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OLFACTORY DISCRIMINATION OF LITHIUM CHLORIDE

BY THE COYOTE (*CANIS LATRANS*)

A Thesis

Presented to the

Faculty of

California State College

San Bernardino

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts.

Psychology

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by

Glenn Carle Martin

May 1979

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Approved by:

Chairperson

5-10-79
Date

ABSTRACT

For many species, including the coyote, food aversions may be formed based on the association of a distinctive taste with subsequent illness induced by lithium chloride. However, nongustatory cues may also be associated with the illness resulting in rejection of the food. Prior research has suggested that the coyote has the ability to detect the odor of lithium chloride in its food. Although it is generally believed that olfaction is important in the coyotes' foraging behavior, a paucity of information is available on this sensory system. The conditioned taste aversion paradigm and the use of lithium chloride as an illness agent therefore provides an excellent method for examining the limits of the coyotes' olfactory acuity. Coyotes were averted to canned dog food laced with lithium chloride. They were simultaneously offered a choice of either plain dog food or dog food containing lithium chloride. Each food was placed in a wooden tray covered with wire mesh and open at one end. The coyote was required to first smell the food then move the tray and insert its paw or muzzle into the open end to obtain the meal. This methodology ensured that the discrimination was based on olfaction rather than on gustatory contact with the food. The quantity of lithium chloride in the laced food was gradually reduced until the

coyotes' performed at chance level in the two-choice situation. The results indicate that the coyote is capable of detecting minute quantities of lithium chloride in food by olfaction. This ability was found to be an increasing linear function of the logarithmic transformation of the quantity of lithium chloride. At 40 mg of lithium chloride/100 g of food the subjects performed at 75 percent correct responses. The subjects' performance remained above 50 percent correct responses, the chance level, until the amount of lithium chloride was reduced in the laced food to 3 mg of lithium chloride/100 g of food. This study indicates that coyotes can form a LiCl salt aversion in a single trial after which they are easily capable of utilizing olfactory cues to detect and avoid the food or bait containing this emetic salt. A likely explanation for this result is the recently proposed synergistic compound potentiation hypothesis.

TABLE OF CONTENTS

ABSTRACT	iii
LIST OF FIGURES	vi
LIST OF TABLES	vii
ACKNOWLEDGEMENTS	viii
INTRODUCTION	1
Conditioned Taste Aversion	2
Lithium Chloride: Properties and Use as a Toxic Agent ..	4
Sensory Cues in Food Selection	9
Olfaction in Mammals	12
Odor Toxicosis	16
Statement of the Problem	17
METHOD.....	19
Subjects	19
Apparatus	19
Procedure	21
RESULTS	27
DISCUSSION	35
Conclusion	44
REFERENCES	45

LIST OF FIGURES

1. Kennels, Exercise Area and Blind	20
2. Feeding Box Apparatus	22
3. Placement of the Feeding Apparatuses within Kennel	23
4. Performance of Individual Subjects as the Quantity of LiCl was Reduced	32
5. Combined Performance as the Quantity of LiCl was Reduced	33

LIST OF TABLES

1. Results of the LiCl Vs Plain Food Discrimination
for the Various Quantities of LiCl 29
2. Results for the Consumption of LiCl as the Quantity
was Reduced in the Stimulus Patty 30

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INTRODUCTION

It has been estimated that each year millions of dollars worth of sheep and livestock are lost to predators throughout the western United States (Balser, 1974). A major contributor to this predation problem has been the coyote, *Canis latrans*. In the past, the principal methods employed to control predatory coyotes have been lethal techniques such as use of guns, traps (coyotes are trapped, then shot), and poisons. Since these methods do not distinguish between those coyotes that kill sheep and those that do not, lethal methods of coyote control have been the target of substantial criticism.

During recent years, a nonlethal technique which saves both predator and livestock has received considerable attention from sheep growers, wildlife specialists and scientists. Conditioned taste aversion, first established as a laboratory paradigm, has been used as a successful method for the control of coyote predation on domestic livestock (Ellins & Catalano, 1978; Ellins, Catalano, & Schechinger, 1977; Gustavson, Kelly, Sweeney, & Garcia, 1976; Stream, 1976). This model entails the lacing of sheep carcasses with an emetic salt, lithium chloride (LiCl), and then placing these carcasses in selected areas around sheep herds. According to the model, coyotes consuming these carcasses become ill and thereafter refuse to consume sheep carcasses or attack live sheep.

Controversy has emerged, however, when some investigators have not produced prey aversions, but lithium salt aversions (Burns, 1977; Conover, Francik, & Miller, 1977; Griffiths, 1978; Lehner & Horn, 1977). Because little information has been available on the parameters of LiCl necessary to produce prey aversions in the coyote, researchers have experimented with a variety of LiCl dosages. This has led to results that are confusing and inconsistent with the previously established findings of the conditioned taste aversion paradigm.

In a recent study (Ellins & Swanson, 1978), it was found that coyotes were able to avoid quantities of LiCl placed in their food. This avoidance was thought to be based on the detection of the odor of the LiCl. This finding may have serious implications for the use of this chemical as a non-lethal poison. Since little is known about the effective dosages of LiCl and a paucity of information exists on the coyotes' olfactory capabilities, the present experiment was designed to examine the coyotes' ability to utilize olfactory cues to detect the presence of LiCl.

Conditioned Taste Aversion

If a rat becomes ill after consuming a poison bait and survives, it develops a "shyness" for the taste of that particular bait (Barnett, 1963). This phenomenon was first observed under natural conditions (Rzoska, 1953) and has since been experimentally demonstrated in the laboratory. Garcia, Kimeldorf, and Koelling (1955) noticed that if healthy rats

were allowed to drink a sweet-flavored water and then made ill with ionizing radiation, the rats drastically reduced their preference for that fluid. On the other hand, when the sweet-flavored water was followed by a punishing electrocutaneous shock, the rats preference for the fluid remained unchanged (Garcia & Koelling, 1966). Because gustatory-visceral conditioning occurred much more easily than gustatory-cutaneous conditioning, this learning phenomenon became known as conditioned taste aversion.

Since the Garcia et al. (1955) study, conditioned taste aversions have been produced under a wide variety of experimental conditions. Mammals (Braveman, 1974; Johnson, Beaton, & Hall, 1975), birds (Capretta & Moore, 1970), fish (Mackay, 1974) and reptiles (Burghardt, Wilcoxon, & Czaplicki, 1973) have been used as subjects. Sweet (Garcia & Kimeldorf, 1957), sour (Zahorik, 1972), bitter (Braun & Snyder, 1973), and salty (Nachman, 1963) have been used as tastes. Ingested toxins (Nachman, 1963), and injected drugs (Garcia & Koelling, 1967), in addition to numerous other methods (Braun & McIntosh, 1973; Garcia, Erwin, & Koelling, 1967; Garcia & Kimeldorf, 1960; Garcia et al., 1955; Kimeldorf, Garcia, & Rubadeau, 1966) have been used as illness inducing agents.

Among the toxic drugs, d-amphetamine (Berger, 1972), apomorphine (Revusky & Gorry, 1973), cyclophosphamide (Garcia et al., 1967) and lithium chloride (Nachman & Ashe, 1973) have been most widely used. Within recent years, the number of conditioned taste aversion studies using LiCl has greatly in-

creased. This, in part, has been due to such advantages as ease of administration, availability, safety, and a short latency of illness onset (30 min. for the coyote) (Gustavson, Garcia, Hankins, & Rusiniak, 1974) without long lasting side effects (Nachman & Ashe, 1973). It also appears that LiCl is one of the most effective substances for producing a conditioned taste aversion in a single trial (Garcia & Koelling, 1967).

Lithium Chloride: Properties and Use as a Toxic Agent

Lithium is the third element in the periodic system after hydrogen and helium. It is the first of the alkali metals: lithium, potassium, rubidium and cesium. Lithium has several properties similar to sodium and potassium (e.g., a single electron in an orbital outside an inert gas core, thereby producing a strong tendency to form a monovalent positive lithium ion) and is commonly found in its chloride form, Li^+Cl^- (Møllerup & Jørgensen, 1975). LiCl closely resembles common table salt, sodium chloride (NaCl), in appearance and taste, but unlike NaCl , LiCl is easily hydrated and will quickly deliquesce.

During the late 1940's LiCl was used as a salt substitute by individuals on low sodium diets (Johnson & Cade, 1975). After several patients on this diet showed severe toxic reactions and died, the use of LiCl for a NaCl substitute was discontinued (Greenfield, Zuger, Bleak, & Bakal, 1950). Consequently, LiCl was labeled as a dangerously poisonous substance

(Corcoran, Taylor, & Page, 1959). In small doses, LiCl has been shown to produce a powerful and specific anti-manic action in humans (Cade, 1949; Gattozzi, 1970). Larger doses, however, produce a variety of toxic reactions. The list of side effects of LiCl poisoning is formidable. Those effects most frequently observed are nausea, abdominal discomfort, muscular weakness, fatigue, lethargy and vomiting (Shopsin & Gershon, 1973).

Although NaCl and LiCl are similar in appearance, they produce very different physiological effects in rats. NaCl is a basic physiological requirement and thirsty rats will show a preference for mildly concentrated NaCl solutions (Braun & Kiefer, 1975; Richter, 1939). On the other hand, consumption of LiCl has been shown to produce gastrointestinal upset. After a single trial in which a LiCl solution is consumed, rats quickly learn to avoid drinking the fluid (Nachman & Ashe, 1973).

Even though the physiological effects of NaCl and LiCl solutions are quite different, the tastes appear to be similar. The neural discharges recorded at the chorda tympani (Fishman, 1957), the solitary nucleus (Doetsch & Erickson, 1970) and the pons (Perrotto & Scott, 1976) are very similar for the two salts when a solution is applied on the tongue. Behaviorally, Nachman (1963) was unable to demonstrate that the rat could discriminate between equimolar NaCl and LiCl solutions in a simultaneous, two bottle discrimination task. Kiefer (1978), however, recently showed that this discrimination could be made

reliably by rats throughout a broad range of equimolar NaCl and LiCl solutions.

The dosages, concentration and route of administration of LiCl necessary to produce the required illness for taste aversions have been determined for the rat (Nachman & Ashe, 1973). The most obvious behavioral symptom of high dosages of LiCl in the rat is inactivity. Perhaps more significant though, is that diarrhea is often present, which is indicative of gastrointestinal distress.

Garcia and Erwin (1968) have suggested that gross LiCl poisoning affects the area postrema, a neural emetic center. The area postrema has been identified by Borison and Wang (1953) as an emetic chemoreceptor trigger zone in the medulla oblongata of the brainstem. Ablation of this structure reduces the incidence of vomiting in cats receiving systemic poisoning by apomorphine. Since taste afferents, along with those afferents monitoring the viscera and the area postrema converge upon the nucleus solitarius emetic circuitry, Garcia and Erwin (1968) and Garcia, Hankins, and Rusiniak (1974) hypothesize that this neuroanatomical convergence provides evidence for the selective association of taste and illness. In support of this, Hartley (1977) found that lesions of the area postrema abolish the effect of LiCl poisoning as an unconditioned stimulus in conditioned taste aversion. It appears, therefore, that among its many physiological effects, LiCl poisoning produces emesis through gustatory-visceral afferent pathways projecting to the area postrema and nucleus solitarius of the

medulla.

In laboratory and field applications of conditioned taste aversions, LiCl has been the toxic agent used most frequently to produce illness in the coyote. Baits have been constructed using several methods and a variety of LiCl preparations and dosages. Gustavson et al. (1974) fed coyotes hamburger containing 6 g of LiCl in gelatin capsules. After consuming this meal, the coyotes became ill and regurgitated the food. When presented with a hamburger meal three days later, the coyotes refused to consume the meat while readily consuming regular dry dog food. This result demonstrated that the conditioned aversion was specific to the hamburger taste. The coyotes were then fed raw sheep hide baits containing chopped mutton laced with 6 g of LiCl. After one or two mutton-lithium trials, coyotes refused to consume safe baits or attack live sheep. In addition, coyotes were fed rabbit carcasses perfused with 5 g of LiCl/50 ml of water. One or two illness trials produced an aversion to the taste of this flesh after which the coyotes refused to consume a safe rabbit carcass or attack live rabbits.

In a second study, Gustavson et al. (1976) fed coyotes rabbits injected with 6 g of LiCl/50 ml of water and bait packages consisting of 3 g of LiCl in gelatin capsules mixed into 340 g of dog feed and sewn into a rabbit hide. Once again, after one or two trials of a flesh followed by illness, the coyotes refused to consume a safe rabbit carcass or attack live rabbits.

Other investigators using different quantities of LiCl have produced salt aversions in coyotes. Conover et al. (1977) fed coyotes chickens laced with several concentrations of LiCl; 6 g of LiCl/20 ml of water, 5 g of LiCl/10 ml of water and 4 g of LiCl/100 ml of water. Because of the extreme concentrations, the coyotes developed an aversion to the "salty" chicken, while continuing to kill and consume "plain" chicken. Burns (1977) used a 6 g of LiCl/20 ml of water solution injected into chicken carcasses to make coyotes ill. After only one or two lithium-illness experiences, the coyotes were able to discriminate which carcass had been injected with LiCl and avoid that carcass. Lehner and Horn (1977) and Griffiths (1978) fed coyotes rabbit carcass baits with dose levels that varied from 3 g to 6 g of LiCl per bait. Several baits were consumed by the coyotes and the exact LiCl/bait dosage for each animal was unknown. In each of these studies, the coyotes were able to avoid LiCl baits after one or two lithium-illness experiences. Ellins and Swanson (1978) also established a LiCl aversion in coyotes. After one lithium-illness on chicken permeated with a solution of 450 g of LiCl/12.7 l of water and a second illness on 6 g of LiCl/432 g of canned dog food, coyotes refused to consume any food containing illness inducing quantities of LiCl. From the results of these studies, it appears that the presence of LiCl adds a salty taste to the food in which it is placed and produces a specific aversion to the now "salty" taste rather than an aversion to the taste of the plain food or prey.

Sensory Cues in Food Selection

The palatability of a food is the primary factor in dietary regulation. When a food is associated with nutritious aftereffects, the palatability of the food tends to be increased (Rozin, 1969; Zahorik & Maier, 1969). When the food is associated with toxic aftereffects, the palatability tends to be decreased (Garcia et al., 1955). This shift in palatability provides a mechanism by which animals are able to avoid toxic foods after consuming only a small quantity. The coyote, for example, after consuming a meal containing LiCl and becoming ill, may avoid the food at a later date because of a shift in the hedonic value of a food's flavor.

For the laboratory rat, taste is the prepotent sensory cue which guides palatability in food aversion learning. Using taste as a conditioned stimulus, rats can learn strong food aversions with a delay in illness of up to several hours (Nachman, 1970; Revusky, 1968). Visual, auditory or tactile cues, even though present at the time of ingestion, do not become as strongly associated with illness (Garcia & Koelling, 1966; Garcia, McGowan, Erwin, & Koelling, 1968). Cues such as the size of the food pellet (Garcia et al., 1968) or features of the food dish (Rozin, 1969) provide relatively ineffective conditioned stimuli for illness in the rat.

Although taste is the prepotent cue used in forming food aversions, nongustatory cues may be secondarily associated with taste and allow an animal to reject a substance without

tasting it again on subsequent trials. After one meal of worms followed by LiCl illness, garter snakes will attack worms but not swallow them, frequently dropping the worms as soon as they strike (Burghardt et al., 1973). When given an opportunity to feed on worms at a later date, the snakes will avoid the worms without attack, and in some cases without even a tongue flick.

Many avian species have highly developed visual systems in comparison to their gustatory systems and rely more heavily on visual cues than gustatory cues when selecting foods and avoiding toxins. For these species, taste aversions may be mediated through visual cues. Quail (Wilcoxon, Dragoin, & Kral, 1971), chickens (Capretta & Moore, 1970), and Buteo hawks (Brett, Hankins, & Garcia, 1976) show aversions to both the taste and color of their food. Strong learned aversions to visual cues have been demonstrated in the quail with delays in illness of up to two hours (Wilcoxon, 1977). The ability to form food-illness aversions to visual cues, however, is not based totally on a highly developed visual system. Anatomical (Walls, 1963) and behavioral (Messing, 1972) evidence suggests that guinea pigs have poor visual acuity, yet these animals are capable of using both taste and visual cues in forming aversions (Braveman, 1974). This finding is inconsistent with the results of a comparable experiment (Wilcoxon et al., 1971) in which rats were unable to associate visual cues with gastrointestinal illness. Although research suggests that the visual acuity of rats and guinea pigs is comparable (Walls, 1963;

Messing, 1972), visual cues may be more important for the guinea pig than for the rat during foraging. According to Rozin and Kalat (1971), animals form aversions to those cues which are related to the ingestion of food. If, for example, the guinea pig utilizes both taste cues and visual cues during its normal feeding behavior, then these cues become effective in mediating food aversions and avoiding toxins (Braveman, 1974).

The sensory modality that becomes associated with illness has also been demonstrated to depend upon the specific food being consumed. In the case of the terrestrial mollusk, learned aversions are mediated by gustatory cues for one food (mushroom) while for another food (cucumber) the aversion is mediated by olfactory input (Galperin, 1975). The use of taste aversion conditioning to control coyote predation demonstrates that nongustatory cues can be used to mediate the avoidance of food (Gustavson et al., 1974). As mentioned previously, after one or two trials in which a coyote ingested a particular flesh (either rabbit or sheep), the coyote not only learned to avoid the flesh, but also suppressed attack behavior on the appropriate prey. Gustavson et al. (1974) attribute this observed behavior to a two-phase conditioning process proposed by Garcia, Clarke, and Hankins (1973). In phase one of this process, the taste of the prey becomes aversive when paired with illness. At this point, the distal cues, i.e., sight, sound and smell of the prey may still elicit approach and attack behavior. In the second phase, these distal cues become associated with

the now aversive taste and inhibit subsequent approach and attack. Thus, through higher order conditioning, nongustatory stimuli can become effective cues for suppressing the coyotes' attack behavior.

Olfaction in Mammals

For many mammalian species, the greater the capacity to detect, recognize and respond to olfactory stimuli, the greater the probability of the animal's survival. Faced with such evolutionary pressures, the ability to detect olfactory stimuli has reached exceptional limits in some mammals. The nocturnal opossum, for example, is said to be able to detect amyl acetate in concentrations as low as 10^{-4} M (M = number of moles of the chemical/number of moles of the chemical + number of moles of the diluent) (Marshall, 1969). The human threshold for amyl acetate is approximately 10^{-3} M (Mullins, 1955), ten times higher than that of the opossum.

The largest quantity of empirical data collected on the olfactory capabilities of any mammal is that for the laboratory rat. Among the many olfactory discrimination tasks it is capable of performing, rats have been trained to discriminate drinking bottles on the basis of odorous substances smeared on the drinking spout (LeMagen & Rapaport, 1951) and to select a correct box containing food on the basis of odorous or non-odorous air admitted from an associated tube (Gruch, 1957). The rat's sense of smell, in fact, was found to be so keen ($10^{-4.5}$ for amyl acetate) (Moulton, 1968), that food cannot be used as a direct reward in experiments designed to determine

olfactory thresholds. Odorous molecules of the food may either mask the test substance or chemically react with it and alter the test chemical's concentration (Eayrs & Moulton, 1960). Olfactory psychophysical parameters for some chemical substances have been established in the rat (Eayrs & Moulton, 1960; Davis, 1973; Moulton, 1968). When compared to the human, the rat's absolute detection threshold for odors was found to be far lower, but the differential threshold was found to be greater (Davis, 1973).

The ability of the domestic dog (*Canis familiaris*) to detect odors in its environment is well established. Neuhaus (1953; 1955) found that the dog's sensitivity to butyric acid was 10^5 to 10^8 times greater than man's. Moulton and Eayrs (1960), however, have reported the dog's threshold for this fatty acid to be only 10^1 to 10^2 times lower than the human threshold. In contrast to these studies, Becker, King, and Markee (1962) found the olfactory thresholds for both the human and dog to be similar for the compounds olive oil and anethole. Using a highly sophisticated olfactometer chamber, Moulton and Marshall (1976) determined the minimum odorant concentration of alpha-ionone detectable by the German shepherd. Thresholds for four dogs ranged from $4 \times 10^{4.5}$ to $4 \times 10^{6.5}$ molecules/cm³. As of this date, the human threshold for alpha-ionone has not been established.

The dog's superior olfactory acuity has been linked to the olfactory receptors. The mammalian neural receptors for olfactory stimuli are located in the olfactory mucosa, which

occupies the medial and posterior region of the nasal cavity. The mucosa consists of bipolar cells (1.0 microns in diameter) which extend peripherally and axons (0.2 microns in diameter) which pass without synapse into the olfactory bulb of the forebrain. The dendrites terminate in a small knob just above the mucosa, and cilia of varying length (3 - 200 microns) extend outward into a layer of mucous. The olfactory knob of most mammals supports 6 - 12 cilia, however, there are an estimated 100 - 150 cilia per knob in the dog (Okano, Weber, & Frommes, 1967). The cilia have been indicated as the possible site stimulated by odorant molecules. The large number of cilia in the dog may, therefore, account for its' olfactory acuity. Current evidence suggests, however, that additional neuroanatomical structures, the vomeronasal (Jacobson's organ), the septal organ of Masera and free nerve endings, are also involved in odor detection (Graziadei & Graziadei, 1976).

At the single receptor level, it appears that the dog has little or no olfactory advantage over the human. Estimates by Neuhaus (1953) for the dog and deVries and Stuver (1960) for the human indicate that one molecule of a specified odorant may be sufficient to excite a single receptor in both species. Apparently, the major difference in olfactory acuity between the dog and the human is the receptor reserve available. Moulton (1977) estimates that there are over 1 billion receptors in the olfactory epithelium of the German shepard, more than 100 times the number of receptors estimated for the human. This receptor reserve may be important in the dog's detection

of compounds at very low concentrations.

Little information is available on the olfactory system or olfactory capabilities of the coyote. The vomeronasal organ, a neuroanatomical structure known to respond to odors in some animals is also present in the coyote. This organ lies ventral to the nasal fossae which connects the buccal cavity via the nasopalatine canal. Although it does not have cilia, its receptors have responded to the same odorants as the olfactory receptors proper, but at higher thresholds (Moulton & Tucker, 1964; Tucker, 1963). The function of the vomeronasal organ in the coyote is unknown. Although Beckoff (1978) has speculated that it might be important in detecting odors, Gier (1978) was unable to find neural connections between the vomeronasal organ and the forebrain and has concluded that this structure may be vestigial and inoperative.

The importance of olfaction in the coyote's predatory behavior has recently been investigated. A tentative hierarchy of the effectiveness of the different senses in determining prey location has been developed by Wells and Lehner (1978). In a laboratory setting, the coyote was found to rely primarily on visual cues to detect its' prey. In the absence of visual stimuli, auditory cues were used by the coyote. Only in the absence of both auditory and visual stimuli did olfactory cues play a significant role in prey location. The generalizability of this study to coyotes foraging for food in the natural environment, however, is extremely limited. It is doubtful that a predator would rely totally on one sense or another to locate

its food, and certainly a myriad of environmental conditions must affect which sensory modality is favored. Regardless of the sensory cues employed in the location of prey and the ensuing chase and capture, taste is the primary cue which monitors and regulates the eventual prey ingestion (Gustavson et al., 1974; Gustavson et al., 1976).

Odor Toxicosis

Since odor and taste are closely related senses, and because gustatory and olfactory stimuli interact in feeding and drinking behavior, the role of odor in learned aversions is of particular interest. Numerous authors have reported that animals tend to avoid ingestion on the basis of odor which has been previously associated with illness (Garcia & Koelling, 1967; Hankins, Garcia, & Rusiniak, 1973; Lorden, Kenfield, & Braun, 1970; Pain & Booth, 1968). Although most odor aversions have been obtained with brief odor-illness delays (less than 10 min.), Takulis (1974) has produced an odor aversion in the rat with a 4 hour CS-US delay. This study, however, has been criticized by Hankins, Rusiniak, and Garcia (1976) because the odor stimulus was directed into the rat's mouth. In any study designed to assess the ability of an animal to associate odor cues with illness, odor cues may possibly be confounded with taste cues because airborne molecules are potential stimuli for both gustatory and olfactory receptors. For this reason, the results of Takulis (1974) cannot be assumed to be due to olfactory stimulation alone.

Hankins et al. (1973) have shown that olfactory cues are not necessary to form a taste aversion since peripherally anosmic rats show little impairment in the acquisition of an aversion to a distinctive taste. Taste cues have been demonstrated to be most effective in flavor-aversion paradigms, but odor cues are most effective in shock-avoidance-paradigms (Hankins et al., 1976). This combination of cues and consequences is highly adaptive since peripheral pain and gustatory cues are seldom associated in the natural environment.

Statement of the Problem

Although olfaction is thought to play a minor role in the regulation of feeding behavior (Hankins et al., 1973), in some cases, olfactory cues may be highly effective in mediating taste aversions. The aversion to LiCl reported in coyotes by Ellins and Swanson (1978), for example, appears to be mediated by odor cues. After two experiences with LiCl, coyotes avoided the LiCl poison without tasting it, while continuing to consume the safe food on which they were previously made ill. In subsequent tests which necessitated that the coyotes use olfactory cues to make a discrimination, two additional foods containing LiCl were quickly avoided while the same safe food was readily consumed.

Almost all of the experiments that have used quantities of LiCl either mixed directly into food or first dissolved into water and then injected into carcasses have produced "salty" tasting baits and resulted in LiCl aversions. If these salt aversion findings are true, and if coyotes are able to

use the odor of LiCl to avoid laced baits in the field, the effectiveness of the conditioned taste aversion paradigm to control predation on domestic livestock could be seriously undermined.

Therefore, the purpose of this thesis was to examine the limits of the coyote's ability to detect the odor of LiCl when placed in its food. Coyotes were first averted to LiCl and then trained to use odor cues to discriminate food containing LiCl from plain food. Then, the quantity of LiCl was gradually reduced until the coyotes performed at chance level in the two-choice situation. Additional information on the potential dosage levels for the field use of LiCl was also examined.

METHOD

Subjects

Three coyotes, donated by the California Department of Fish and Game, served as subjects for this thesis. Two of the coyotes, S₁ and S₂ were males, and one S₃ was female. All of the animals were hand-reared from 3 weeks of age and were approximately 1 year old at the beginning of this study. S₁ and S₂ had been subjects in a previous LiCl taste aversion experiment during which they had consumed a rabbit carcass injected with 6 g of LiCl/50 ml of water. After this treatment, it was observed that neither of the coyotes would consume LiCl laced food. The third coyote, S₃, was naive to LiCl.

Apparatus

The research facility consisted of three adjoining kennels, an exercise area and a blind containing a one-way mirror (Figure 1). The sides of the kennels were constructed of heavy gauge chain-link fence with chain-link doors that opened outward into the exercise area. The floors were concrete slabs and the roof covering the kennels was constructed of corrugated aluminum sheeting. Each kennel was separated from the other by .65 cm plywood sheeting attached to the chain-link fence.

The exercise area was constructed of 3.05 m x 1.8 m high chain-link panels. The overhead was covered with 5.08 cm chicken wire to prevent the coyotes' escape by jumping or

FIGURE 1. KENNELS, EXERCISE AREA AND BLIND

climbing. Buried 15 cm beneath a dirt floor was a 10.16 cm square hardware cloth skirt. The skirt was wired to the chain-link side panels and extended 1.35 m inward toward the center of the exercise area. This prevented the coyotes escape by digging.

Within each kennel was a ceramic water 27.5 cm diam. x 10.5 cm deep, and 2 identical wooden feeding boxes (Figure 2). The bottom and three sides of the feeding boxes were constructed of 1 cm thick plywood. The top of the box was concave and constructed of wire netting with 1.3 cm squares. One end was open allowing the coyotes to reach into the apparatus to obtain the food. The feeding boxes were positioned with their open ends against the door (Figure 3).

Either 50 g or 100 g of Skippy Regular canned dog food, pressed into a 8.33 cm diam. x 2.2 cm high mold, was used as the standard food. A plain patty and a patty containing varying quantities of reagent grade LiCl was placed on separate white paper plates, 23 cm in diameter, and then inserted into the feeding boxes.

Procedure

Each coyote was assigned to a kennel (kennel numbers 1-3) where it remained for the duration of the study. All subjects were fed and tested daily between 6 and 11 AM.

Pretraining. The subjects were habituated to eating their daily meal from the wooden feeding apparatuses for 14 days. Fifty gram patties containing no LiCl were used during the

FIGURE 2. FEEDING BOX APPARATUS

FIGURE 3. PLACEMENT OF THE FEEDING APPARATUSES WITHIN KENNEL.

habituation period. Each animal was given 5 trials per day during which 2 of the 50 g patties, one in each box, were available for consumption. In order to obtain the food patties, the coyotes were first required to move the open end of the box away from the door, and then insert their paw or muzzle to remove the paper plate.

The activity of the experimenter placing the food patties inside the boxes was visually shielded from the coyotes by a portable cardboard screen 90 cm long x 76 cm high. After each patty had been placed in the approximate center of a clean paper plate and then placed within the box, the boxes were positioned against the kennel door. The experimenter then closed the door, walked directly to the blind and began the trial. The coyotes behavior was observed through the one-way mirror. The 1st and 2nd choice of boxes (left or right), the method of obtaining the food from within the box, and the consummatory behavior of each animal was recorded. The trial was terminated when the coyote consumed the food and returned to the plywood house.

Treatment. On the 15th day, each coyote was offered one 100 g patty of dog food laced with 6 g of LiCl on a paper plate in the center of the kennel. Subjects S₁ and S₂ consumed approximately 50 g and S₃ consumed the entire 100 g patty. Between 30 min. to 1 hr. later, all animals became ill and regurgitated the LiCl laced food.

Testing. On the day following treatment, the coyotes were simultaneously offered a choice of two patties. One stimulus

patty consisted of 100 g of plain dog food while the comparison patty contained 6 g of LiCl mixed with 100 g of food. All patties were prepared on the day prior to testing, wrapped in Handi-Wrap and stored at room temperature. Each subject received 5 successive trials per day for 2 consecutive days, totalling 10 trials per animal and 30 trials overall. For each trial, the stimulus positions were alternated according to the Gellerman series (Gellerman, 1933). The design of the feeding apparatus and its positioning with its open end against the door ensured that the subjects initial discrimination was based on olfaction rather than on gustatory contact with the food. The third day after treatment was designated as a "safe" day and each animal was allowed to consume 500 g of plain dog food placed on a paper plate in the center of the kennel.

Upon completion of the 30 trials at 6 g of LiCl, three manipulations were performed to determine the nature of the olfactory aversion. First, to determine if the aversion was specific to the odor of LiCl, the coyotes received 30 discrimination trials of 6 g of NaCl vs plain food. Second, to determine if coyotes could discriminate between the odors of NaCl and LiCl, the subjects received 30 trials with 6 g of NaCl vs 6 g of LiCl as choices. Third, to demonstrate that the avoidance of the "salty" smell was due to a learned aversion and not to a neophobic response to the odor of a novel food, the coyotes received 30 trials with 6 g of minced garlic vs 6 g of NaCl as choices. During these 90 trials and throughout the remainder of the study, every third day was also a "safe" food

day.

After testing the various control substances, the quantity of LiCl in the LiCl vs plain food discrimination was gradually reduced from 6 g to 4 g, 2 g, 1 g, 500 mg, 250 mg and 125 mg. At and below 125 mg, the number of trials was increased to 20 trials per animal, 60 trials overall. The quantity of LiCl was then further reduced from 125 mg to 80 mg, 50 mg, 20 mg, 10 mg, 5 mg, 3 mg and 1 mg. At the levels 5 mg, 3 mg and 1 mg of LiCl, solutions of .15 M LiCl were used to supply the LiCl since the precise weighing of such small quantities was difficult by mechanical scales. In addition, at levels of 50 mg and lower, after the subject made a correct discrimination, the LiCl laced food was removed from the kennel to prevent the extinction of the discrimination. In order to maintain the discrimination at the 50 mg level or lower, 5 trials of 2 g of LiCl/100 g of food were given to the subjects the day prior to the beginning of each new level.

RESULTS

On the initial discrimination with 6 g of LiCl vs safe food, the coyotes avoided the LiCl on all 30 trials. During five of these trials, after consuming the safe food, the coyotes then made oral contact with and rejected the LiCl food.

After establishing the 6 g of LiCl vs safe food discrimination, the three sets of control substances were tested. On the 6 g of NaCl vs plain food discrimination, the coyotes also avoided the NaCl on all 30 trials. A chi square goodness of fit revealed this result to be significant ($\chi^2 = 36.67$, $df = 1$, $p < .001$). Again, on eight of the trials the NaCl patty was rejected after oral contact.

On the 6 g of NaCl vs 6 g of LiCl olfactory discrimination, the coyotes avoided the LiCl on 80 percent (25 choices NaCl, 5 choices LiCl) of the trials. Analysis of this data revealed a significant difference ($\chi^2 = 13.3$, $df = 1$, $p < .001$). The selection of the NaCl patty, however, did not result in consumption of this food. Typically, after sniffing both foods, the coyotes would taste and then reject the NaCl patty. The LiCl patty was then tasted and also rejected.

For the discrimination trials with 6 g of minced garlic vs 6 g of NaCl as choices, the coyotes selected and consumed the minced garlic on 87 percent (26 choices minced garlic, 4 choices NaCl) of the trials. A chi square analysis showed this

difference to be significant ($\chi^2 = 16.13$, $df = 1$, $p < .001$). Again, in four of the trials, the NaCl patty was tasted and rejected.

After testing the control substances, the quantity of LiCl in the stimulus patty was systematically reduced from 6 g. Table 1 presents the results for the various quantities of LiCl that were tested. When the quantity of LiCl in the stimulus patty was reduced from 6 g to 4 g, 2 g and 1 g, the coyotes' performance remained at 100%. As the quantity of LiCl was reduced from 500 mg to 5 mg, the percentage of correct responses decreased. For the quantities 3 mg, 2 mg and 1 mg LiCl, the coyotes performed at chance level in the two-choice situation. This result was due to a position habit that the subjects developed at 3 mg and maintained for the quantities 2 mg and 1 mg LiCl. For these 3 quantities of LiCl, regardless of the placement of the stimulus patty, each subject selected the food on its left as it approached the two patties.

Although the coyotes did not consume any LiCl at 6 g, 4 g and 2 g, they occasionally returned to taste the stimulus patty after initially smelling and avoiding the LiCl. As the quantity of LiCl in the stimulus patty was reduced to 1 g or less, however, the subjects frequently returned to consume the LiCl patty after consuming the safe food. Between the quantities 1 g and 50 mg of LiCl, the consumption of a sufficient quantity of LiCl to cause regurgitation occurred once for each subject. Table 2 presents the results for the consumption of LiCl as the quantity of LiCl was reduced in the

TABLE 1. RESULTS OF THE LiCl VS PLAIN FOOD DISCRIMINATION FOR THE VARIOUS QUANTITIES OF LiCl. THE STIMULUS FOOD CONTAINED THE LiCl.

QUANTITY OF LiCl	FREQUENCY OF OBSERVED CHOICES		PERCENT CORRECT RESPONSES
	COMPARISON FOOD	STIMULUS FOOD	
6 g	30	0	100
4 g	30	0	100
2 g	30	0	100
1 g	30	0	100
500 mg	28	2	93.33
250 mg	27	3	90.0
125 mg	49	11	81.66
80 mg	47	13	78.33
50 mg	45	15	75.0
20 mg	42	18	68.33
10 mg	37	23	61.66
5 mg	35	25	58.33
3 mg	30	30	50.0
2 mg	30	30	50.0
1 mg	30	30	50.0

TABLE 2. RESULTS FOR THE CONSUMPTION OF LiCl AS THE QUANTITY WAS REDUCED IN THE STIMULUS PATTY.

QUANTITY OF LiCl AVAILABLE IN THE STIMULUS PATTY FOR EACH TRIAL	TOTAL QUANTITY OF LiCl CONSUMED	FREQUENCY OF ORAL CONTACT WITH STIMULUS PATTY BEFORE COMPARISON PATTY	FREQUENCY OF ORAL CONTACT WITH STIMULUS PATTY AFTER COMPARISON PATTY
6 g	0	0	5
4 g	0	0	3
2 g	0	0	8
1 g	4.25 g	0	11
500 mg	2.5 g	2	7
250 mg	2.375 g	3	8
125 mg	4.025 g	11	25
80 mg	3.76 g	13	47
50 mg	3.0 g	15	45

stimulus patty. Column 2 lists the total LiCl consumed for all trials at that quantity. Regurgitation occurred at 1 g LiCl when subjects S₁ and S₂ consumed approximately 2.5 patties containing 2.125 g of LiCl and at 500 mg when S₃ consumed 5 patties containing 2.5 g of LiCl. Below the 500 mg level, each subject consumed many LiCl patties, but regurgitation did not occur. Columns 3 and 4 of Table 2 present a breakdown of the number of oral contacts made with the stimulus patty prior to and after the selection of the comparison patty. As the quantity of LiCl in the stimulus patty was reduced, the number of oral contacts with this food increased. At 80 mg of LiCl the subjects made oral contact with and consumed the stimulus patty on almost every trial. Since this comparison resulted in no visible signs of illness (such as regurgitation), the stimulus patty was removed after the consumption of the safe food for quantities less than 50 mg of LiCl.

Figure 4 presents the performance of the individual subjects as the quantity of LiCl in the stimulus patty was reduced. The percent correct responses was found to be an increasing linear function of the logarithmic transformation of the quantity of LiCl present. The data for S₁, S₂ and S₃ was combined (Figure 5) and a regression equation, $y = 8.12 \log (x) + 99.8$, was determined to estimate the coyotes' performance for any given quantity of LiCl. The standard error of estimate was calculated to be 1.82 percent, and no observed data point was found to differ significantly from the regression line.

Two measures used to evaluate sensitivity in olfactory

FIGURE 4. PERFORMANCE OF INDIVIDUAL SUBJECTS AS THE QUANTITY OF LiCl WAS REDUCED. ABOVE THE ABCISSA IS THE ACTUAL WEIGHT OF LiCl IN GRAMS/100 GRAMS OF FOOD. BELOW THE ABCISSA IS THE LOG QUANTITY OF LiCl/100 GRAMS OF FOOD.

FIGURE 5. COYOTES' PERFORMANCE AS THE QUANTITY OF LiCl WAS REDUCED. ABOVE THE AB-
 CISSA IS THE ACTUAL WEIGHT OF LiCl IN GRAMS/100 GRAMS OF FOOD. BELOW
 THE ABCISSA IS THE LOG QUANTITY OF LiCl/100 GRAMS OF FOOD.

psychophysical experiments are the Just Noticeable Difference (JND) and the Weber fraction. The JND is the smallest intensity difference a subject can detect and was defined in this study as the stimulus quantity necessary to produce a percent correct score halfway between 50 and 100 percent correct discrimination performance (Engen, 1971). The horizontal and vertical arrows on Figure 4 represent the 75 percent correct response level and the estimated stimulus quantity for the JND. For this study, the 75 percent correct stimulus quantity was found to be 50 mg of LiCl.

The Weber fraction is defined as a constant representing the change in stimulus intensity required to produce one JND.¹ The Weber fraction for the coyote was computed to be 2.0. Following the example of Miller (1947) for acoustical stimuli, Stone (1963; 1964) has suggested that a modified Weber fraction be used for odors.² Therefore, the adjusted Weber fraction was calculated to be 1.8 for the coyote.

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¹If ΔI is the amount by which a given stimulus must be changed (increased or decreased) in order to produce a second stimulus just noticeably different from the first, then the Weber fraction may be stated as $W = \frac{\Delta I}{I}$ (D'Amato, 1970).

²Except at very high and very low intensities, the Weber fraction is apparently constant over more than 99.9 percent of the usable range of stimulus intensity. As ΔI approaches threshold, however, some interfering stimuli or "noise" exists in the sensory system preventing the subject from identifying the true stimulus. Therefore, a small addition I_R (intensity at the 50 percent threshold) can be added to the Weber fraction to help correct for this problem. The modified Weber fraction then becomes $W = \frac{\Delta I}{I + I_R}$ (Stevens, 1951).

DISCUSSION

The results of this study indicate that the coyotes' ability to detect LiCl in its food is an increasing linear function of the logarithmic transformation of the quantity of LiCl present. This finding is in agreement with previous olfactory discrimination research in which performance has been found to be a logarithmic function of stimulus intensity (Ashton, Eayrs, & Moulton, 1957; Becker et al., 1962; Eayrs & Moulton, 1960; Moulton et al., 1960).

The results of the 6 g of LiCl vs safe food discrimination indicate that after consuming 100 g of LiCl laced food, coyotes have little difficulty using odor cues to detect and avoid the same food laced with 6 g of LiCl on subsequent trials. At the same time, the coyotes will readily consume that food containing no LiCl. This finding confirms the result of Ellins and Swanson (1978), indicating that coyotes consuming food laced with 6 g of LiCl apparently become averted to the taste of the LiCl food mixture, rather than to the taste of the plain food alone. The taste aversion in this study appears to be mediated by olfactory cues, allowing the coyote to avoid the lithium laced food without tasting it a second time. Exceptions to this did occur, however, during several trials at 6 g, 4 g, 2 g and 1 g quantities of LiCl. After making the initial olfactory discrimination and consuming the safe food, the coyotes

returned to taste and reject the LiCl patty. Thus, the coyotes' ultimate rejection of the LiCl food was presumably due to its "salty" taste. This result agrees with the data of Hankins et al. (1973; 1976) for the rat, who found that odor serves as a distal cue to guide the approach response to food, while taste serves as a proximal cue to guide food's consumption. The results presented in Table 2 indicate that as the quantity of LiCl in the stimulus patty was reduced, the coyotes first line of defense (odor) faltered, increasing the probability of the coyotes tasting the poisoned food. The final decision to consume or reject the food, however, occurred only after the coyotes had tasted the LiCl patty.

The results of the 6 g of NaCl vs plain food discrimination indicate that the learned aversion was not specific to the taste of LiCl, but generalized to the taste of another salt. Again, during several trials, after the safe food had been consumed, the coyotes returned to taste and reject the "salty" NaCl food. Thus, following a single treatment with 6 g of LiCl in 100 g of food, coyotes develop a generalized aversion to the taste of salt.

The results of the 6 g of LiCl vs 6 g of NaCl discrimination are of particular interest since both stimuli had "salty" odors. Previous research has indicated that following prior experience with a two bottle discrimination task that involved LiCl (LiCl vs sucrose), rats can rapidly discriminate between the tastes of equimolar (.15 M) LiCl and NaCl solutions (Kiefer, 1978). If the solutions are strong enough ($> .10$ M),

rats with LiCl vs NaCl discrimination experience can detect and avoid the LiCl on the basis of odor cues (Miller & Erickson, 1966). Rats with no previous LiCl vs NaCl experience, however, do not discriminate between these salts (Kiefer, 1978). Since the coyotes in this study were naive to LiCl and NaCl, it was expected that like naive rats, they would be unable to discriminate between the odors or tastes of the two patties. Based on olfaction, however, the coyotes avoided the LiCl patty on 80 percent of the trials. Following this olfactory discrimination, oral contact with either of the patties resulted in the rejection of the "salty" tasting food. It appears that even though there was a substantial generalization between the "similar" tastes of the two salts, as evidenced by the eventual rejection of both patties, there was little generalization between the LiCl and NaCl odors. Thus, naive coyotes, unlike naive rats, may be able to discriminate between LiCl and NaCl laced foods on the basis of olfactory cues.

Upon first examination, the 50 mg JND observed in this study appears relatively large in comparison to what might be predicted for a canid species reputed to have excellent olfactory capabilities. Since most animal psychophysical studies present a single fluid stimulus compound in a successive discrimination paradigm intending to measure the absolute threshold, the resulting odor detection threshold generally corresponds with a very low concentration. In contrast, the present study made no attempt to determine the coyotes' absolute threshold for LiCl. This study employed a simultaneous discrimination

technique in which the stimulus odor was combined with a masking odor and then compared against the masking odor alone. Therefore, several factors may have been responsible for the large JND. First, the psychophysical measures resulting from a simultaneous discrimination methodology are usually higher than those resulting from a conditioned suppression or a single-stimulus, successive discrimination technique (McBurney, Krasschau, & Bogart, 1967; Davis, 1973; Shaber, Brent, & Rumsey, 1970; Shumake, Smith, & Tucker, 1969; Shumann, 1898). Shaber et al. (1970), for example, have used a conditioned suppression technique with aversive brain stimulation as reinforcement to obtain odor detection thresholds that were three to six times lower than those values previously reported from behavioral experiments. Second, in comparison to a single stimulus, successive discrimination task in which the odor of the LiCl stimulus is presented alone, the LiCl in this study was mixed with 100 g of dog food. Thus, this discrimination may have been more difficult than a single stimulus presentation since the LiCl odor was masked by the odor of the dog food. And third, the actual distribution of LiCl on the surface of the patty available for olfactory detection was substantially less than the total quantity of LiCl in the patty. Thus, the observed 50 mg JND represents a differential threshold which was considerably elevated due to the methodology of this study. The purpose in using this methodology, however, was to approximate the procedures and quantities of food and LiCl used in presenting LiCl laced food in other

studies.

Although olfactory intensity discrimination has been extensively studied in the human (Gamble, 1898; Pangborn, Berg, Roeseler, & Webb, 1964; Stone, 1963; Zigler & Holway, 1935) relatively little research has been conducted to determine these thresholds for other mammals. Davis (1973) has examined olfactory intensity thresholds for the rat and found them to be higher than those for the human.

In the present study, a Weber fraction of 2.0 (1.8 corrected) was obtained for the coyote. This provides the first information on the odor differential threshold for a species in the canid family. In comparison, calculated ranges of values for odor differential thresholds, expressed as corrected Weber fractions for other species, vary from 2.2 to 2.6 for the rat (Davis, 1973) to .2 to .5 for the human (Stone, 1963). From these studies, Davis (1973) has concluded that although the rat's odor detection threshold is $2.5 \log_{10}$ units lower than the humans', the Weber fraction indicates that the human may be able to resolve smaller odor concentrations than the rat. The results of the present study indicate that the coyote, with a corrected Weber fraction of 1.8, may also have poorer capabilities to detect odor intensity differences compared to the human. According to Davis, this relationship may be expected since a sensory system optimized for the detection of the lowest amplitude suffers from an attendant loss in resolving power. The converse of the principle is also expected to be true. Davis cites as an example, the highly sen-

sitive but poor wavelength-resolving rod system in the eye, compared with the less sensitive but more selective response properties of the cone system in the same eye. Thus, if the coyote has exceptional olfactory sensitivity as this study suggests, due to the minute quantity of LiCl that it is able to detect in its food, a large Weber fraction for differential sensitivity might be expected. The observed Weber fraction of 2.0 for the coyote supports this prediction.

Since the discovery of the conditioned taste aversion phenomenon (Garcia et al., 1955) it has not been clear how the closely related senses of odor and taste are integrated into a sequence of behaviors leading to the avoidance of poisoned food. Research with rats has indicated that taste cues are more effective than odor cues in flavor aversion paradigms (Hankins et al., 1973) and odor cues are more effective than taste cues in shock-avoidance paradigms (Hankins et al., 1976). The way in which these sensory cues become associated, allowing an animal to avoid poisoned food from a distance, however, has received little examination.

At present, there have been two hypotheses advanced to explain the association of nongustatory and gustatory cues in food aversion learning. The first hypothesis, the two-phase conditioning sequence mentioned earlier, was proposed by Garcia et al. (1973) to explain the behavior of wild canids toward poisoned prey. In phase one of this hypothesis, the taste of a prey becomes aversive due to its association with illness.

In phase two, the distal cues become secondarily associated with the taste and subsequently suppress approach and attack behavior. Thus, in the Gustavson et al. (1974; 1976) studies, it was hypothesized that before the coyotes' attack behavior was suppressed, it took at least two trials to associate the taste with the distal cues.

The second hypothesis, synergistic compound potentiation, has been proposed by Rusiniak, Hankins, Garcia, and Brett (in press). Synergistic compound potentiation refers to the strengthening of a weak food cue by association with an effective taste cue in flavor aversion paradigms. Thus, if a weak cue such as odor is associated with a stronger taste cue in a compound stimulus, the weak odor cue becomes as effective as the taste cue in mediating the aversion, and much more effective than if the odor cue had been conditioned alone.

Evidence for this type of potentiation has been found in hawks and pigeons. Following one LiCl illness, Brett et al. (1976) found that the coat color of a mouse prey was a weak cue for buteo hawks. If the coat color was accompanied by a distinctive taste, however, it became an effective cue in mediating the aversion. Likewise, Clarke, Irwin, and Westbrooke (in press) found that pigeons did not acquire a visual aversion for blue-tinted water after one LiCl illness. If, however, blue-salty water was followed by LiCl illness, a strong visual aversion was established in a single trial. Similar but weaker potentiation effects have been found in rats (Braun & Ryugo, 1974; Lorden et al., 1970). Other evidence for the po-

tentiation of nongustatory cues has been found in coyotes. Ellins and Swanson (1978) showed that coyotes avoided a familiar food in a novel place due to the synergistic potentiation of cues associated with the novel place by being paired with taste cues associated with illness.

Rusiniak et al. (in press) recently compared the two-phase hypothesis with the synergistic compound potentiation hypothesis to determine the possibility of either occurring in flavor aversion paradigms in the laboratory rat. Using odor as the distal cue and taste as the proximal cue, they found only weak evidence for the two-phase hypothesis. Strong evidence was found, however, indicating that taste synergistically potentiated the distal cue of odor. Odor alone became a powerful cue in the avoidance of poison food.

This finding appears to contradict the well established interference effect (Kamin, 1969; Mackintosh, 1974; Pavlov, 1928) in which strong component of a compound stimulus overshadows or blocks conditioning to the weaker component. Interference effects, however, are usually observed when visual or auditory cues signal the onset of a reinforcing stimulus such as a cutaneous insult or a taste food reward. Since both cues serve the same functional role, the stronger cue tends to overshadow the weaker cue. In the ingestion sequence, odor and taste do not serve the same functional roles (Garcia et al., 1974), thus, potentiation of the weak odor cue by the taste cue occurs rather than the overshadowing of the odor cue by the taste cue.

In the present study, by taking on strong aversive qualities due to its association with taste and illness, odor became a strong cue for the coyote. After a single LiCl treatment, odor became a telereceptor cue to avoid the LiCl poison. This suggests that the odor of the LiCl was potentiated by the "salty" taste of the LiCl in the food. Since this conditioning occurred in only one treatment instead of two, it appears that the two-phase hypothesis would provide an unlikely explanation for the results of this study. The synergistic compound potentiation hypothesis, however, provides a likely explanation for the coyotes' avoidance of the LiCl laced food. Much like Rusiniak's rats, the coyotes in this study formed an aversion for the distal cues that control the approach response, allowing them to avoid the poisoned food at a distance.

The present study indicates, therefore, that in some circumstances, synergistic compound potentiation of nongustatory cues may occur in the coyote. This potentiation of cues may also provide a possible explanation for the coyotes' avoidance of poisoned prey. During many of Gustavson et al.'s (1974; 1976) trials with live prey, coyotes suppressed attack behavior on the second trial after "mouthing" the prey. Perhaps this close contact allowed the coyote the opportunity to smell the now potentiated odor and avoid the prey without tasting it. Since the present study did not include the use of live prey, this hypothesis remains to be tested in future research.

CONCLUSION

The present study indicates that after one illness on 6 g of LiCl in 100 g of food, coyotes can discriminate between plain food and food containing quantities as small as 50 mg of LiCl. This finding provides a likely explanation for the results of research that has deviated from the established conditioned taste aversion procedures of Gustavson et al. (1974; 1976). Ellins, Gustavson and Garcia (in press) have previously offered a word of caution to researchers who use this emetic agent in prey aversion paradigms. If the taste of LiCl is allowed to predominate in a food, the resulting aversion will be to the salty taste, rather than to the taste of the prey. The results of the present study provide the necessary data to substantiate their warning. Furthermore, coyotes can form a LiCl salt aversion in a single trial after which they are easily capable of detecting and avoiding the food or bait containing this emetic salt.

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