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SPECIFIC HUNGERS AND POISON AVOIDANCE AS ADAPTIVE SPECIALIZATIONS OF LEARNING[1]

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Learning and memory are considered within an adaptive-evolutionary framework. This viewpoint is illustrated by an analysis of the role of learning in thiamine specific hunger. Consideration of the demands the environment makes on the rat and the contingencies it faces in the natural environment, appreciation of the importance of the novelty–familiarity dimension for these animals, and the realization of two new principles of learning, permit a learning explanation of most specific hungers. The two new principles, "belongingness" and "long-delay learning" specifically meet the peculiar demands of learning in the feeding system. In conjunction with the importance of the novelty dimension, they are discussed in an attempt to develop the laws of taste-aversion learning. It is argued that the laws or mechanism of learning are adapted to deal with particular types of problems and can be fully understood only in a naturalistic context. The "laws" of learning in the feeding system need not be the same as those in other systems; manifestation of a learning capacity in one area of behavior does not imply that it will be accessible in other areas. This notion leads to speculations concerning the evolution and development of learning abilities and cognitive function. Full understanding of learning and memory involves explanation of their diversity as well as the extraction of common general principles.

The application of the basic principles of evolution and adaptation to learning and memory offers a hopeful means of conceptualizing and ordering the increasingly diverse data of these fields. Learning and memory, being the result of natural selection, should be expected to be best developed in situations and species where other solutions to the problems at hand are less adaptive. Furthermore, when learning or memory capacities are brought to bear on a particular type of problem or situation, it stands to reason that these capacities should be shaped by or adapted to the situation.

We propose to treat learning and memory as any other biological characteristic, subject to natural selection and therefore adapted to handle specific types of problems. Insofar as an important environmental problem (e.g., obtaining adequate foods) presents unique demands or contingencies, we would expect to find appropriate modifications of learning and memory abilities, closely articulated with one another and with the natural behavior

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of the organism. Biologically speaking, there is no reason to assume that there should exist an extensive set of generally applicable laws of learning, independent of the situation in which they are manifested. This is not to say that there might not be some general laws, at a minimum resulting from basic constraints and features of the operation of the nervous system, and perhaps reflecting general principles of causality in the physical world. However, if we look at learning within an adaptive-evolutionary framework, we should seek not only to uncover some of the greatest common denominators among the behaviors we study, but also to explore the plasticity of the mechanisms themselves, as they are shaped through selection to deal with particular types of problems. For many years, the leading ethologists (e.g., Lorenz, 1965; Tinbergen, 1951) have espoused a position consistent with this. They have emphasized the importance of considering learning within a naturalistic context; learning is viewed as being genetically programmed to occur at specific points in an ongoing behavior sequence. The thesis presented here is in harmony with the ethologists' position, but emphasizes differences in learning *mechanisms* themselves, as a function of the situations in which learning occurs.

In the face of recent evidence, coming most significantly from the work of Garcia and his colleagues (Garcia, Ervin, & Koelling, 1966; Garcia & Koelling, 1966), challenging two important generalities in learning, a framework for ordering the suggested diversity of laws of learning is desirable. We propose such a framework in terms of the notion of adaptive specializations. Consideration of learning from the adaptive point of view offers two advantages: (*a*) it provides a heuristic, for ordering and predicting the types of learning one will see in different situations, and (*b*) it provides a type of explanation of behavior, in that one aspect of understanding behavior can be considered to be explication of its adaptive value.

Adaptive considerations have proved useful in many areas of biology and are a significant part of our understanding of sensory psychology and physiology. Specializations in sensory function, as shown in the classic works of Lettvin, Maturana, McCulloch, and Pitts (1959) in the visual system of the frog, Capranica (1966) on the remarkable tuning of the frog auditory system to mating calls, and Roeder (1963) on detection of bat sonar by the moth auditory system, can be fully understood only in the context of adaptations to natural problems. The incredible diversity of the visual system (e. g., variations in the proportion of rods and cones in the retina as a function of species and ecology) can be ordered and comprehended in a phylogenetic adaptive framework, as shown in the classical work of Walls (1942). We would like to suggest that there are similar possibilities in the area of learning and memory.

In the major portion of this paper, we shall discuss specific hungers and poisoning in rats. We shall argue that some basic features of learning and memory as applied to food selection in the rat are strikingly different from features characterizing the rat's learning in more traditional laboratory situations, that these differences make sense in terms of evolutionary adaptation, and that an understanding of the role of learning and memory in food selection involves an elucidation of specifically adapted learning mechanisms and an integration of these with genetically determined behavior patterns.

In the remaining portion of the paper, we shall discuss whether the feeding system is a unique case or representative example, relate our position to somewhat similar theoretical positions, including ethology and the recent papers of Garcia (Garcia & Ervin, 1968; Garcia, McGowan, & Green, 1971), Revusky (Revusky, in press; Revusky & Garcia, 1970), Seligman (1970), Lockard (1971), and Shettleworth (1971), and discuss the implications of our position in the areas of comparative psychology of learning and human function.

SPECIFIC HUNGERS

Basic Phenomenon and Problems with a Learning Interpretation

The phenomena of specific hungers were beautifully demonstrated in the classical work of Richter (1943). The question raised by this work was, How is the animal (in particular, the rat) able, when deficient in a particular nutrient, to select those foods containing it? In the case of sodium, it is quite clear that sodium deficiency releases an *innate* preference for substances containing sodium (Nachman 1962; Richter, 1956; Stricker & Wilson, 1970). However, it is hard to believe that the rat comes equipped with prewired recognition systems for each of the many substances for which it can show a specific hunger. The alternative view holds that rats can learn about what foods "make them better" when they are ill and in this manner come to select the proper nutrients (Harris, Clay, Hargreaves, & Ward, 1933; Scott & Quint, 1946). Rats would, in their lifetime, learn preferences for the tastes of only those foods associated with recovery from the deficiencies they happen to have experienced. This notion has the distinct advantage of simplicity in that it accounts for all of the specific hungers (except sodium) with one basic mechanism.

There was, in fact, some evidence for a learning interpretation of specific hungers. Scott and Verney (1947) offered a distinctively flavored vitamin supplemented food and an unflavored deficient food to deficient rats. After a preference developed for flavored, enriched food, the flavor was switched to the deficient food. By and large, rats now preferred the flavored deficient food, suggesting a learning mechanism.

The problem with a learning interpretation, so far as psychologists were concerned, was the long delay of reinforcement. The recovery (reward) effects produced by an ingested nutrient would not occur until many minutes or hours after ingestion. This poses serious problems for a learning mechanism within the context of traditional learning theory. If specific hungers were in fact learned, then some new type of learning had to be involved. This served as the impetus for our investigation of specific hungers.

The first demonstration of vitamin B hunger was that of Harris et al. (1933), who found that given a choice of three foods, one supplemented with B vitamins, B vitamin deficient rats would quickly come to choose the correct food. For convenience, Rozin, Wells, and Mayer (1964) decided to study a more simplified situation. One vitamin, thiamine, was selected, since a clear specific hunger for thiamine had been reported (Richter, Holt, & Barelare, 1937; Scott & Quint, 1946). The most pronounced symptoms of thiamine deficiency in the rat are weight loss and anorexia. (More details about this and other aspects of thiamine hunger are available in a review by Rozin, 1967a). Following injection or ingestion of thiamine, deficient rats show clear signs of reversal of symptoms within a few hours, at most. The basic design consisted of raising weanling rats on a thiamine deficient diet for 21 days, at which point they showed clear signs of deficiency. At this point they were offered a choice between this deficient diet and the same diet supplemented with thiamine.

Thiamine deficient animals strongly preferred the thiamine enriched choice, while control animals who were not deficient, but otherwise treated identically, did not. A few rats with a choice between deficient and *highly enriched* diet showed no clear preference during the first few choice days, but in the meantime ingested great amounts of thiamine and showed marked recovery. Subsequently, these rats developed a clear preference for the thiamine rich diet. It seemed highly unlikely that a rat would show a preference for what it would have needed a few days ago without showing that same preference when the thiamine presumably had reinforcing value. This anomalous observation was confirmed in an experiment in which rats were made deficient in thiamine and then recovered from deficiency by injection of high amounts of thiamine while consuming the deficient diet. After a period of recovery, the rats were offered a choice of thiamine enriched and deficient diets. Preferences for the thiamine enriched diets in rats that had been deficient emerged at all the recovery intervals studied (Rozin, 1965).

This result raises a second problem for a learning interpretation of thiamine hunger: How could rats develop a learned preference for something that at the time the preference appeared, had no known reinforcing effects? If the preference developed because of the initial reinforcing effects of the thiamine, why did it not appear until much later? We shall call this problem *Preference after recovery.*

Careful consideration of the specific hungers situation and contingencies gave rise to additional problems that could not be easily solved within the traditional learning framework. Given that a rat might learn with the delays of reinforcement that seem to hold here, how would the recovery be specifically associated with a particular food? If the animal had eaten from a number of the choices available (or both choices in the two-choice situation), how could one of these choices, presumably the one containing thiamine, show a specific increase in preference? In other words, if an ingestion of two or more foods is followed by recovery, how does one of these foods acquire positive properties? We shall call this third problem, *Which food?*

A logical extension of this notion raises the question of how food or the eating of food becomes associated with recovery when many other potential candidates for association exist in the environment. After all, following ingestion of foods including the vitamin enriched food, and before recovery can ensue, the rat performs many acts, such as chewing, grooming, exploring, and sleeping, and receives many stimuli. By what principle does he elect to respond to food stimuli instead of other stimuli? We call this fourth problem, *Why food?*

We have, then, four problems in the application of traditional learning principles to the explanation of specific hungers:

1. Delay.
2. Preference after recovery.
3. Which food?
4. Why food?

Reinterpretation of Specific Hungers

The first step in the resolution of the problem as formulated came with the appreciation of the importance of novelty in the determination of food preferences in deficient rats (Rodgers & Rozin, 1966). Deficient rats show an immediate and almost complete preference for new foods, even when the new food is thiamine deficient and the old food has a thiamine supplement. In this case, the new-food preference reverses after a few days. The results *suggested* that the "specific hunger" for thiamine may be simply a reflection of the thiamine deficient rat's preference for new foods: If the new food contains thiamine, a learned preference could develop (mechanism still unknown).

Rodgers (1967a) succeeded in demonstrating quite conclusively that there is no specificity to thiamine specific hunger. Reasoning that the novelty response might overwhelm an existing tendency to prefer the vitamin, Rodgers offered deficient rats the choice of a deficient novel diet or the same novel diet supplemented with thiamine. The usual strong specific hunger did not appear. Furthermore, when the choice was between two different novel diets, one enriched, preferences for the enriched source did not develop rapidly. Finally, separate groups of thiamine deficient rats and pyridoxine deficient rats were offered their basal diet in two forms: one supplemented with thiamine, the other with pyridoxine. If there were any specificity, one would expect each group to show a preference for the vitamin that would produce recovery. There were no significant differences between the groups.

There seemed to be two types of explanations for the novelty effect. One is that the deficiency experience triggers an innately programmed "neophilia." A more attractive hypothesis is that the novelty effect comes about through learning. The paradigms described all pit the new food against the familiar food that has been associated with deficiency. The new-food preference could be a reflection of an aversion to the old food. Put more colloquially, we could ask whether preferences for new foods appear because the rat "loves the new stuff or hates the old stuff." The issue can be clarified by watching the behavior of deficient animals toward different foods (Rozin, 1967b). Rats housed in relatively large individual cages were observed during the first 15 minutes of an 8-hour food presentation each day. Their responses were classified into a number of categories, such as grooming, sleeping, eating, and chewing. The experimental rats were placed on a thiamine deficient diet. As deficiency developed, less time was spent eating during the first 15 minutes, and two striking behaviors, quite rare in normals, appeared. One was spillage of the food: the rat would approach the food cup, sniff at the food, and then paw at the food in a scooping motion, spilling it out of the cup, so that it fell through the wire mesh floor. (This spillage phenomenon in deficient rats was actually quite familiar, since we have always had some difficulty measuring the food intake of deficient rats on this account.) The other new behavior was what we call "redirected feeding." Following this initial investigation of the food cup, rats would occasionally move over to the wooden barrier separating the nest area from the rest of the cage and begin to chew it vigorously. They would also, occasionally, chew on the cage wires. These two behaviors suggested an aversion to the familiar diet. The redirected feeding suggests conflict between desire to eat and the aversiveness of the food offered. Spillage is often seen in normal rats with highly unpalatable foods, such as quinine adulterated diets.

When offered the old deficient food in a new container (metal instead of glass) in a new location, these deficient rats showed little potentiation of eating and continued to show the behavior described above. Apparently the vessel and its location were not controlling the aversion. However, when a completely new deficient food was offered in the familiar vessel and location, uninterrupted avid eating ensued, suggesting that the aversion was specific to the food. The deficient rats were subsequently allowed to recover on a new, vitamin enriched diet. Following one week of recovery, and after a 16-hour period of food deprivation, they were presented again with the familiar deficient food for the first time since the onset of recovery. These food deprived rats, showing no signs of deficiency at this time, responded to the familiar deficient food as they had before, with minimal ingestion and occasional spillage and redirected feeding. In this case, a "normal" hungry rat prefers staying hungry to eating its original diet which provides, in fact, perfectly adequate nutrition for him at the time, and is normally quite palatable. Preference of hunger (eating nothing) to ingestion in hungry rats and the similarity in the rat's behavior toward deficient and highly unpalatable (quinine adulterated) diets suggests strongly that we are dealing with an aversion to the familiar food.

The learned aversion interpretation places specific hungers in a new perspective. We can consider the deficient diet as a CS and the nausea or other ill effects produced by its ingestion as a UCS. Presumably, the classically conditioned "ill effects" lead to avoidance of the familiar food. The mechanism suggested for the specific hunger phenomenon, as seen in the standard two-diet choice, would then be that the rat learns an aversion to the familiar deficient food. Before the time of choice, he has already done a most significant part of his learning: He knows what not to eat. The initial preference for the new food follows. Its maintenance when the new food is enriched could be accounted for as an additional learned preference for the new food or as a failure to develop an aversion to it (see section on learned preference).

To the extent that specific aversions play a key role in specific hungers, there is an obvious parallel between specific hungers and poisoning. Both involve learned aversions; vitamin deficient diet is a slowly acting poison. The aversion experiment thus suggests that these two sets of phenomena are closely related. Furthermore, the same basic problems raised here (Delay, Which food? Why food?) arise with respect to poisoning. Since poisons are designed and synthesized by man, it is unreasonable to hold that rats show innate aversions to them. In comparing the literature on poisoning (see Barnett, 1963; Richter, 1953; Rźoska, 1953) to that on specific hungers, there is one apparent contrast. We have reported an increased *preference* for new foods in white rats, while the poisoning literature which focuses on wild rats strongly indicates the opposite: an exaggerated neo*phobia* following poisoning. That is, wild rats, who show a much greater base-line tendency to avoid new objects or events than do white rats (e.g., see Galef, 1970), show a further exaggeration of this tendency, often to an extreme (Richter, 1953) following poisoning experiences. This disparity can be accounted for as a procedural difference, since the new-familiar choices we offered to our domestic rats were different from those usually offered poisoned wild rats. In particular, in the novelty experiments, which were done before we realized that specific aversions were involved, the rat was offered a choice between a familiar food associated with deficiency and a new food. Even if the white rat were somewhat neophobic, this might not appear since the alternative choice was a strongly aversive familiar diet.

In order to provide a meaningful comparison between poisoning and specific hungers, both sets of phenomena would have to be demonstrated under the same sets of conditions and in the same strain of rats. In an experiment meeting these criteria and comparing half-wild and domestic rats, a paradigm was employed that allowed fuller expression of the rat's neophobic or neophilic tendencies. Rats were raised on Diet A, prior to induction of aversive consequences. Deficiency or poisoning (or nothing in the case of controls) occurred in the presence of Diet B. In the final test, rats were offered these two diets and a completely new one, Diet C. Therefore, rats were faced with a choice among a familiar *safe* diet (A), a familiar aversive diet (B), and a completely new diet (C) (Rozin, 1968).

The single important result is that all rats suffering poisoning or deficiency showed an increased preference for the familiar safe food, that is, a ***neophobia.*** Half-wild rats showed a stronger neophobia following the aversive experience, but half-wild controls also showed a higher base-line neophobia. All experimental rats almost completely avoided the familiar aversive food (B), but ate some of the completely new food. There were no major differences between the specific hunger and poisoning groups. Therefore, it appears that we can consider specific hungers as a parallel to poisoning. Again, the behavior makes sense in an adaptive framework: following an unpleasant food-related experience, the rat tends to return to a known, *safe* food.

Resolution of the Inconsistencies with a Learning Interpretation

The specific aversion explanation of specific hungers, the realization of the importance of the familiarity-novelty dimension, and the appearance of two articles of major significance by Garcia and his colleagues enable us to resolve the four basic problems with a learning interpretation.

Preference after recovery. This can be accounted for as a retained aversion to the familiar food. Rats made deficient in thiamine and then recovered by injection for 12 hours or 5 days (while continuing to eat the same deficient diet) show a strong initial novel-food preference when offered a novel-familiar food choice, with thiamine *absent* from both choices (Rozin & Rodgers, 1967). In these experiments, recovery took place in the presence of the familiar food. The existence of a novelty effect suggests that the aversion had not fully extinguished by the time of testing. It is significant in this regard that in most of our experiments (some unpublished) the recovery effect showed some diminution as time of recovery increased. The recovery effect should be maximal when recovery is associated with a new food, so that the old diet aversion does not extinguish. Strong "recovery' effects are in fact seen under such circumstances in the aversion experiment, with a single choice (Rozin, 1967b) and in typical two-choice experiments with long recovery periods (Rozin, unpublished data).

Which food? In the "standard' two-choice situation, this problem is easy to deal with; the rat learns to avoid the deficient food when it is the only diet available. There is no Which food? problem here. Because of this learned aversion, rats show an immediate, virtually complete preference for the novel food, thus making it possible for them to learn about its consequences.

The testing situations described up to this point, with the partial exception of the testing environment in the aversion experiment, have been very limited, well defined, and unnatural. Rats normally live in a much larger area than was permitted to them in these studied, have an elaborate social life, and seldom face simple binary food choices. It is not unreasonable to assume that one or only a few foods might be available to the rat during the deficiency period in nature, since with a wide variety of foods available, a deficiency would be quite unlikely. In their classic work on B vitamin hungers, Harris et al. (1933) offered deficient rats a choice among a large variety of foods, with only one containing B vitamins in significant amounts. By and large, they found that with large numbers of choices (6–10 foods), rats were unable to select the vitamin enriched source, and they found it necessary to "educate" the rats by offering only the enriched food for a period of days in order to establish a maintained preference for this food. Examination of the day-to-day intake of these animals before the education period suggests a distinctly nonrandom food selection pattern: food intake seemed to be restricted to only a few of the many choices on any particular day. This seemed to be an adaptive way of unconfounding the situation and suggested an analysis of the meal patterns of deficient rats faced with the choice of a number of new foods (Rozin, 1969a). A thiamine supplement was placed in one of four diet choices for each rat. Feeding was restricted to eight hours a day, and the food intake from each cup was measured at hourly intervals. Four of the 10 deficient rats studied developed clear preferences for the enriched choice within a few days, and two other rats developed strong preferences for two of the four choices, where one of the preferred choices was enriched. Analysis of the meals indicates a characteristic pattern, both on a daily and hourly basis. Means, except for an initial daily sampling of many or all of the choices, tended to be restricted to one food. The rat's feeding pattern maximizes the possibility of associating each diet with its appropriate consequences, since meals tend to be isolated in time and to consist of a single food. The emergence of a strong preference for the enriched food is, in each case, preceded by a clearly defined meal of that food. Furthermore, no rat failed to develop a clear enriched food preference if it ate an isolated meal of at least 1 gram from the enriched food. The rats that failed to show adaptive preferences in the initial part of the experiment failed to sample significant amounts of the enriched food. Similar, though less well defined, sampling patterns are seen in normal rats. Normals mix meals more, but this may be a direct consequence of the fact that their meals are larger. The anorexia of deficiency may, in and of itself, exaggerate in an adaptive way the normal feeding pattern of the rat. It is clear that we have here another part of the answer to the Which food? problem.

Finally, social factors have become implicated in food selection in some significant recent experiments. Galef and Clark (in press) studied responses to poisoning in colonies of wild rats observed in the laboratory under seminaturalistic conditions. They offered a group of wild rats two foods, one of which was poisoned. After a short period of time, all rats avoided this food. The poison was removed, but the rats still completely avoided the base. A litter was born, and the behavior of the young toward these new foods was observed. The parents and young were fed for three hours a day and were constantly under observation during this period. During a two-week period (Days 14–28 of life in the pups), the pups came out to eat, but ate only the safe food (possibly because this was the only food being eaten by the parents). When the young were fully weaned and placed in a new cage, separated from their parents, they continued for a six-day period to eat only the safe diet and ignore the formerly poisoned diet. Further experiments (Galef 1971; Galef & Clark, in press) suggest a straightforward explanation for this effect. Rat pups tend to approach areas where adults are located and begin feeding there. In this way, they become familiar with the foods eaten by the adults and avoid alternative diets as a result of their neophobia. More recent work (Galef & Clark, 1971; Galef & Henderson, in press) suggests an additional mechanism: chemical cues from mother's milk seem to function to familiarize the young with certain characteristics of the mother's food and produce initial postweaning preferences.

Why food? Rats in the aversion experiment (Rozin, 1967b) did not show an aversion to the container or the location of the deficient food. While introduction of a new food dramatically increased ingestion, change to a new location and container did not. Apparently what the animal learned was specific to the food.

In an independent and much more compelling experiment, Garcia and Koelling (1966) provided evidence that there was a specific tendency for taste "CSs" to be associated with certain types of visceral "UCSs," while exteroceptive CSs such as light and sound would be preferentially associated with exteroceptive UCSs, such as shock. They paired light, sound, and taste simultaneously with either electric shock or poisoning in different groups of animals. The shocked animals developed an avoidance of the light and sound, but not of the taste. The poisoned animals, subjected to the same light-sound-taste pairing, avoided the taste and not the sound or light.

Delay. The reinterpretation of specific hungers, in itself, does not bring us much closer to solving this important problem. It does not appear to be possible to reinterpret what appeared to be long-delay learning in terms of short delays. However, a critical experiment by Garcia et al. (1966) demonstrates that long-delay learning can occur in this system. They induced an aversion to saccharin in rats by injections of apomorphine, a drug that presumably produces gastrointestinal upset. Aversions were produced when the interval between termination of drinking and injection of the drug was one-half hour or more. Only a few trials were necessary to establish a clear aversion.

A New Problem—Are There Learned Preferences as well as Learned Aversions?

Before we leave the problem of specific hungers, there is one new issue to resolve. Much of the specific hunger phenomenon can be explained in terms of aversion; Is there a positive side also?

Up to this point we have provided evidence for three categories of foods based on the animal's experience (Rozin, 1968). These are unexperienced or novel, familiar-safe, and familiar-aversive. The question is, Is there a fourth category, familiar-positive? That is, is the experiencing of positive consequences any different from the experiencing of neutral consequences when these experiences are contingent upon ingestion of a particular substance?

Much of the evidence which appears to demonstrate positive preferences can be reinterpreted in terms of learned aversions. For example, Harris et al. (1933) found that when only one of a large number of diets contained adequate thiamine, most deficient rats were not successful in selecting the correct diet. However, if the rats were "educated" by being offered *only* the adequate food for several days, they showed a preference for this food when the larger number of diets were again offered. This experiment does not distinguish between learned-preference and learned-aversion interpretations. Rats could be avoiding the nonthiamine diets by a combination of learned aversions and neophobia. That is, after "education" the rats have learned that the thiamine-containing diet is "safe," but it is not certain whether they have learned that it has any special "recovery from deficiency" properties which distinguish it from other safe diets, since we know that deficient rats prefer "old safe" foods to either old aversive or novel foods (Rozin, 1968). Similarly, in the sampling experiment (Rozin, 1969a), the fact that the rat eventually prefers the only enriched diet in a four-choice situation could mean that he had developed aversions to the other choices.

There are some recent experiments which present more serious challenges to a pure aversion model. Garcia, Ervin, Yorke, and Koelling (1967) repeatedly made rats thiamine deficient and produced recovery by thiamine injection. Just prior to thiamine injection, rats drank saccharin solution. At all other times, water was the only fluid available. When thiamine deficient, the rats showed an increase of saccharin intake over trials, both with respect to their own water intake and to the saccharin intake of similarly treated animals where thiamine injection was not contingent on saccharin ingestion. Campbell (1969) has also demonstrated that thiamine deficient rats show an increase in their absolute intake of a sucrose solution which has been associated with recovery from deficiency. Zahorik and Maier (1969) used Garcia et al.'s (1967) procedure but with a modified test and found that rats prefer the taste associated with recovery to both the taste associated with deficiency and a novel taste. Furthermore, this preference was apparent in both deficient and recovered rats.

These experiments, which certainly provide evidence for learned preferences, can nonetheless be explained in terms of the three basic categories of food. A more decisive experiment would have to show that rats prefer a "recovery" solution to an old "safe" solution, that is, one they drank without aversive consequences at a time when then were not vitamin deficient.

Revusky (1967; Revusky & Garcia, 1970) performed a series of experiments to demonstrate that food with clear positive consequences would be preferred to foods with relatively neutral consequences. In his simple design, rats were fed one nutrient solution while hungry and a different one when satiated. After five days of this training, a significant preference developed in a two-bottle test for the solution drunk while deprived. This result is interpreted in terms of the greater (delayed) reinforcing effect of the solution drunk during deprivation. Since both solutions were equally familiar and the rats drank the solution offered in satiated conditions voluntarily (so that an acquired aversion would be unlikely), this experiment meets the requirements for demonstrating a learned preference. The effect is clear, though not large by comparison to the aversion data (see Revusky & Garcia, 1970, for additional data).

It is noteworthy that the positive preference effects reported have been rather small by comparison with learned aversions, and difficult to obtain (Kalat & Rozin, unpublished; Revusky & Garcia, 1970). We cannot satisfactorily explain this asymmetry. Possibly the rat is better prepared to learn aversions because rapid learning there has particular survival value; that is, mistakes are very costly. This remains, for the moment, an intriguing problem, with possibly great implications for the regulation of food intake.

Other Specific Hungers

We have offered a theory of thiamine specific hunger. We believe that it holds for other learned specific hungers as well. Novel-food preferences, which imply a learned aversion mechanism, have been demonstrated in calcium, sodium, and magnesium deficient rats (Rodgers, 1967a) and in pyridoxine and riboflavin deficient rats (Rozin & Rodgers, 1967). The preference after recovery phenomenon appears in identical form in thiamine, riboflavin, and pyridoxine deficiency (Rozin & Rodgers, 1967).

It seems reasonable to assume that the anorexia characteristic of most vitamin deficiencies reflects, at least in part, a learned aversion to the deficient food. This is dramatically clear in the case of thiamine deficiency, where the anorexia symptom disappears precipitously when a new diet is offered. On the other hand, there is relatively little anorexia in vitamin D or vitamin A deficiency, and in both cases there has *not* been a clear demonstration of a specific hunger.

There is an impressive body of research on amino acid specific hungers and responses to amino acid imbalance (Harper, 1967). These "deficiencies" are characterized by anorexia and seem to fit into the scheme we have described. Recently, Rogers and Harper (1970) presented evidence for a positive preference for a solution that corrects an amino acid imbalance.

We cannot complete this reconsideration of specific hungers without mentioning one particularly serious shortcoming of all the mechanisms we have discussed. Although, in principle, they can account for most of the individual vitamin or mineral specific hungers, it is not clear how the classic "cafeteria" self-selection of Richter (1943) can be accounted for. Rats appear to self-select an extremely well balanced diet. Unless we assume that they develop incipient deficiencies of a variety of nutrients and learn aversions and preferences on the basis of these minimal symptons and their abatement, we have no explanation of this remarkable phenomenon. At this time, long-delay learning mechanisms appear inadequate to the task, since we cannot identify obvious candidates for unconditioned stimuli.[4]

WHY IS SODIUM HUNGER INNATE?

An alternative to the mechanism we have discussed is an almost completely genetically preprogrammed specific hunger. Sodium hunger seems to be such a case. Rats sodium deficient for the first time show a strong preference for sodium immediately upon tasting it (Nachman, 1962; Richter, 1936, 1956; Stricker & Wilson, 1970). They also show strong preferences for similar-tasting salts which will not actually alleviate their deficiency (Nachman, 1962), and they will work at a high rate in extinction at a lever which previously produced a salt solution which they drank while sodium replete (Krieckhaus & Wolf, 1968).

We do not know why sodium differs from other specific hungers, but at least three explanations are available. First, the great importance of sodium in body fluid balance, its common scarcity in the environment (witness salt licks and salt wars), and the large amount needed by the individual organism might place particular selection pressure in favor of a surefire sodium hunger. The various physiological adaptions directed toward regulation of body sodium are impressive. Second, it is conceivable, as Rodgers (1967b) has suggested, that sodium ingestion by sodium deficient organisms may have initial negative effects[5] associated with large-scale electrolyte shifts. There is not much evidence on this point. Sodium deficient animals do develop an aversion to sodium deficient diet (Rodgers, 1967a). However, *injections* of sodium into sodium deficient animals have not successfully produced preferences for foods ingested just prior to injection (Rodgers, 1967b). These possible initial negative events may prevent the operation of the learning mech-

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[4] Another remaining problem concerns the difficulty in demonstrating specific hungers with the nutrients in an aqueous solution (Appledorf & Tannenbaum, 1967; Rozin, Wells, & Mayer, 1964). This contrasts with Richter, Holt, and Barelare's (1937) dramatic demonstration of a specific hunger for thiamine in solution. We are inclined to believe that the difficulty frequently encountered with aqueous solutions derives from pure water being one of the choices available. Water's great familiarity might protect it from becoming aversive (Garcia & Koelling, 1967; Maier, Zahorik, & Albin, 1971; Nachman, 1970a). Palatability differences in the various choices solutions might also be involved Rogers & Harper, 1970).

[5] Scott, Verney, and Morissey (1950) noted that magnesium deficient rats selected magnesium deficient food in preference to magnesium enriched food. Rodgers (1967a) confirmed this "inverse" specific hunger and suggested that the initial ingestion of magnesium by magnesium deficient rats produces aversive consequences. Here, those consequences might be considered as "coming down" from the hyperirritability or "high" characteristic of magnesium deficiency.

anisms normally implicated in specific hungers. Third, sodium as a stimulus is well defined by the taste system. It would be easy for a genetic program to tie into the proper class of stimuli. (Conversely, one might argue that the fact that sodium recognition seems to be so fundamental to the taste system suggests again the great importance of sodium as a directive force in evolution.) Although a unique learning ability might have evolved to meet this particular problem, the actual genetically programmed solution seems preferable. However, important biological functions are often overdetermined; this may be one example. It has been shown that normal rats can learn the location of sodium sources in their environment and go to them promptly when a sodium need is induced (Krieckhaus & Wolf, 1968).

But now we must turn the question around and ask, Why are all specific hungers not innate? One basic learning mechanism can provide an adaptive solution for almost all specific hungers (and also poisoning). Instead of programming specific innate recognitions of a variety of nutrients, the organism can rely on the fact that the malaise produced by most deficiencies (and possibly the consequent recovery on ingestion of the needed nutrient) is adequate to establish aversions (and preferences). There remains the fascinating question of whether long-delay learning originally evolved in response to proper selection of nutrients or the regulation of food (caloric) intake, or both.

Sodium hunger raises the general issue of the factors influencing the role learning will play in solving a particular problem. With alternative mechanisms available to deal with an environmental problem, the solution achieved by a species should be determined by factors of economy (cost) dictated by the actual situation and features of the development of the organism. We can see the interplay of these factors in the case of what Stricker (personal communication, 1971) has pointed out is another specific hunger: thirst for water. Morgan (1894) studied the development of drinking in young chicks and found that they apparently had no innate recognition of water. For example, they would run through water trays without drinking. At some point in the first few days of life, the bird would ingest water by pecking at a water drop or at an irregularity on the surface or in the bottom of the water pan. As soon as water entered the bird's mouth, it would adopt characteristic drinking movements, and after only one or two such experiences, would show a clear visual recognition of water. Hunt and Smith (1967) repeated and extended these results.

This system is highly predetermined: all components seem to be genetically programmed, except the recognition of the visual stimulus for water. Even a reasonably precise regulation of water intake is programmed, ready to come into operation as soon as water is experienced. Stricker and Sterritt (1967) have shown that on its very first drink, a chick's water intake is proportional to its deficit. We suggest that the visual recognition of water is learned because this is an efficient way of accomplishing the task at hand. The situation in the environment is such that a bird looking for food (defined as small irregularities) will certainly end up with water in his beak, and since he is prepared to learn this and has all of the other genetic equipment necessary to handle water ingestion and balance, he is "home free." We emphasize that this mechanism is successful because the bird's normal pecking and eating behavior (genetically programmed) invariably brings it into a position where water enters the beak. Hunt and Smith (1967) show that the first time a bird pecks at a dew drop (likely to be his first experience with water in the real world), it responds with a "feeding" peck, which is characteristically different from an approach to water. Only after the water enters the beak does drinking-type behavior appear, and subsequently, the peck at dew drops can be seen to be qualitatively different from the peck at food.

We are suggesting that there are two types of advantages (and therefore evolutionary pressures) to learned solutions to problems. The first, and most obvious, has to do with the variable environment. In the face of a changing and variable environment, it would be maladaptive to program specific modes of response, since these would often be inappropriate. Clearly, a plastic organism can do better in a plastic environment. (We expect that monophagous animals are less capable of learning about food than omnivorous ones.) The second factor predisposing to learning has to do with the "cost of preprogramming." This has two components. First, preprogramming of a particular behavior or stimulus configuration preempts a portion of the total genetic material, which could otherwise be used for some other purpose. Second, there may be greater costs associated with the evolution of genetically programmed solutions, insofar as built-in solutions involve more genetic reorganization.

Of course, in some cases, a genetically programmed recognition may be *replaced* by a learning mechanism. If an animal had the capability of learning something that was genetically programmed, otherwise favorable mutations in the genetic material responsible for this behavior could be selected for, even though the genetic basis for the behavior would be destroyed. Given a general learning capability, it could often be cheaper to allow the environment to supply the appropriate stimulus configurations, even if these will not vary much throughout life. We suggest that this "balance sheet" type of approach may be fruitfully applied to all specific hungers. In the case of the chick, we suggest that it is necessary to genetically specify those portions of the feeding and drinking system which are distinctively different (the ingestive responses and regulation). Since the chick's behavior leads to water in the beak *anyway*, because the preprogrammed food recognition overlaps with this aspect of drinking, a cheap way out can be found. The costs are minimal, and the genetic savings, significant.

SUMMARY

The reanalysis of specific hungers rests on three fundamental points: (*a*) The actual contingencies in the feeding situation are not what they were thought to be. (*b*) The novelty-familiarity dimension is of particular importance to the rat. (*c*) To account fully for the phenomenon, two new "principles" of learning were needed: belongingness and long delay. It is remarkable that each of Garcia et al.'s two "classic" experiments (Garcia & Koelling, 1966; Garcia et al., 1966) dealt directly with one of these problems at just the time that these two issues became *the* two problems in specific hungers.

In the context of the problems of specific hungers, it seemed clear that the basic principles demonstrated in these experiments must be essentially correct. Both principles, belongingness and long-delay learning, seem highly adapted to the properties of the feeding system. Tastes are in fact causally linked to gastrointestinal events, and there is a long inherent delay between the taste and its consequences. We suggest that specific learning mechanisms have evolved in response to specific problems. In the following section, we shall consider taste-aversion learning in greater detail, in order to demonstrate the extensive ways in which learning mechanisms may be modified to satisfy particular demands.

TASTE-AVERSION LEARNING: AN EXAMPLE OF ADAPTIVE SPECIALIZATION OF LEARNING

In this section we shall consider learning about food. In considering whether it is a "new type" of learning, we shall examine both the belongingness and delay principles in some detail, consider the importance of familiarity and novelty, and explore other possible differences between learning in the feeding system and more traditional types of learning.

Principles of Stimulus Selection

We can presume, from the material on specific hungers, that when faced with a bewildering array of stimuli as candidates for association with a gastrointestinal event, the rat has available principles with which to sort them out. One concerns his past experience with these stimuli, the novelty-familiarity dimension, and the other certain presumably built-in tendencies to associate certain categories of stimuli with certain relevant events (belongingness). We shall consider each in turn.

Novelty-Familiarity Dimension and Associability

We have argued that the novelty (or familiarity) of a stimulus is of particular importance for a rat (see Galef, 1970; Rozin, 1968). This distinction has particular significance in determining the magnitude of a learned aversion to a given taste. Revusky and Bedarf (1967) and Wittlin and Brookshire (1968) showed that rats learn aversions much more readily to novel than to familiar solutions, even when the familiar solution is drunk after the novel solution (and, of course, before poisoning). In these experiments, familiarization occurred over a period of days, but, in fact, a 20-minute exposure to a solution followed by neutral consequences will produce virtually the same effect, for such a solution is then quite resistant to association with poisoning (Kalat & Rozin[6]). This minimal (single) experience can have occurred three weeks before the poisoning without significant attenuation of the effect.

Belongingness

The "belongingness" (Garcia & Koelling, 1966) or "preparedness" (Seligman, 1970) or "stimulus relevance" (Capretta, 1961) phenomenon—that is, the tendency to associate tastes with aversive internal consequences as opposed to associating either element with anything else—seems eminently sensible from an adaptive point of view. Gastrointestinal and related internal events are, in fact, very likely to be initiated or influenced by substances eaten, and taste receptors, by virtue of their location, provide information about these same substances. It is essential for an omnivore to have the ability to learn rapidly which substances to eat and which to avoid. However, an equal ability to associate lights and sounds with gastrointestinal consequences would be far less adaptive; in fact, the common result would be "superstitious" learning. The belongingness phenomenon receives support not only from these adaptive arguments but also from neurological considerations. The gustatory receptors and the gut receptors are similarly classified as visceral sensory inputs and show close neurological relationships, specifically in the medulla and possibly in the hypothalamus.

It appears that under *some* circumstances, exteroceptive cues can become associated with poisoning (Garcia, Kimeldorf, & Hunt, 1961; Rozin, 1969b). Rather rapid learning of aversion to locations and shape of drinking vessel can be demonstrated if the UCS (apomorphine) is introduced *during* drinking from the appropriate vessel (Rozin, 1969b). On the other hand, even with a modest 30-minute CS–UCS interval and the use of a concatenation of nontaste cues including vessel shape, location, solution texture, and temperature, virtually no aversion appears after many trials (Rozin, 1969; but see Nachman, 1970a, for a demonstration that under proper circumstances oral temperature—a nontaste but interoceptive cue—alone may be an effective cue). The suggestion here is that at least part of the "weakness" of exteroceptive cues derives from a very rapid decay of their associability with time.

The belongingness principle in relation to taste-aversion learning is elaborated by Garcia and Ervin (1968) and Garcia et al. (1971). Further extensions of the principle to areas outside of feeding have been discussed by Seligman (1970) and Shettleworth (1971).[7]

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[6] J. Kalat and P. Rozin. Learned safety as an explanation for taste-aversion delay of reinforcement gradients. In preparation.

[7] The principle of belongingness makes some predictions about what aversive stimuli should be employed in various types of aversion therapy. For example, it would be expected that nausea-producing drugs such as apomorphine should be more effective than electric shock in treating alcoholism. At the present time, the data are not clear on this point (Rachman & Teasdale, 1969). The issue is complicated because it may be the case that humans learn different things with electric shock or nausea as UCSs.

Salience. There is evidence for "intramodality" belongingness. Rats tend to associate poisioning with some novel solutions more than others (Kalat & Rozin, 1970). Rats drank one novel solution briefly, 15 minutes later drank a second novel solution, and another 15 minutes later were poisoned. The following day, the rats were offered both solutions simultaneously. Under these conditions, certain solutions, which we describe as highly salient, became more aversive than others. The salience of a solution proved to be a more potent predictor of amount of acquired aversion than temporal proximity to poisoning. It was found possible to rank novel solutions in a stable, transitive "salience" hierarchy, such that each solution proved more salient (associable with poisoning) than all solutions lower on the list. Evidence for a salience effect on the "positive" side (recovery from thiamine deficiency) has been reported (Campbell, 1969).

As yet it is not known what constitutes the defining characteristics of the salience dimension. It is probable that the "relative novelty" of these operationally novel solutions contribute to the effect. By this we mean that more salient solutions may be more different from previously experienced solutions. There may be additional factors associated with intrinsic properties of the solutions. Certain tastes (e.g., bitter) may have a particular tendency to be associated with aversive consequences.

A functional definition of belongingness. At this time we know that some category of CSs, including tastes, preferentially associates with some category of UCSs, including "gastrointestinal distress." We would like to define these categories more precisely. The unconditioned stimuli employed have been described variously as "poisoning," "nausea," and "gastrointestinal upset." But the category of effective stimuli may include stimuli not suggested by these terms. Ingested foods can certainly produce significant internal effects outside of the gastrointestinal system, and it is indeed possible that the primary action of some of the UCSs presently employed is outside of the gastrointestinal system. On the other hand, it is hard to understand, from an adaptive point of view, why pain in the lungs or heart, for example, should be selectively associated with taste. As a matter of fact, it is not known whether gastrointestinal *pain* is selectively associated with taste. Much more research is needed to better define the range of visceral sensations with which tastes have high associability. The extensive Russian literature on interoceptive conditioning (see Bykov, 1957) demonstrates that exteroceptive cues can be attached to visceral UCSs. Whether there is some belongingness operating here remains to be seen.

Yet another dimension of belongingness concerns the temporal parameters of the various CSs and UCSs. In the taste-visceral system, stimuli tend to have slow onsets and to last for long periods. Exteroceptive CSs and UCSs, in contrast, are characteristically brief and well defined in time. The importance of these dimensions and the visceral field for taste-aversion learning could both be determined by using experimentally controlled UCSs, such as electric shock to the stomach mucosa instead of the ill-defined poisoning procedures.

The category of effective CSs should differ from species to species. It was argued above that the specific ability to learn taste-poison associations is highly adaptive because foods are the usual cause of any aversive gastrointestinal stimulation. This argument assumes that the animal identifies its food by taste. However, some species use other modalities as well. In particular, there is reason to believe that birds put main emphasis on visual cues in the identification and selection of food. A number of experiments by Brower (1969) indicate that birds can readily learn aversions to the sight of food,[8] and experiments by Wilcoxon, Dra-

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[8] One type of mimicry is based on the fact that many birds and some other species readily learn to avoid toxic or unpalatable prey. In these cases, a safe, palatable species evolves coloration similar to that of an unsafe or unpalatable one and thereby obtains some protection due to the predator's generalization of its learned aversion (Brower, 1969; Rothschild, 1967; Wickler, 1968).

goin, and Kral (1971) indicate that Japanese quail learn poison-based aversions more readily to the color (or optical density) than to the taste of a solution. Rats and bobwhite quail were poisoned half an hour after drinking a solution which was either blue, sour, or both blue and sour. The rats subsequently showed considerable aversion to the sour water, but none to the blue (dense) water. The quail, however, showed an aversion to both; furthermore, the quail poisoned on blue-sour water generalized their aversion to blue water and not to sour water. To show that the aversion to blue water was not based on the taste of the blue coloring, the investigators showed that quail could form an aversion to plain water in a distinctively colored tube.

We suggest that the critical dimension for poison-based aversion learning may not be "taste versus other modalities" but "eating-related cues versus other cues." This type of functional categorization of input is in harmony with Gibson's (1966) view of perceptual systems. Eating-related cues would be whatever type of cue—gustatory, visual, or otherwise—a particular species uses to identify food. Because of the intimate and relatively invariant relationship between taste receptors and food ingestion, and because of the neurological association between taste and visceral receptors, it is likely that taste cues would always be classified as eating-related so that taste-poisoning belongingness should be practically universal. However, in some species, other modalities may also be eating related.

Nontaste sensory modalities could include both eating-related and non-eating-related cues. For instance, it may be that birds can form poison-based aversions to the sight of potential prey, but not to other sights. Also, it is known that odors are less effective than tastes in poison-based aversions in rats. Possibly odors are more effective when they emanate from a food source or if they are experienced simultaneously with a taste. It would be interesting to investigate the effective cues for poison-based aversion learning in other species in which food recognition is known to occur partly via nongustatory cues. For instance, frogs have specific visual cells which respond maximally to flying insects and similar stimuli (Lettvin et al., 1959). The above analysis suggests that stimuli which excite these "bug detectors' might be more easily associated with poison than other types of visual stimuli.

LONG-DELAY LEARNING

Until recently it appeared that learning of both classical and operant types was almost impossible with delays of reinforcement exceeding a few seconds. The importance of close temporal contiguity has been demonstrated in a considerable variety of experimental paradigims, and apparent exceptions seemed to depend on secondary reinforcement (Kimble, 1961). There were cogent theoretical and adaptive reasons for assuming the universal importance of close temporal contiguity. Premonitions existed, however, of a possible problem with learning about food ingestion.

History

The first such reference is Pavlov (1927). Using morphine as a UCS, Pavlov noted signs of nausea and profuse salivation in response to the touch of the experimenter, which preceded injection. Needless to say, the UCS (i.e., nausea, etc.) did not occur until many minutes after the morphine was administered. Pavlov evidently regarded the effect as a species of conditioning, thus implicitly accepting the possibility of learning over long delays:

> This experiment provides a clue to the well-known fact that dogs will eat meat the first time it is offered them, after removal of their parathyroids, or after an Eck fistula and tying of the portal vein, but on all subsequent occasions will refuse it. Evidently in these cases the appearance and smell of meat produce of themselves a reaction identical with that produced through direct pathological action in the absence of the parathyroids or the portal circulation, by those toxic substances resulting from digestion of the meat [p. 36].

A similar recognition of the phenomenon of long-delay learning is present in the biological literature on poisoning, regulation of food intake, and specific hungers. Thus, Harris et al. (1933), Scott and Verney (1947), Rźoska (1953), and LeMagnen (1969) explicitly implicated learning mechanisms; to biologists without any particular commitments to psychological theory, this explanation seemed perfectly plausible.

One way of reconciling these data to traditional S–R learning theory was to assume that animals associated a food with the consequences of a previous meal of the same food, thus achieving temporal contiguity (Rozin et al., 1964; Smith & Capretta, 1956). But rats need only a single exposure to a toxic food to learn to avoid it (Rźoska, 1953); thus some other explanation is necessary.

The discovery that long CS–UCS intervals are possible in learning about the consequences of foods occurred gradually. Garcia et al. (1961) in their early work found that rats learned food aversions on the basis of simultaneous exposure to X rays. Although it was known that X rays had their main effect with a considerable delay ("radiation sickness"), it was assumed that some immediate effect of X rays was involved in the learning, and slight evidence was offered to support this position. McLaurin (1964) was the first to operationally manipulate CS–UCS intervals over a wide range in taste-aversion learning with long delays of reinforcement. However, a methodological flaw precluded meaningful interpretation of this result; McLaurin tested for aversion immediately after exposure to X rays, and it was later demonstrated (Smith & Schaeffer, 1967) that the rats were learning aversions to the test solution during the test itself. That is, the drinking of the solution during testing was simultaneous with the development of aversive consequences of the X rays, and temporal contiguity was achieved. Garcia et al. (1966) avoided this problem by giving the test for saccharin aversion three days after exposure to apomorphine. This experiment successfully demonstrated learning with long delays of reinforcement of the order of *one hour*. Smith and Roll (1967) found similar results using X rays and either saccharin (up to 12-hour delays) or sucrose (up to 6-hour delays). Replications by Revusky (1968) using sucrose CS and X-ray UCS and Rozin (1969b) (using saccharin or casein hydrolysate as CSs and apomorphine as UCS) confirmed this effect.

Hypotheses to Explain the Long Delay

Peripheral—the aftertaste theory. Because of the revolutionary nature of this finding, there was considerable interest in the possibility that the apparent absence of temporal contiguity was illusory. Although the CS–UCS interval was ostensibly long, some peripheral trace of the CS might remain throughout the interval in the form of an aftertaste, regurgitation, or a high concentration in the blood. It could be this trace that was involved in the conditioning. However, a fair amount of data are now available to oppose this explanation. The main import of the data is that taste-aversion learning is possible under conditions that should greatly minimize any aftertaste.

First, taste-aversion learning to sucrose and saccharin solutions occurs on a single trial with maximum delays of poisoning of about 7 and 12 hours, respectively (Revusky, 1968; Smith & Roll, 1967). It is very doubtful that an aftertaste or perceptible change in blood concentration persists for such long periods. It is even less plausible to suggest that enough sucrose or saccharin remains in the stomach at this time to be tasted by regurgitation. Actually the regurgitation model never had much applicability to rats anyway, since rats rarely if ever vomit. A second argument against the aftertaste and related models is the fact that rats can learn aversions to a .05% HCl solution with a one-hour delay of reinforcement (Garcia, Green, & McGowan, 1969). A litmus paper test showed no measurable amount of HCl on the tongue two minutes after the animal stopped drinking. Thus, the likelihood of a conventional peripheral aftertaste an hour later is minimal. Furthermore, the solution was less concentrated than the HCl already in the stomach. Consequently, this experiment is peculiarly effective in eliminating regurgitation, stomach-tasting, and blood-tasting models. A third line of evidence is Rozin's (1969b) demonstration that rats can learn an aversion to a specific concentration of a solution as opposed to other concentrations of the same solution. The animal learned the aversion just as easily to the lower as to the higher concentration. Presumably after the 30-minute delay used in this experiment, the aftertaste of a more concentrated solution should taste more like a less concentrated solution of the same substance. Similarly, the blood or stomach concentration of the substance at the time of poisoning should not be uniquely related to a particular concentration of original solution by a function known independently by the rats. A fourth line of evidence is Nachman's (1970a) demonstration that rats can learn an aversion to a particular temperature of water; an aftertaste of a temperature is difficult to imagine. Fifth, rats can learn an aversion to a solution even if one or more solutions is drunk between the first solution and poisoning (Kalat & Rozin, 1970, 1971a; Revusky & Bedarf, 1967). The intervening solutions would surely minimize any aftertaste of the first. Finally, it has been argued (Revusky & Garcia, 1970) that even if the aftertaste model were correct, it would be difficult to reconcile the taste-aversion learning results to conventional learning theories. Even if there is an aftertaste, it would have been present and declining in intensity for such a long period that there would be no precedent for expecting learning to occur—let alone in one trial.

It may be argued that none of these arguments completely demolishes an aftertaste theory, and that certain other tests could be conducted, for example, attempting to produce aversions to solutions intubated intragastrically. Some recent evidence suggests that if such aversions occur at all, they are much smaller than taste-mediated aversions (Smith, 1970). However, even if demonstrable, intragastric aversions would not solve the delay problem, as the HCl experiments (Garcia et al., 1969), concentration aversions (Rozin, 1969b), and solution temperature aversions (Nachman, 1970a) are no easier to explain in terms of contiguity with intragastric stimuli.

Bradley and Mistretta (1971) have demonstrated the development of aversions to intravenously introduced solutions (saccharin) in rats, using X rays as the UCS. A circulating "slug" of high-concentration saccharin stimulates taste receptors in the tongue. This interesting experiment provides *another* mechanism of learned aversions, but it cannot be the only mechanism involved in orally mediated aversions. The blood concentrations used in these experiments are much higher than any which would occur naturally or in the long-delay experiments, and the same experiments discussed above as raising problems for an intragastric-tasting mechanism would be equally troublesome for a "blood-tasting mechanism."

At present there is no evidence in favor of an aftertaste theory and a considerable body of evidence against it. Establishment of an alternative theory seems a more appropriate strategy than accumulation of still further evidence against aftertaste interpretations. Of course, from the point of view of this paper, long-delay learning is exactly what should be expected in this situation, and the central-mediation alternative appears quite acceptable.

Central mechanisms—interference. Revusky (in press; see also Revusky & Garcia, 1970) proposes that the maximum CS–UCS interval in all types of learning depends not on time per se, but on the number of other potential CSs that intervene between the CS being tested and the UCS. That is, the animal tends to associate the UCS with the most recent potential CS, or perhaps the last several such stimuli. As the CS–UCS interval expands, the probability increases that the organism will perceive other sights, sounds, etc., and consequently the probability decreases that the animal will associate the UCS with the CS in question. In taste-aversion learning, the argument holds, the range of potential CSs is much more restricted. Only tastes have a substantial tendency to be associated with aversive gastrointestinal stimulation, and typically the test solution is the most recent taste the animal experienced prior to poisoning. Since no other potential CSs are present, there is nothing to interfere with learning over long delays. In taste aversion as in other learning, the animal tends to associate a UCS with the last potential CS; the only difference is that in taste-aversion learning, the potential CSs are fewer and less frequent. We would like to point out that the taste modality differs from the commonly studied exteroceptive modalities, in that virtually all stimulation comes from contacts initiated by behavior. Rats do not taste unless they approach something and introduce it into their mouth.

This theory is very attractive because it proposes that the differences between taste-aversion learning and other types of learning may all be derived from the general principle of belongingness, without postulating an independent difference in the delay of reinforcement function.

Nevertheless, the theory, if taken as the sole of primary explanation of delay, faces two serious problems. It predicts that in the absence of interfering taste cues, there should be little or no decrement in learning as the CS–UCS interval is increased. This is not the case. Garcia et al. (1966), Nachman, (1970a), Revusky (1968), and Kalat and Rozin (1971a) have all found an orderly decrease of aversion with increasing CS–UCS interval. Furthermore, all experiments have found a maximal interval, varying from about 2 to 12 hours, beyond which no learned aversion can be demonstrated. Kalat and Rozin (1971a) deprived rats of both food and water during the CS–UCS interval, and still observed an orderly decrease in learned aversions with increasing CS–UCS interval.

Not only is there a decrement in learning in the absence of explicit interference, but the addition of explicit interfering cues does not markedly reduce learning. The consumption of two or even three salient novel solutions during a 30-minute delay between sucrose consumption and poison does not eliminate the sucrose aversion (Kalat & Rozin, 1971a). The *maximal* interference effect we observed using three novel interfering solutions following sucrose, and one poisoning, left sucrose equally palatable with water, to which it is normally strongly preferred.

These experiments, then, suggest that retroactive interference can clearly weaken a potential association, but it is highly unlikely that the normal delay function can be largely accounted for in these terms: What could interfere with drinking of a test solution during six hours of no eating or drinking that would be *more* effective than three novel solutions? Proactive interference is an unlikely explanation. Effects from past taste experiences should be minimal, since most rats have experienced only highly familiar rat chow, water, and mother's milk.

Recent findings by Wilcoxon et al. (1971) pose further problems for Revusky's theory. Unlike rats, bobwhite quail poisoned 30 minutes after drinking unflavored water from a blue tube learn an aversion to drinking from that tube. Since the quail presumably saw a great many visual stimuli in the 30-minute delay, their ability to learn over long delays in this situation cannot be explained simply in terms of absence of interference.

Although it seems unlikely that interference represents the only basis for the CS–UCS delay gradient, it does appear to be a contributing factor. Since a rat normally experiences fewer tastes than other stimuli within a given period, the Revusky theory may account for part of the difference in the delay gradients between taste-aversion and other types of learning.

Slow decay of associability as an inherent property of the taste system. An alternative to the view that the delay-of-reinforcement gradient is a function of interference is the view that the delay gradient is an inherent property of the system itself; memory or associability decays much more slowly for taste than for other modalities. This leaves unanswered the question, What accounts for this decay?

One possibility is that the delay function represents the decay of short-term memory. According to this hypothesis, a stimulus is associable with other events only while it is held in short-term memory, and tastes remain in short-term memory for unusually long periods. (Although there is extensive data on short-term memory in humans, virtually none has been collected on taste, and it is conceivable that tastes do not compete with exteroceptive cues for space in short-term memory.)

One way of testing this hypothesis is by means of electroconvulsive shock, which has been assumed to eradicate short-term memories or to block their conversion to long-term memories. If taste associations must be made from short-term memory extended in time, it should be possible to demonstrate disruptive effects of electroconvulsive shock, presented within the CS–UCS interval but with longer delays following the CS than are ordinarily effective in disrupting other types of memory. In a very careful study, Nachman (1970b) found amnesic effects of electroconvulsive shock in some rats when electroconvulsive shock was presented immediately after 10 seconds of drinking but not after 30 seconds of drinking. He also found some amnesic effects from electroconvulsive shock presented 25 seconds after a 5-second drinking period. Kral (1970) also found small amnesic effects with electroconvulsive shock, using delays of 2 or 25 *minutes* following a 10-minute drinking period. As is usual with electroconvulsive shock experiments, the temporal parameters seem to vary widely from one experiment to another. However, in both cases, the effect of electroconvulsive shock is small; it impeded but did not prevent learning. And in both cases, the effective electroconvulsive shock times were within the range of times reported for electroconvulsive-shock-amnesic effects in other systems. Thus there is no evidence that the transfer of taste stimuli into long-term memory is unusually slow, or that tastes remain in short-term memory for a long time.

Another possible mechanism for the delay function is that some central long-term "trace" of the taste is decaying over time. Unfortunately, this is a difficult hypothesis to test. One experiment (Rozin & Ree[9]) at least puts certain constraints on the type of decay which is possible. Rats were anesthetized for 6–8 hours during the interval between consumption of a sucrose solution and LiCl poisoning. These rats showed strong learned aversions at delays of poisoning considerably longer than those which are effective in the absence of anesthesia. Thus anesthesia seems to retard whatever process mediates the delay of reinforcement gradient. If this process is to be described as "decay," it is evidently an active rather than a passive type.

Central mechanisms—learned safety. The suggestion of an "active decay" process raises still another possibility, which is not a decay mechanism at all. Perhaps the delay gradient should be viewed not as a forgetting curve but as a learning curve. That is, in the absence of unfavorable gastrointestinal events, as time passes following consumption of a novel solution, the animal *learns that the solution is safe* (Kalat & Rozin, see Footnote 6).

As evidence for this, it has been demonstrated that an animal does learn something about a solution when consumption of that solution is followed by no negative consequences. We have already discussed the evidence indicating that rats learn less aversion to familiar solutions than to novel solutions (Revusky & Bedarf, 1967) even when the familiar solution was experienced once for only 20 minutes, three weeks before poisoning (Kalat & Rozin, see Footnote 6). This interpretation goes on to make a stronger claim: The learning of "safety" takes place within the period measured by the maximum delay of reinforcement. At the end of that period,

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[9] P. Rozin and P. Ree. Long extension of effective CS–UCS interval by anesthesia between CS and US. In preparation.

the "trace" has not decayed; it has merely been associated with the *absence* of aversive consequences. At intermediate delays, the intermediate amount of learned aversion reflects the fact that the animal has learned an intermediate amount of safety. Although this interpretation is grossly different (and not inconsistent with) the interference or trace-decay interpretations, it is not easy to separate the alternatives experimentally. The results of Rozin and Ree (see Footnote 9), which suggest that indefinitely long CS–UCS intervals will support aversion learning if the rat is anesthetized during the interval, are consistent with learned safety, since it is reasonable that the rat would be unable to learn safety while anesthetized.

WHAT ALL THIS MEANS TO THE RAT

We are now prepared to describe how a rat can handle some of the complex problems in food selection. The first thing to realize is that the situation is probably less complex than it might appear when the rat's natural behavior is considered. For example, the rat who gets sick in the garbage dump probably did not recently sample all the choice delicacies available (Rozin, 1969a). His choice behavior itself will help to unconfound the situation. He *may* have eaten a few different foods. He "knows" it was a *food* that made him sick (the belongingness principle) and can discount any familiar safe foods (the novelty principle). With the capability of forming associations over long delays, he is now likely to associate his illness with the last relevant (as defined above) thing or few things he ate over the last few hours. Although some of these foods may become more aversive than others because of their intrinsic properties (salience effect), the rat will acquire a significant aversion to each of them (small interference effect), with those closer in time to the aversive event picking up somewhat more aversion (temporal contiguity). Similar mechanisms would be employed to account for important aspects of the regulation of food intake.

What Kind of Learning Is This?

We have already described a number of differences between taste-aversion learning and traditional learning. We shall now consider some additional evidence in order to determine how fundamental this distinction is. Recent experiments have suggested two additional differences. First, it appears that rats can learn taste aversions when poisoned under anesthesia (Berger[10]; Roll & Smith, in press). Anesthesia was continued for a long period following UCS administration, so that it was highly likely that the learning occurred under anesthesia. Second, one of the more "complex" characteristics of classical conditioning, the Kamin blocking effect (Kamin, 1969), is either nonexistent or relatively weak in taste-aversion learning (Kalat & Rozin, 1971b; Revusky, in press).

One interpretation of why taste-aversion learning does not clearly show the Kamin-type effects is that the taste does not become a *signal* for poison in the sense that a tone or light becomes a signal for shock. In taste-aversion learning, the animal's perception of the taste itself or of its affective value may change (suggested by H. Gleitman, personal communication, 1971). The taste itself may become aversive or unacceptable, as if it were unpalatable (Rozin, 1967b). By contrast, stimuli associated with shock do not themselves become aversive; they evoke little avoidance outside the training situation. This difference seems related to the reported "*irrationality*" of learned taste aversions; humans commonly maintain an aversion to foods they ate prior to becoming nauseous, even when they are sure that some other agent was responsible for the nausea.

Seligman (1970) has suggested that taste-aversion learning may be a particularly primitive type of learning. The evidence mentioned above is quite consistent with this view. Furthermore, in a biological context, it makes sense that this ability should be primitive. The problems

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[10] B. Berger. Learning in the anesthetized rat. In preparation.

of food selection and the regulation of food intake are pervasive ones, and both are likely to involve long-delay learning. The essential problems are relatively invariant across species: any new food has some probability of being toxic, and for almost all species, the caloric density of foods will vary. Therefore, it makes sense that taste aversion and related types of learning should be more or less the same throughout most of the vertebrate subphylum.

ADAPTIVE SPECIALIZATIONS OF LEARNING: GENERALITY AND RELATION TO OTHER POSITIONS

The work on specific hungers and poisoning suggests that there are two aspects of adaptive specializations of learning. First, some mechanisms of learning may differ markedly (at least in terms of large quantitative differences in basic parameters) in the feeding system, as compared to other systems. Second, understanding of an adaptive specialization includes delimitation of the situations in which it applies and elaboration of its relationship and interaction with the animals' natural behavior (e.g., sampling, neophobia) in the relevant situation. The variation in interplay among naturalistic context, genetic programming, and learning is clearly illustrated in the contrast between water or sodium hunger, and other specific hungers.

Our emphasis has been on the first aspect of adaptation, while the ethologists have focused more on the context of learning and interplay of prestructured and acquired components:

> The student of innate behavior, accustomed to studying a number of different species and the entire behavior pattern, is repeatedly confronted with the fact that an animal may learn some things much more readily than others. . . . In other words, there seem to be more or less strictly localized "dispositions to learn." Different species are predisposed to learn different parts of the pattern. So far as we know, these differences between species have adaptive significance [Tinbergen, 1951, p. 145].

> . . . innumerable observations and experiments tend to show that modifiability occurs, if at all, only in those performed places where built-in learning mechanisms are phylogenetically programmed to perform just that function. How specifically these mechanisms are differentiated for one particular function is borne out by the fact that they are very often quite unable to modify any but one strictly determined system of behavior mechanisms [Lorenz, 1965, p. 47].

We are aware of only two well-studied systems showing adaptive specializations of learning. One is feeding, which we have already discussed, and the other involves imprinting, as a mechanism of species recognition.

Two of the prominent features of imprinting—the special sensitivity during a critical period early in life and the great resistance to extinction—can be seen as adaptations to limit the likelihood of errors in species recognition. The learning should take place soon after hatching, since the probability of exposure to a conspecific (i.e., the mother) is highest at this time, and the bird should be less sensitive to later experiences, since the frequency of contact with members of other species is likely to increase greatly after the nestling period.

Feeding and imprinting can be considered as two exceptions to an otherwise correct "general process" view of learning, or they can be considered as examples of a basic adaptational principle pervading much or all of learning. We prefer the latter alternative and believe that the absence of additional known instances of adaptive specializations may reflect learning psychologists' reluctance to study potentially learned behaviors which do not fit into the general process paradigms. (Significantly, the case for adaptive specializations in both imprinting and feeding came from outside the psychology of learning.)

At this point one can only speculate about what other systems will show special adaptations of learning. Bees may possess a wide variety of adaptive specializations (von Frisch, 1953, 1967). A particularly promising example is their navigational ability. First, there is evidence for "belongingness."

> Honey bees can learn to use irregular forms, like those of trees or rocks, as landmarks by which to steer a course to and from the hive; but they cannot,

> even by the most subtle conditioning technique, be taught to use the same forms as positive or negative signals indicating the presence or absence of food in a tray, as von Frisch (1914) has shown. As signals for food, bees can distinguish different forms only if they are geometrically regular, preferably radially symmetrical (Hertz, 1937) [Lorenz, 1965, p. 47].

Second, a limited amount of experience in observing a piece of the sun's arc enables the bee to "project" the rest of the arc. That is, bees raised without the opportunity to see the sun have great difficulty compensating for sun movement during navigation. But bees that have observed sun movement only during a limited period in the morning are fully capable of compensating for sun movement in the afternoon (von Frisch, 1967). In this situation, the environmental input produces a long-term change, and does not act "associatively," but rather provides a reference point. Other examples of such "calibrational learning" (Lorenz, 1965) might include adaptation to visual displacement produced by prisms and caloric regulation.[11]

The naturalistic literature is replete with other examples of surprising abilities of animals—such as digger wasps' memory of the location and state of their nests (Baerends, 1941), gobies' latent learning of the location of tidepools (Aronson, 1951), salmon's recognition of home-stream odor (Hasler, 1966), doves' individual mate recognition (Morris & Erickson, 1971), sparrows' acquisition and storage of song dialects (Marler, 1970), etc. These have not been thoroughly studied as possible specialized learning mechanisms.

The "heuristic" value of an adaptive evolutionary point of view can be suggested by considering the types of predictions that might be made about some basic learning and memory relationships. For example, an organism's memory of some aspect of the environment is useful only if that aspect is predictable or controllable; otherwise, rapid forgetting might be advantageous. It is probably of no use for bees, birds, or other organisms with complex navigational abilities to remember whether it was cloudy *yesterday* or which way the wind was blowing, though both may have been important at the time. Under these circumstances one might expect to find a specialization in short-term memory such that information could be stored for longer periods and in greater quantities than usual without entering long-term memory.

Another example concerns extinction. Extinction, from an adaptive point of view, allows an organism (*a*) to correct for mistakes (fortuitous conditioning) and (*b*) to constantly reshape itself to adapt to a variable environment. One might expect the rapidity of extinction to depend on the probability that either of these events would occur. In the case of imprinting, we have great resistance to extinction in a case where clearly the environment will not vary (i.e., the species will not change), and the proper imprinting object is almost certain to be present at the time of imprinting. The great resistance to extinction of avoidance conditioning (Solomon & Wynne, 1954) may be an adaptively selected feature of this learning: the costs of errors of omission here are high. One might expect rapid extinction of the learned location and stimulus properties of food sources, where these sources are subject to marked seasonal or other temporal variations. An example might be extinction of responses to particular types and locations of flowers in foraging bees. One might observe slow learning, but high resistance to extinction in a situation where the environment is stable but a critical

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[11] We can suggest a role for "calibrational learning" in the regulation of food intake. It has been known for some time that rats and other mammals respond to changes in caloric density of food by appropriate modulation of volume intake. In the rat, this compensation occurs largely as an increase in meal size, rather than in number of meals (Snowdon, 1969; Teitelbaum & Campbell, 1958). When a standard diet is diluted, the rat ends up eating larger meals: he has "recalibrated" his meal size on the basis of the metabolic aftereffects of his meals. It is possible to imagine a mechanism which compares some measure of the amount ingested with its delayed metabolic effects, and adjusts future intake downward or upward so that the metabolic consequences will approach some preferred or ideal value. The demonstration of a long-delay learning mechanism makes this type of explanation feasible and subject to investigation.

difference is relatively hard to detect (e.g., prey density), and "averaging" must be done before a clear choice or preference is established. One might observe rapid learning and rapid extinction in a rapidly changing environment (see Shettleworth, 1971, for additional comments on this point).

Recently, a number of authors have expressed positions related to ours (Garcia & Ervin, 1968; Garcia et al., 1971; Revusky, in press; Revusky & Garcia, 1970; Seligman, 1970). We differ from all of these authors in the sense that they see belongingness, in one form or another, as *the* unique phenomenon to be explained, whereas we see it as an example of the general adaptational principle; animals may not only learn some things more easily than others, but they may also learn some things in a different way than others. The contrast is clearest in the case of Revusky, who attempts to preserve traditional learning theory intact, with the introduction of a new "belongingness" assumption.

Seligman (1970) proposes a new dimension, "preparedness," based on the belongingness relationship, to incorporate recent findings into a more viable learning theory. Preparedness represents the tendency of certain inputs (and/or outputs) to be associated with one another, this tendency resulting from natural selection. Seligman proposes that highly prepared associations are established with a minimal input (e.g., number of pairings). In addition to very rapid learning, prepared associations would tend to show learning with long delays of reinforcement and perhaps high resistance to extinction. We are certainly in accord with the general flavor of Seligman's position, but we feel that in his desire to reorder the phenomena of learning, he has not fully appreciated the diverse natural forces that can shape behavior and learning mechanisms. In imprinting, for example, where Seligman's view of rapid learning (and high resistance to extinction) fits very well, the presence of the critical period cannot be accommodated without additional assumptions. More significantly, the long-delay learning found in feeding is probably not characteristic of other "prepared" associations, and in our view, it should not be, since in most cases close temporal contiguity is the best predictor. Furthermore, we see no reason to expect a consistent relationship between rapid learning and high resistance to extinction (see discussion of extinction above).

In short, we disagree with Seligman that diversity can be ordered along any single, operationally meaningful dimension, that is, preparedness. If preparedness meant adaptedness to situational demands, it would be an acceptable but not clearly meaningful dimension. Seligman has given it operational meaning, but narrowed the scope of the phenomena he can account for in the process. In a more recent statement of the preparedness position, Seligman and Hager (in press) have acknowledged some of these possible limitations.

Shettleworth (1971), in a paper written concurrently with this one, has presented a position very similar to ours. It focuses on belongingness, broadly conceived, but also describes learning in general in terms of adaptive specializations, and provides examples from the naturalistic literature. A recent paper by Lockard (1971) also explicitly discusses the diversity of learning mechanisms as an important feature ignored by most psychologists and implies that the search for common elements in learning across species and situations is almost hopeless.

We differ slightly from Shettleworth and markedly from Lockard with respect to our optimism about the possibility of finding order within the diversity of learning mechanisms. Given the constraints on adaptations produced by basic properties of the nervous system, the cost of evolving specializations, and the fact that most species face a common set of problems, we doubt that a separate learning mechanism would exist for every situation, or that there would be separate laws for each species. It may yet be possible to formulate laws of some degree of generality, taking ecological factors into account (see

Walls, 1942, for an example in the area of vision).

SOME SPECULATIONS

It follows from the point of view presented here that an organism may have an ability that manifests itself in only a small number of the total possible situations in which an experimenter might test for it. The ability in question might be inaccessible to or "unconnected" with the machinery for modulating and controlling most behavior. Using a computer analogy, we might suppose that a particular routine is designed (evolved) to handle a specific problem. At this point in time, it is physically connected only into the relevant inputs, outputs, or systems, and is inaccessible to the rest. Under these circumstances, it would be difficult to describe a species' learning capacity.

The interesting demonstrations by Bitterman (1968), Gonzalez and Bitterman (1969), and Mackintosh (1965) of differences in learning abilities in certain situations between a few species of fish and mammals do not in themselves indicate complete absence of these abilities in any species of fish (see Gleitman & Rozin, in press, for a general review of this issue with respect to learning and memory in fish). A species should be tested for any ability in those situations where its existence would have the greatest survival value. The failure of a few fish species to demonstrate abilities such as progressive improvement in habit reversal in a few laboratory situations does not meet this demand.

However, the data gathered by Bitterman, by Gonzalez and Bitterman, and by Mackintosh do suggest some interesting phylogenetic generalizations about learning capacities. Since the laboratory apparatus used to study rats and other mammals is often not ideally suited to *their* natural behavior, just as the fish apparatus is not, it *is* quite interesting that mammals reliably show the greater plasticity in these "unnatural" situations. One possible explanation for this, offered by Bitterman (1964), is that the rat possesses certain higher learning abilities that "fish" do not possess. Another not mutually exclusive possibility is that the rat and probably most other mammals are "generalists," compared to the majority of other vertebrates. That is, abilities initially evolved to handle a specific situation and limited in application to the appropriate system may turn out to be useful in others and may through evolution be "connected" into new systems. To what extent do the higher abilities of the mammals represent an increase in accessibility of specialized capacities, an "emancipation," to borrow a word from the ethologists, of a capacity from its original tight motivational system?

The proposed increase in accessibility of capacities in phylogeny may have a parallel in ontogeny. Within the Piagetian framework, it is apparent that particular cognitive structures may have only limited applicability at any point in development. Piaget applies the name "decalage" to this feature of development. (Flavell, 1963, pp. 21–24). For example, in the Piagetian scheme, the same cognitive structure is necessary for the achievement of mass and weight conservation, yet the latter occurs about two years after the former. Cognitive development may consist, in part, of the extension of existent capacities to new situations, in parallel to our scheme for phylogeny.

We have argued for the existence of adaptive specializations in learning and memory. Since, by their nature, such specializations are limited to a relatively narrow range of situations, we have pointed out that they must be inaccessible to most functioning systems. We believe that this general formulation has a wide application, and we are presently applying it to an understanding of the difficulties in initial acquisition of reading (Rozin & Kalat, in press; Rozin, Poritsky, & Sotsky, 1971).

It is the basic thesis of this paper that in a biological-evolutionary framework, specifically adapted abilities are extremely important and should not suffer from neglect as a consequence of the search for great generalities. To understand a set of phenomena, within humans or across the animal kingdom, is to be able to describe and explain diversity, as well as to extract common elements.

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