duction among individuals born into confined laboratory populations (*18*) may result partly because these animals are familiar with each other before puberty.

The following conclusions can be drawn from the results of this experiment: (i) Sibling mating results in inbreeding depression in *P. m. bairdi*. (ii) Siblings paired at weaning age do not reproduce as readily when mature as do siblings paired when sexually mature. This may reduce the probability of inbreeding in mouse populations. (iii) The delay in reproduction due to prepubertal familiarity is independent of genetic effects since nonsibling pairs also exhibit it. The exact mechanism regulating this delay in reproduction due to familiarity of the pair is not yet known. Such a delay may result from any of several factors, such as interference of other behaviors with copulatory behavior, delayed sexual maturation, blockage of fertilization or implantation, resorption of embryos, or early abortion and ingestion of embryos. Elucidation of this mechanism, including the role played by pheromones (*19*) in delaying reproduction in familiar pairs, should be the object of further research.

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15. Weights of testes and seminal vesicles or ovaries and uteri did not differ between reproductive and nonreproductive individuals. Of the nonreproductive females, 13 had not recently ovulated, 6 had corpora lutea, and 1 was pregnant with two embryos.
16. The age in days of the youngest female to give birth in each group was: early siblings, 60; early nonsiblings, 61; late siblings, 73; and late nonsiblings, 74.
17. The difference in reproductive performance developed within the first 2 weeks. By day 9 (the median value for all groups combined) the early-mated pairs had produced only 25 percent (12/48) of their litters, while the late-mated pairs had produced 75 percent (39/52) of their litters.
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11 June 1974; revised 29 July 1974

Antihistamines Block Radiation-Induced Taste Aversions

Abstract. *When rats are treated with an antihistamine prior to being given sublethal doses of ionizing radiation, the formation of a conditioned saccharin aversion is completely inhibited. A profound aversion could be conditioned with histamine diphosphate as the aversive stimulus. The increase in histamine production after radiation exposure represents the physiological basis of radiation-induced taste aversions.*

Garcia, Kimeldorf, and Koelling (*1*) found that a taste aversion to saccharin-flavored water could be conditioned in rats by pairing consumption of the sweetened fluid with a 37-r whole body exposure to gamma rays. Similar taste aversions have been conditioned by pairing saccharin intake with injections of lithium chloride (*2*), apomorphine (*3*), cyclophosphamide (*4*), and many other poisons. All of these treatments have been presumed to cause the animal to become "sick," and the pairing of sickness with intake of the novel saccharin solution resulted in the subsequent conditioned taste aversion. The injections of lithium chloride, apomorphine, or cyclophosphamide make the rats ill, and these rats can easily be discriminated from sham-injected controls. With whole body x-ray and gamma-ray exposures up to 100-r (*5*), the rats do not appear to be sick and cannot be distinguished from sham-exposed controls except by the subsequent aversion to the taste solution. This subtle and interesting reaction of the rat to the radiation stimulus was first demonstrated in 1955, and the physiological basis of a radiation-induced taste aversion has been the topic of considerable research.

The aversion phenomenon was formerly attributed to gastrointestinal disturbances (*6*), but considerable doubt has been cast on this explanation (*7*). Partial body exposures have shown that it is not necessary to irradiate the head of the rat in order to produce the taste aversion, thus eliminating vision, olfaction, taste, or audition as necessary for conditioning the aversion (*8*).

The studies by Hunt and his coworkers (*9*) with parabiont pairs of male rats indicated that some humoral factor may be involved in conditioning the taste aversion. When the shielded (nonirradiated) partner of the parabiotic pair was allowed to drink saccharin 30 minutes after the nonshielded partner received a whole body exposure of 360-r, the shielded partner avoided the saccharin solution during a saccharin-water preference test administered 24 hours later.

We have shown that the maximal saccharin aversion develops 30 to 90 minutes after the onset of the radiation exposure (*10*), implying that the aversive consequence of the irradiation reaches a peak during this interval.. The histamine concentration in the blood of rats exposed to 600 r of x-rays reaches a peak 60 to 120 minutes after the exposure (*11*). The purpose of the experiments reported below was to determine if the injection of an antihistamine prior to radiation exposure would inhibit the formation of a saccharin aversion, thus providing evidence for a causal relation between aversiveness of the irradiation and radiation-induced histamine production.

Chlorpheniramine maleate was chosen as the antihistamine because it is an active histamine antagonist, but it has a minimum of undesirable side effects (*12*). Naive male albino rats ($N = 28$) were placed on a 23.5-hour water de-

privation schedule. For 5 days they were given access to water for 30 minutes per day. On day 6 (conditioning day), 14 rats were injected intraperitoneally with chlorpheniramine maleate (20 mg/kg). Immediately after the injection seven rats were exposed to 100 r of gamma rays at 9 r per minute (Chlor/100 r), and the other seven rats were sham-exposed (Chlor/sham). The remaining 14 rats were injected intraperitoneally with 0.15*M* NaCl (2 ml/kg). Again, seven rats were exposed to 100 r (NaCl/100 r) and seven were sham-exposed (NaCl/sham). Thirty minutes after the onset of the radiation or sham exposure all rats were allowed to drink approximately 10 ml of a 0.1 percent (weight to volume) sodium saccharin solution. This treatment regimen was chosen to assure maximal taste aversion conditioning (*13*). One day later, on day 7 (test day), all rats were allowed 20 minutes access to the saccharin solution. The mean intakes in milliliters) of saccharin for the 20-minute test were: Chlor/100 r, 15.6; Chlor/sham, 17.6; NaCl/100 r, 5.3; and NaCl/sham, 18.4. An analysis of variance across these means yielded an F of 16.6, and d.f. = 3,24, which was significant beyond the .01 level of significance. An orthogonal comparison indicated that the NaCl/100 r group was significantly different from the other three groups, which were not different from each other ($F = 48.0$; d.f. = 1,24; $P < .01$). These data show that the antihistamine injection completely inhibited the formation of a radiation-induced taste aversion.

Whereas the above results implicate histamine in the formation of radiation-induced taste aversions, it was necessary to demonstrate that histamine itself could indeed produce a conditioned taste aversion. Using a water deprivation regimen similar to that outlined above, we injected 16 rats subcutaneously on the back with either histamine diphosphate (75 mg/kg) or 0.15*M* NaCl (1.5 ml/kg) immediately after giving the animals 20 minutes access to saccharin (mean consumption = 10 ml). Twenty-four hours later the rats were given the usual 20-minute saccharin drinking test. Rats injected with histamine diphosphate drank significantly less saccharin (mean = 5.0 ml) than the NaCl injected controls (mean = 17.8 ml) ($t = 6.31$; d.f. = 14; $P < .01$). These results show that it is possible to condition a pronounced taste aversion with histamine as the aversive stimulus.

Since antihistamines, in addition to their antihistaminic and antiemetic properties, produce certain central nervous system depressant effects (*12*), we thought it necessary to demonstrate that rats treated according to the procedure described above for chlorpheniramine do not lose their ability to learn taste aversions. Using a similar procedure, on day 6 we injected 8 rats intraperitoneally with chlorpheniramine maleate (20 mg/kg), and 16 rats intraperitoneally with 0.15*M* NaCl (2 ml/kg). Thirty minutes after these injections, all rats were allowed to drink approximately 10 ml of 0.1 percent saccharin solution. Immediately after saccharin drinking, 16 rats were injected intraperitoneally with a volume of 0.3*M* LiCl equal in weight to 1 percent of their body weight (groups Chlor/LiCl and NaCl/LiCl). The remaining eight rats were injected intraperitoneally with a corresponding amount of 0.3*M* NaCl (group NaCl/NaCl). Mean intakes of saccharin (in milliliters) for the 20-minute test on day 7 were: Chlor/LiCl, 6.7; NaCl/LiCl, 5.2; NaCl/NaCl, 17.5. An analysis of variance across these means was significant ($F = 62.9$; d.f. = 2,21; $P < .01$). An orthogonal comparison indicated that the intakes of the two groups injected with LiCl did not differ and were significantly less than that of the NaCl injected group ($F = 124.1$; d.f. = 1,21; $P < .01$). These data indicate that rats treated with chlorpheniramine maleate are still able to learn avoidance of a taste solution if LiCl is the aversive stimulus.

Since histamine produces many different physiological effects, most of which can be blocked by appropriate doses of antihistamines, it would be premature at this time to speculate about the specific mechanisms involved in the suppression of taste aversion after irradiation. However, we do have evidence that suggests that the antiemetic properties of antihistamines are not instrumental in blocking the taste aversion formation. Prior treatment of rats with Tigan (100 mg/kg; Roche Laboratories), an effective antiemetic drug, does not inhibit the formation of radiation-induced taste aversions. The importance of the findings presented is that no other treatment has been found which could conclusively block the formation of a radiation-induced taste aversion. Marked taste aversions were observed even when the irradiation was performed while the animals were under the influence of deep ether or sodium pentobarbital anesthesia (*14*).

Antihistamines thus appear to be unique in their ability to suppress a radiation-induced taste aversion, a fact which strongly suggests that there is a causal relation between histamine production and "aversiveness of irradiation." This conclusion is strengthened by reports which indicate that antihistamines are effective in reducing a number of different physiological reactions associated with radiation exposure (*15*). For example, antihistamines have proved effective in preventing radiation-induced contraction of the gut (*16*) as well as reducing the early, transient incapacitation of monkeys exposed to high doses of radiation (*17*). Similar studies with humans have demonstrated that radiation therapy patients treated with antihistamines immediately after radiation exposure showed a marked decline in the incidence of nausea, vomiting, irritability, anorexia, and similar symptoms of radiation sickness (*18*). It therefore appears that increased histamine production after exposure to ionizing radiation may be the prime cause for many of the adverse physiological reactions observed in irradiated mammals.

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13 May 1974; revised 2 July 1974

Tandem Calling: A New Kind of Signal in Ant Communication

Abstract. Leptothorax acervorum, L. muscorum, *and* L. nylanderi *recruit nest mates to a new food source by tandem running, with only one nest mate being recruited at a time. This technique is initiated by a special "tandem calling" behavior; the recruiter slants its gaster upward and discharges poison gland secretions from the extruded sting. Nest mates are attracted, and as soon as one of them touches the calling ant, tandem running starts. Further details of the full recruitment sequence are provided. Evidence is presented to suggest that tandem running is the evolutionary precursor of odor-trail communication and sex attraction within certain phylogenetic lines of myrmicine ants.*

When a scout ant discovers a new food source or a better nesting site it usually returns to its colony and recruits nest mates to these places. The recruitment techniques employed by different groups of ant species vary considerably. The so-called tandem running behavior is generally considered to be one of the most primitive recruitment methods. Only one nest mate is recruited at a time, and the follower has to keep close antennal contact with the leader ant. This behavior has been described in a phylogenetically scattered array of species, including *Camponotus sericeus* (*1*), *Ponera eduardi* (*2*), *Cardiocondyla venestula* and *C. emeryi* (*3*), *Leptothorax acervorum* (*4*), and *Bothroponera tesserinoda* (*5*), but until recently nothing was known about the precise nature of the signals involved. For *B. tesserinoda* and *C. sericeus* we were able to demonstrate that a recruiting ant first stimulates a nest mate by a special motor display, which we called invitation behavior, before tandem running starts. During tandem running the leader ant and the follower are bound together by a continuous exchange of tactile signals and by a surface pheromone discharged by the leader (*5*, *6*).

Analyses of the signals involved in tandem running of *L. acervorum* have now led to the discovery of a new kind of signal in ant communication, for which we propose the term "tandem calling" (Fig. 1). When a successful scouting forager returns to the colony it first regurgitates food to several nest mates. Then it turns around and raises its gaster upward into a slanting position. Simultaneously the sting is exposed and a droplet of a light liquid extruded (Fig. 2a). Nest mates are attracted by this calling behavior. When the first ant arrives at the calling ant, it touches the caller on the hind legs or gaster with its antennae and tandem running starts (Fig. 2, b and c).

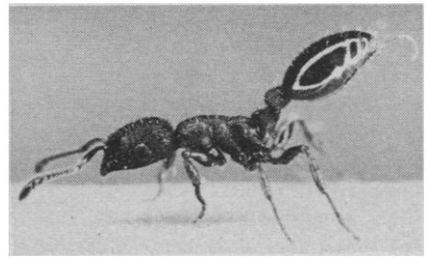

Fig. 1. Chemical tandem calling behavior of a worker ant of *Leptothorax acervorum*. The gaster is raised upward into a slanting position. Simultaneously the sting is exposed and poison gland secretion is extruded.

Table 1. Dummy experiments with *Leptothorax acervorum*. A series of different dummies was presented to tandem followers which had lost their leader ants. Various materials, such as filter paper, were used for dummies. If an ant accepted a dummy and followed behind it, the reaction was considered positive; N = number of trials.

Dummy	N	Positive (%)
Scentless control dummy	10	0
Sting with poison and Dufour's glands	56	100
Gaster without sting glands	126	5.6
Dummy with poison substance	312	100
Dummy with Dufour's gland secretion	69	0

The recruiting ant leads the nest mate to the newly discovered food source. During tandem running the leader ant lowers its gaster, but the sting remains extruded (Fig. 2d). However, it is not dragged over the surface, as it is in the case of ant species which lay chemical trails from their stings. The follower keeps close antennal contact with the leader, continuously touching its hind legs and gaster. Whenever this contact is interrupted, as when the follower accidently loses its leader or is removed experimentally, the leader immediately stops and resumes its calling posture. It may remain in this posture for several minutes, continuously discharging the calling pheromone. Under normal circumstances, the lost follower rather quickly orients back to the calling leader ant and tandem running continues. *Leptothorax muscorum* and *L. nylanderi* show the same tandem calling behavior, with the latter species raising its gaster less conspicuously.

To analyze this interesting recruitment behavior, we attempted first to answer the question: What causes a leader ant to resume tandem calling after it has lost its follower? As mentioned above, if a tandem pair has been separated the leader immediately stops and assumes the calling posture. However, when we touched the ant carefully with a hair at the hind legs or gaster and continued to do so with a frequency of at least two contacts per second, the leader stopped its calling behavior and continued running to the target area. This simple experiment shows that the absence of the tactile signals normally provided by the follower ant is sufficient to cause a leader ant to resume tandem calling.

Second, we asked: Which signals attract and bind the follower to the leader ant during tandem running? The fact that the leader ant extrudes its sting suggested that it discharges a short-lived pheromone, which stimulates the nest mate to follow closely behind. In subsequent experiments we were able to show that the calling pheromone originates from the poison gland. Workers were strongly attracted to dummies contaminated with poison gland secretions, but not to dummies contaminated with secretions of the Dufour's gland. Further experiments revealed that poison gland substance not only functions as a calling pheromone, it also plays an