connecting the basal bodies of adjacent cilia as a neuromotor system, transmitting regulatory impulses from an undetermined control center (*9*). More modern versions have proposed that the rhythm of a group of cilia is dependent upon a pacemaker cilium and, in some instances, that potential changes occur during a ciliary beat which then spread electrotonically to adjoining cilia causing them to beat in turn (*10*).

The mechanical theory has been refined and coordination according to this view is now considered to arise from viscoelastic coupling in the medium between autonomously beating oscillators. Accordingly, synchrony or metachrony results because the energy dissipation in overcoming the viscous drag of the medium is minimized when neighboring cilia beat in phase or with a constant phase relationship (*11*).

Recent studies have shown the neuroidal theory to be implausible, and the mechanical model of coordination is now generally accepted (*12*). Curiously, the ctenophore used in the study responsible for the inception of the neuroidal theory (*8*) seems to represent a special case which provides the only well-documented exception to the mechanical theory. In ctenophores, the existence of both neuroidal and mechanical mechanisms of coordination have been demonstrated, each characteristic of a particular class of ctenophore (*13*). However, since the swimming plates of ctenophores comprise up to thousands of cilia, the motion and coordination of these structures may represent phenomena distinctly different from the motion and coordination of individual cilia.

The synchronous movement of flagella in the isolated apparatus of *Chlamydomonas* may present another and different exception to the mechanical theory. The synchrony is clearly not explainable by neuroidal mechanisms involving elements of the cell cytoplasm and has been shown to be unaffected by solubilization of the flagellar membranes. However, it is also unlikely that the coordination of flagellar beat results from viscoelastic coupling through the medium since the two flagella sweep away from each other during the effective stroke and generate opposing waves during the recovery stroke. Thus one flagellum is not passively following the line of least resistance created by the beat of the other.

Another possibility is that flagellar motion in this organism represents a new category of coordination in which the movement of the individual flagella is coupled by structural elements intrinsic to the apparatus itself. Some such coupling mechanism at the base of the flagella seems required by (i) the structural simplicity of the functional apparatus and (ii) the apparent exclusion of the other theories of coordination. A plausible candidate for the coupling of motion in the flagellar apparatus might be the striated fiber connecting the basal bodies (*1*).

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Taste Aversions to Sexual Attractants

Abstract. *The vaginal secretion of female hamsters serves as a sexual excitant or attractant for the male even in the absence of previous sexual experience, but attraction to the secretion can be altered with surprising ease by pairing ingestion of the secretion with gastrointestinal illness.*

Many mammalian species rapidly learn to avoid tastes or odors which have been paired with gastrointestinal illness (*1*), and these learned aversions have been demonstrated with a wide variety of taste and odor stimuli and several different methods of producing illness (*2*). Although dozens of different tastes have been used in these studies, there is little evidence that the nature of the taste (for example, sweet, bitter, or salty; palatable or unpalatable) is an important factor in the formation of taste aversions: as long as the taste is readily distinguished from other tastes, the animal can form an aversion to it. While the particular taste employed has little effect on the strength of aversions, past experience with the taste is extremely important. Familiar tastes are less readily associated with illness than are novel tastes (*3*), and tastes which have been paired with recovery from illness are even more resistant to association with illness than are other familiar tastes (*4*). Perhaps experience confers a new meaning on a taste—"This taste is safe" or "This taste always makes me feel better"—and that new meaning can then interfere with later associations between the "meaningful" taste and illness.

The important variable here may not be experience per se, but the "meaning" or information which experience provides. If that is the case, certain tastes or odors which communicate important information to a species even without prior experience might also be difficult to associate with illness. A number of these pheromone-like substances have been implicated in the communication of various mammalian species, and one of the most thoroughly studied examples is the vaginal secretion of the female hamster. This secretion has several effects on the behavior of male hamsters: its odor alone is highly attractive to males and elicits approach, sniffing, and licking behavior (*5*), and when the secretion is applied to a variety of inappropriate hamster partners, such as castrated or anesthetized males, it elicits attempted copulation (*6*). These behavioral responses are not dependent on experience with the vaginal secretion after weaning (*7, 8*). Females deposit the secretion on the substrate with a special scent-marking behavior, the frequency of which varies cyclically with the estrous cycle (*9*); the secretion is also sniffed, licked, and consumed by males when females extrude it as part of normal mating sequences (*6–8*). Thus the variety of male responses to the vaginal secretion and the various conditions under which females extrude it suggest that the secretion serves at least two communication functions: the attraction of males to females and scent-marked areas and the elicitation of male sexual behavior. If the strong sexual "meaning" of this secretion interferes with the formation of new associations to its taste and odor, it should be difficult to produce aversions to the secretion by pairing it with illness; on the other hand, if it is possible to produce strong aversions to this biologically important substance, then responses to this pheromone-containing secretion are more easily altered by experience than we have supposed.

Having first established that hamsters (like all other rodents tested) show strong, long-lasting aversions to tastes which have been paired only once with gastrointestinal illness (*10*), we performed a standard taste-aversion experiment using vaginal secretion from estrous females as the taste stim-

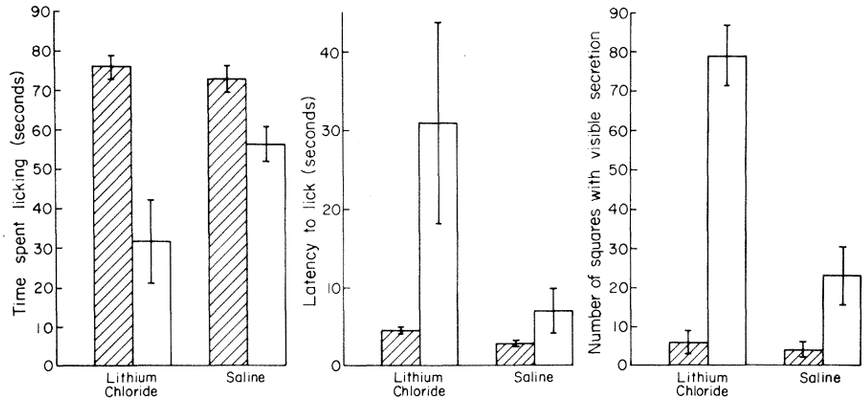

Fig. 1. Three measures of the attractive properties of hamster vaginal secretion before and after injections. The shaded bars represent measurements taken just before the subjects were injected with either lithium chloride or saline, and the unshaded bars are the measurements taken 48 hours later. The height of each bar represents the mean, and the standard errors of the means are also plotted. Data points are based on 11 animals, with the exception of measurements of number of squares with visible secretion before injections, which are based on 6 animals.

ulus. The subjects were 22 naive male hamsters (*Mesocricetus auratus*), born and reared in our laboratory under standard feeding and lighting conditions and housed individually in metal cages; they were about 1 year old at the time of the experiment and had no previous experience with vaginal secretion or with female hamsters after weaning. Subjects were first given 2-minute exposures to clean glass plates (7.62 by 12.70 by 0.32 cm) on three successive days; on the fourth day vaginal secretion from estrous females was presented by spreading it thinly over a 2.54 by 3.81 cm area in the center of the glass plate just before the plate was placed in the hamster's home cage. During the 2 minutes the plate was left in the cage, each hamster was given a score on latency to lick the secretion (from the time his nose crossed the edge of the plate) and a score on time spent licking the secretion. When the glass plate was removed at the end of this 2-minute trial, each hamster was removed from its cage and given an intraperitoneal injection: 11 of the subjects received 1 percent of their body weight of 0.2*M* lithium chloride, which rapidly produces severe but brief gastrointestinal illness (*11*), while the other 11 hamsters received 1 percent of their body weight of saline. The subjects were then returned to their cages and left undisturbed for 48 hours. Because the vaginal secretion forms an opaque film on the transparent glass plates, it was possible to get an estimate of the amount of secretion each hamster actually removed from the plate by simply placing each plate over a grid of 0.32-cm squares and counting the number of squares over which the secretion was still visible. These scores were obtained immediately after all the injections had been given.

After 48 hours, each subject was given a second 2-minute presentation of a glass plate spread with the vaginal secretion; measures of licking time, latency to lick, and the amount of secretion left on the plate were taken as in the first presentation of the secretion.

The results of both presentations are summarized in Fig. 1, and suggest that naive male hamsters show strong aversions to female vaginal secretion after a single pairing of the secretion with gastrointestinal illness (*12*). In comparison to the control animals, the hamsters poisoned after ingesting the vaginal secretion showed a greater decrease in time spent licking ($.05 < P < .10$) and a greater increase in latency to lick ($P < .01$), and left more secretion on the plate ($P < .01$) (*13*). A Kendall coefficient of concordance showed that the average correlation between these measures was + .564 ($P < .05$), suggesting that all three are at least in part measures of the same variable. One interesting feature of the data was the very large increase in variability among the experimental hamsters in the time spent licking and in the latency to lick: although all of the animals approached the plates, a few then retreated and never licked the secretion. Even those poisoned hamsters which did lick the secretion did not remove much from the plate, confirming our impression from observation that their licking was hesitant and lacked vigor.

We were surprised that a single pairing of a brief gastrointestinal illness with consumption of the vaginal secretion so seriously disrupted several of the normal responses to this sexually meaningful substance, namely, approach, licking, and consumption. The results thus provide additional evidence that the nature of the flavor does not seem to affect the ability of an animal to form taste aversions, and further suggest that this is true regardless of the flavor's biological functions.

The potential effects of this aversion on normal sexual behavior are unknown. The vaginal secretion is only one of several cues which summate to cause sexual behavior in male hamsters (*8, 14*), and the aversions we produced might not disrupt sexual behavior in situations where other cues from females are present. The olfactory mechanisms underlying copulation and those mediating attraction to and licking of the vaginal secretion are neuroanatomically separable (*15*), suggesting that these two functions of the vaginal secretion are not necessarily correlated. Whether or not the aversions we observed will actually disrupt sexual behavior as well as altering attraction and licking, our data demonstrate a change in responsiveness to a communication signal due to experience, and they argue against the common view that responses to pheromones are stereotyped and nonmodifiable. This view is based on studies of insect pheromones and may be an inappropriate framework for investigations of mammalian systems.

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