as presenting the saccharin and the poisoned partner at the same time.] The 18 pairs of rats in the unfamiliar group received exactly the same exposure to saccharin as the familiar group. They differed in that following their initial exposure to the saccharin the normal visitor to a particular host rat was replaced by the injected visitor from another cage. The nonpoisoned partners in this group will be referred to as Group UNFAM.

The above procedure meant that, in both the familiar and the unfamiliar groups, the host and visitor animals had experienced

identical treatments up until the time of injection. They differed in that following injection of the visitor animals, the rats in Group FAM spent the second 2-h period in the presence of sick rats that were familiar to them, whereas the rats in Group UNFAM spent it in the presence of sick rats that were unfamiliar to them. The remaining three pairs of animals formed Group CONT. They were exposed to the procedure described for Group FAM except that neither host nor visitor was injected following exposure to the saccharin.

Day 7 served as the test day, on which each animal received 15 min individual access to the saccharin solution. Amount consumed was taken as an index of strength of aversion.

Results and Discussion

During their 2-h exposure to the saccharin solution on the conditioning day, the pairs of animals forming Group FAM drank 17.6 ± 7.8 ml, those forming Group UNFAM drank 16.2 ± 6.8 ml, and Group CONT drank 16.2 ± 3.1 ml. None of these differences were significant. The result of greatest interest is the saccharin consumption of the various groups on the test day. This is illustrated in Figure 3.

A one-way analysis of variance on these data was significant [$F(2,39) = 4.6$, $p < .05$]. Newman-Keuls tests indicated that the only significant difference was between Groups FAM and CONT, with Group FAM consuming less of the saccharin solution than Group

Figure 3. Mean consumption of the saccharin solution on the test day for each of the three groups in Experiment 3. FAM stands for the nonpoisoned rats that were familiar with their sick partners, UNFAM stands for the nonpoisoned rats that were unfamiliar with their sick partners, and CONT stands for control. Vertical lines denote standard deviations.

CONT ($p < .05$). This finding replicates that of Experiments 1 and 2 in demonstrating the PPE. The present study was designed to examine whether the NPP had to be exposed to a familiar sick rat in order to display the PPE. The results suggest that this is so in that Group UNFAM did not differ significantly from Group CONT.

That the NPP should be familiar with the sick rat in order to display the PPE seems eminently reasonable. Wild rats are colonial, forming closed anonymous groups. That is, they can discriminate colony members from strangers, although they cannot discriminate individuals within the colony (Barnett, 1963). Given this social organization and their antagonism towards strangers, rats will clearly be predisposed to learn about the aversive properties of food only from colony members with whom they are familiar.

Interestingly, there was a distinct difference between Groups FAM and UNFAM in their reactions to their sick partners. Casual observation indicated that Group UNFAM spent much more time investigating their sick partners than did Group FAM. This observation indicates that whatever it is about the sick rat that the NPP associates with the novel flavor, Group UNFAM was certainly in a position to perceive it.

Following the completion of this study, Revusky et al. (1982) published the results of a study indicating that the PPE can be obtained when the NPP is not familiar with its poisoned partner. Specifically, in their Experiment 1, they exposed their NPPs to a procedure in which the NPP was visited by a different partner for 2 h each day every other day for 14 days. Following this pretraining, the NPPs were exposed to yet another partner on the conditioning day. Despite the numerous changes in partners, they did display the PPE. It would appear from these results that if the NPP is accustomed to frequent changes in partner, then the PPE can be obtained using an unfamiliar poisoned partner. Interestingly, and in support of this suggestion, Revusky et al. did not use this elaborate pretraining procedure in a second experiment but did pair their NPPs with unfamiliar poisoned partners and failed to observe a robust PPE.

Finally, the finding that the PPE is not observed when the NPP is unfamiliar with its sick partner or has not gone through the pretraining described above suggests that this may have been the reason Revusky et al. (1981) failed to observe the PPE in guinea pigs. Clearly, this possibility must be examined before we can accept the conclusion that guinea pigs do not display the PPE.

EXPERIMENT 4

The previous experiments established that the PPE is a reliable phenomenon, that it is based upon asso-

ciative learning, and that it requires that the NPP be familiar with the sick rat. Thus far, there has been little examination of the temporal parameters important in demonstrating the PPE. Coombes et al. (1980) have demonstrated that the NPP can exhibit a flavor aversion when there is a temporal gap of up to 6 h between consumption of the flavor and exposure to the sick rat. This delay gradient compares favorably with that produced when an animal is made sick itself following consumption of the novel flavor (Revusky & Garcia, 1970). The final two experiments reported here were concerned with delineating the temporal parameters associated with actual exposure to the sick rat. First, Experiment 4 examined the question of how long the NPP and the sick rat need to be together for the former to display a PPE. Previous research and the experiments reported here all exposed the NPP to the sick rat for a constant 2-h period.

Method

Subjects and Apparatus. Fifty-four male Wistar albino rats, weighing 283 to 450 g, were used. They were housed, trained, and tested under conditions similar to those described for Experiment 1.

Procedure. The procedure for the first 5 days for all 27 pairs of rats was identical to that described for Experiment 1. Day 6 served as the conditioning day. Twenty-four pairs of rats were exposed to the .6% saccharin solution together for 2 h. At the end of this period, they were removed and weighed and the visitor was injected with 10 ml/kg of .3 M LiCl. At the same time, the saccharin was removed and the amount consumed noted. Subsequently, the host and visitor were returned to the host's cage with no fluid present. For six pairs, the rats remained together for 15 min before the sick visitor was returned to its own cage. This group is designated NPP-15. The remaining 18 pairs of rats stayed together for 30, 60, or 120 min with no fluid present ($n = 6$, in each case). These groups are designated NPP-30, NPP-60, and NPP-120, respectively. The remaining three pairs of rats formed Group CONT. They were exposed to the procedure described for Group NPP-120 except that neither host nor visitor was injected following exposure to the saccharin.

Day 7 served as the test day, each animal receiving 15 min of individual access to the saccharin solution. Amount consumed was taken as an index of aversion strength.

Results and Discussion

The pairs of rats drank 13.5 ± 4.0 ml of the saccharin solution on the conditioning day. The result of greatest interest is the saccharin consumption of the various groups on the test day. This is illustrated in Figure 4.

A one-way analysis of variance on these data was significant [$F(4,28) = 5.6$, $p < .01$]. Newman-Keuls tests indicated that Groups NPP-120, NPP-60, and NPP-30 differed significantly from Group CONT. No other differences were significant. These results indicate that the PPE can be obtained when the NPP is exposed to a sick rat for as little as 30 min (Group NPP-30 vs. Group CONT). Since the lithium chloride would have reached its maximal effect after 30 min, it would seem that whatever the putative UCS is in determining the occurrence of the PPE,

Figure 4. Mean consumption of the saccharin solution on the test day in Experiment 4. NPP stands for nonpoisoned partner. The suffix indicates the length of time the NPP was paired with its poisoned partner immediately following injection of the latter. CONT stands for control. Vertical lines denote standard deviations.

it appears to be related to the temporal influence of the LiCl.

EXPERIMENT 5

In Experiment 4 it was determined that the PPE could be obtained if the NPP was kept with its sick partner for 30 min immediately following its consumption of the novel saccharin solution and its partner's injection with LiCl. If this finding resulted from the NPP's being with its sick partner during the period of maximal effect of the LiCl, then exposure at any other time should be less effective in producing the PPE. Experiment 5 tested this prediction. Three groups of rats were paired with sick partners for 40 min immediately following a 2-h exposure to a novel saccharin solution. They differed in that, the partners of one group were injected with LiCl immediately before, the partners of a second group 40 min before, and the partners of a third group 80 min before being placed with their NPPs. Thus, the rats of all three groups consumed saccharin immediately before their poisoned partners were placed with them; they differed only in terms of how long previously their poisoned partners had been injected.

Method

Subjects and Apparatus. Fifty-four male Wistar rats weighing 355 to 486 g were used. They were housed, trained, and tested under conditions similar to those described for Experiment 1.

Procedure. The procedure for the first 5 days was identical to that described for Experiment 1. Day 6 served as the conditioning day. Thirty rats received a 2-h exposure to a .6% (w/v) saccharin solution in their home cages. At the end of this period, the rats were weighed, the saccharin solution was removed, and the amount consumed was recorded. Eighteen of the rats were then joined in their home cages by their normal partners for 40 min. The partners of six of the rats had been injected with 10 ml/kg of .3 M LiCl immediately prior to placement (Group IMM-40). The partners of a second group of six rats had been injected with LiCl 40 min prior to placement (Group DEL(40)40). The partners of a third group of six rats had been injected with LiCl 80 min prior to placement (Group DEL(80)40). To give an indication of what might be called the "normal" PPE, that is, the level of the PPE observed in previous experiments, six rats were paired with their poisoned partners for 2 h following their consumption of the saccharin (Group IMM-120). The remaining six rats formed the control group (Group IMM-CONT). Following their consumption of the saccharin, they were paired for 2 h. Neither host nor visitor was poisoned.

Day 7 served as the test day, each animal receiving 15 min individual access to the saccharin solution. Amount consumed was taken as an index of strength of aversion.

Results and Discussion

The 30 rats exposed to the saccharin solution on the conditioning day drank 12.7 ± 3.0 ml in the 2-h period. Of greatest interest is the saccharin consumption of the various groups on the test day. This is illustrated in Figure 5.

A one-way analysis of variance on these data was significant [$F(4,25) = 3.5$, $p < .05$]. Newman-Keuls tests indicated that Groups IMM-120 and IMM-40 differed significantly from Group CONT. No other differences were significant.

The present results replicate those of Experiment 4 in indicating that a PPE can be obtained with pairings of the NPP and its poisoned partner in as short a time as 40 min (Group IMM-40 vs. Group CONT). They also indicate that the time of pairing following injection of the poisoned partner is also important. Rats paired with their poisoned partners either 40 min (Group DEL(40)40) or 80 min (Group DEL(80)40) after they had been injected did not display a significant PPE. As suggested previously, the occurrence of the PPE appears to be correlated with the effects of the LiCl. One would expect some waning of the effects of the LiCl in Groups DEL(40)40 and DEL(80)40 and, as a result, some waning of their ability to produce a PPE in their NPPs. Just such a result was obtained in the present experiment. Together with the results of Experiment 4, the present data indicate that, for a PPE to occur, it is important for the NPP and sick rat to be paired together not only for a particular duration but also at a particular time.

Figure 5. Mean consumption of saccharin solution on the test day in Experiment 5. Groups IMM-120 and IMM-40 were paired with their poisoned partners for 120 and 40 min, respectively, immediately following injection of the latter. Groups DEL(40)40 and DEL(80)40 were paired with their poisoned partners for 40 min, 40 or 80 min following the injections. CONT stands for control. Vertical lines denote standard deviations.

GENERAL DISCUSSION

To summarize, the experiments reported here serve to establish the PPE as a robust effect, Experiment 1 providing a replication of Lavin et al. (1980) and Experiment 2 indicating that the effect is not due to sensitization. Furthermore, they indicate some of the parameters associated with the effect. Experiment 3 demonstrated that the NPP has to be familiar with the sick rat for a PPE to be observed. Experiment 4 established that the NPP and the sick rat had to be paired together for at least 30 min following poisoning of the latter for the PPE to occur. Finally, Experiment 5 determined that this pairing had to occur immediately following the poisoning episode; if it was delayed for even 40 min, the PPE was attenuated.

These results set some of the boundary conditions of the operation of the putative UCS leading to the PPE; however, they do not determine what that UCS is. Following the completion of this series of experiments, Stierhoff and Lavin (1982) reported that an intact olfactory system is necessary for obtaining the PPE. Specifically, NPP rats rendered anosmic prior

to being paired with a poisoned partner failed to display the PPE. This result suggests that the putative UCS leading to the PPE is olfactory in nature and is associated with the administration of the LiCl.

The present results suggest that whatever the nature of the olfactory stimulus produced, it is somewhat volatile and short-lived, delays of 40 min and 80 min successively attenuating the PPE (Experiment 5). Furthermore, while this olfactory stimulus may be necessary for the occurrence of the PPE, it is not sufficient. Thus, in Experiment 3, it was noted that nonpoisoned rats did not display the PPE if they were paired with unfamiliar poisoned rats. This was so despite the fact that causal observation indicated that there was considerable interaction between the nonpoisoned rats and their unfamiliar partners. Perhaps the unfamiliar surroundings and companion led the poisoned rats to secrete a somewhat different odor, which attenuated the PPE, or perhaps the unfamiliarity of the poisoned rats interfered with the nonpoisoned rats capacity to associate consumption of the novel flavor with the odor produced by the poisoned rat. Further research is needed to answer this question.

It would appear from the above that the sick rat acts as a quasi-UCS, and the olfactory stimulus that it emits leads the NPP to display a variety of effects similar to those that would be observed if the NPP had been poisoned itself following consumption of the novel flavor. Thus, preexposure of the NPP to a number of sick rats prior to the training day diminishes the PPE, as does preexposure of the poisoned partner to LiCl (Revusky et al., 1982). The insertion of a delay between the NPP's consumption of saccharin and exposure to the sick rat attenuates the PPE (Coombes et al., 1980). Furthermore, the PPE appears to be directly related to the length of time that the NPP is exposed to the sick partner (Experiment 4). Finally, the PPE is an associative phenomenon, not an outcome of sensitization (Experiment 2; Bond, 1982).

The PPE is clearly adaptive. If members of a colony can learn about the toxic consequences of particular foods as a result of the acute poisoning of only one of their number, the selective advantage of such a strategy in an omnivore such as the rat is obvious. The data reported in the present paper testify to the replicability of the PPE. What is needed now is further research to indicate the exact nature of the olfactory stimulus emitted and the mechanism by which the NPP associates this olfactory stimulus with the novel flavor or odor to which it has just been exposed.

REFERENCES

- BARKER, L. M., BEST, M. R., & DOMJAN, M. (1977). *Learning mechanisms in food selection*. Waco, TX: Baylor University Press.

- BARNETT, S. A. (1963). *The rat: A study in behavior*. Chicago: Aldine Press.
- BOLLES, R. C., HAYWARD, L., & CRANDALL, C. (1981). Conditioned taste preferences based on caloric density. *Journal of Experimental Psychology: Animal Behavior Processes*, **7**, 59-69.
- BOND, N. W. (1982). Transferred odor aversions in adult rats. *Behavioral and Neural Biology*, **35**, 417-421.
- COOMBES, S., REVUSKY, S. H., & LETT, B. T. (1980). Long-delay taste-aversion learning in an unpoisoned rat: Exposure to a poisoned rat as the unconditioned stimulus. *Learning and Motivation*, **11**, 256-266.
- GALEF, B. G. (1977). Social transmission of acquired behavior: A discussion of tradition and social learning in vertebrates. In R. A. Hinde, E. Shaw, & C. Beer (Eds.), *Advances in the study of behavior* (Vol. 6, pp. 77-100). New York: Academic Press.
- LAVIN, M. J., FREISE, B., & COOMBES, S. (1980). Transferred flavor aversions in adult rats. *Behavioral and Neural Biology*, **28**, 15-33.
- REVUSKY, S., COOMBES, S., & POHL, R. W. (1981). Failure of albino guinea pigs to exhibit Lavin's poisoned partner effect. *Behavioral and Neural Biology*, **32**, 111-113.
- REVUSKY, S., COOMBES, S., & POHL, R. W. (1982). US preexposure: Effects on flavor aversions produced by pairing a poisoned partner with ingestion. *Animal Learning & Behavior*, **10**, 83-90.
- REVUSKY, S. H., & GARCIA, J. (1970). Learned associations over long delays. In C. H. Bower & J. T. Spence (Eds.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 4) New York: Academic Press.
- ROZIN, P., & KALAT, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Review*, **78**, 459-486.
- STIERHOFF, K. A., & LAVIN, M. J. (1982). The influence of rendering rats anosmic on the poisoned partner effect. *Behavioral and Neural Biology*, **34**, 180-189.

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