ROLE OF ATTENTION IN EXTEROCEPTIVE-CUE-AVERSION LEARNING

BY

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ABSTRACT

Exteroceptive-cue-toxicosis associations are usually difficult to produce and generally less robust than flavour-toxicosis associations. The following series of experiments investigates the paradoxical enhancement of aversion conditioning to exteroceptive cues induced by the presence of a novel flavour at the time of exteroceptive-cue-toxicosis conditioning.

It was found that this flavour facilitation effect is due, in part, to the operation of a mechanism that directs subjects' attention to stimulus attributes of ingesta (Chapter 3). Further experiments suggested that the attentional mechanism is not robust enough to facilitate visual-cue-aversion conditioning over long delays (Chapter 4) and that, consistent with an attentional interpretation, only certain stimuli were subject to the operation of the attentional mechanism (Chapter 5). Apparently rats are more likely to treat certain stimuli as attributes of food objects and these stimuli are more readily associated with toxicosis.

Adaptive-evolutionary accounts that dichotomize stimuli into those that are and those that are not associable with toxicosis or theories that suggest that all exteroceptive cues are contraprepared to be associated with toxicosis cannot account for the present finding of graded exteroceptive-cue-toxicosis conditioning with distance from the food object. The experiments of this thesis suggest that stimulus salience is not an inflexible characteristic of the stimulus itself. Rather, it is suggested that stimulus salience varies as a function of

several factors amongst which the type of reinforcement and time of onset of reinforcement, the presence of other stimuli, the animal's past experience with the stimuli and the relation of the stimuli to the food object appear to play central roles.

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This thesis is dedicated to my wife and son.

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CHAPTER 1

INTRODUCTION

Within the general process view of associative learning it is usually assumed that any stimulus or emitted response can be paired with any biologically significant event to produce learned associations (Pavlov, 1927; Skinner, 1938; Estes, 1959). Although differences in either the salience of stimuli or strength of reinforcers can affect the rate or strength of conditioning, any stimulus can be associated with any other in any species that has the appropriate receptor and effector capacities to respond to the stimulus. This premise of equal associability has allowed researchers to study arbitrarily selected organisms in arbitrarily selected situations with the full expectation that results so generated would be generalizeable to behavior in a wide variety of situations (Seligman, 1970).

Also, within the framework of general process theory, temporal contiguity between stimulus events was considered to be a necessary condition for the production of associations. It was believed that associations would not be formed if the interval between stimulus events exceeded a certain critical value, usually on the order of a few seconds (Kimble, 1961). These two features, the premise of equal associability and the contiguity requirement, were considered central to the enterprise of constructing general laws of learning.

1.1 Two Challenges to General Process Theory

In a now classic series of experiments Garcia and Koelling (1966) demonstrated the existence of a selective relation between

certain stimuli and certain classes of subsequent biologically significant events. Garcia and Koelling presented rats with a compound stimulus composed of a light, a tone and sweetened water, followed by either illness or shock. Animals made sick after experiencing the compound stimulus subsequently exhibited aversions to the flavour component, while animals shocked after experience of the compound stimulus avoided the exteroceptive components. Apparently, the nature of the reinforcer determined the stimulus with which it would be associated.

Garcia and Koelling's demonstration of selective association has been replicated and extended in a number of laboratories, perhaps most importantly by Domjan and Wilson (1972) who reported that irrespective of whether stimulus events were presented singly or in compound, with or without requiring the animal to make a response, gustatory stimuli were selectively associated with changes in internal milieu and exteroceptive stimuli were selectively associated with changes in external milieu.

The demonstrations by Garcia and Koelling (1966) and Domjan and Wilson (1972) that cues may interact with consequences in the production of associations directly challenged the premise of equal associability central to general process learning theory.

A second challenge to learning theory was provided by Garcia, Ervin and Koelling (1966), who demonstrated that associations between tastes and illness could be produced even when a 1-hour delay intervened between stimulus presentation and reinforcement. In the light of later experimental demonstrations of effective conditioning

even over delays between gustatory stimuli and reinforcers of up to 12 hours (Smith and Roll, 1967) it became exceedingly difficult to maintain the contiguity requirement, central to general process theory.

1.2 Responses to the Two Challenges

In the present section three broad classes of response to the challenges to general process theory posed by taste-aversion learning are discussed, first briefly and then in greater detail. The first class of explanation for both stimulus selectivity and long delay learning in taste-aversion conditioning introduced principles drawn from the twin disciplines of animal behavior and ethology into the theory of animal learning. Explanations of this sort required that all learning and memory be viewed in an adaptive-evolutionary framework. On this view, one might expect specialized learning abilities to evolve so that associations between foods and gastrointestinal effects could bridge the normally occurring delay between ingestion and the aftereffects of ingestion. Proponents of this view suggested that variations and divergences from the mechanisms of Pavlovian and Instrumental conditioning occur when general processes interact with the environment and become specialized to promote the organisms level of adaptive functioning.

A second class of response to the anomalies provided by taste-aversion learning was to make minor modifications of the general process theory in an attempt to encompass the new findings while preserving existing theoretical structures. On this view, factors other than the phylogenetic history of the organism were proposed to account for the apparent preparedness of the organism to associate flavour stimuli with illness over long delays.

The third class of explanation incorporated the findings of stimulus selectivity and long delay learning into existing theory by positing the existence of peripheral mediational mechanisms.

1.3 Evolutionary Accounts

The discovery of stimulus selectivity and tolerance of long delays between CS's and US's in flavour-aversion learning by Garcia and his co-workers provoked attempts to incorporate the findings from taste-aversion experiments (as well as some anomalous findings from more traditional learning experiments) into a more adequate account of the processes involved in learning (Seligman, 1970; Shettleworth, 1972). An essential feature of these accounts was the proposition that a consideration of the demands that the natural environment places upon the associative and memorial apparatus of species members must be included to provide a complete account of the learning capabilities of organisms. This approach to the problem looks to the phylogenetic history of the organism for clues to unravel the anomalies of stimulus selectivity and long delay associations in taste-aversion learning.

1.3.1 Anatomical Convergence Hypothesis

Garcia and Ervin (1968) suggested that selective associations between flavours and internal malaise might be predicted from neuroanatomical evidence indicating that nerve tracts from mouth and viscera converge on the same area of the brainstem, the nucleus tractus solitarus. They argued that this convergence of fibre inputs probably evolved in response to the invariant relation that exists in the natural world between gustatory sensations and gastrointestinal events. Because taste sensations are usually indicative of toxicosis animals

capable of rapidly associating flavours and toxicosis would be at a selective advantage. The evolution of animals with this specialized physiological apparatus presumably reflects a particular aspect of the causal structure of their natural environment.

Garcia and Ervin (1968) suggested that anatomical convergence may also account for the ability of the system to tolerate long delays between stimuli and reinforcers and still form associations. While the anatomical evidence is indisputable, it is as yet unknown how such convergence might facilitate the formation of associations over long delays. Garcia and Ervin (1968) also postulated anatomical convergence of telereceptor-cutaneous inputs to account for the selective association of exteroceptive stimuli and exteroceptive reinforcers. If a similar convergence of inputs exists for exteroceptive stimuli as for gustatory stimuli, then the absence of long delay learning in the telereceptor - cutaneous system cast doubts on the adequacy of anatomical convergence to account for long-delay learning in the gustatory-visceral system.

1.3.2 Adaptive Specializations of Learning

Like Garcia and Ervin (1968), Rozin and Kalat (1971) argued that taste-aversion learning is an adaptive specialization that results from regularities in the environmental demands on animals over evolutionary time. They argued that natural selection, acting on variations in the learning capacities of organisms, produced adaptive learning specializations of which poison avoidance learning is only one example. In particular, Rozin and Kalat proposed a functional classification of the stimuli that are employed in learning about

foods. Rather than relying upon a distinction drawn between tastes and other stimuli (as had Garcia), Rozin and Kalat suggested that a division between 'eating-related' and 'non-eating-related' cues might be more appropriate. According to Rozin and Kalat (1971) the stimuli that a species normally employs to select or reject food items in the natural setting will be the stimuli that are quickly and selectively associated with toxicosis.

The Rozin and Kalat account is better able to incorporate the findings that certain species, presumably those which employ their visual system in selecting ingesta, can associate the visual characteristics of food items with delayed toxicosis (e.g. Braveman, 1975; Cavea porcellis; Martin & Bellingham, 1979, Gallus gallus; and Wilcoxon, 1977, Colinus virginianus) than is the account of Garcia and Ervin (1968). Rozin and Kalat consider the long-delay effect in flavour-aversion learning to be another adaptive specialization of learning that has evolved in response to environmental demands.

1.3.3 The Preparedness-Contrapreparedness Continuum

Seligman (1970) proposed that phylogeny has prepared animals to form certain associations and contraprepared them to form others. According to Seligman, evidence of preparedness can be found when rapid one trial learning of associations occurs and of contrapreparedness when learning is minimal, even following protracted periods of training. Seligman drew examples from the results not only of flavour-aversion experiments but also of traditional learning experiments. According to Seligman, instincts, autoshaping and taste-aversion learning are at the prepared end of the

preparedeness-contrapreparedness dimension. Most other learning preparations are in the middle of the dimension and are somewhat unprepared, while exteroceptive-cue-toxicosis learning lies at the contraprepared end of the dimension. The location of behaviors along the dimension will vary between species as a function of the physiological and associative apparatus with which natural selection has equipped them.

A problem for Seligman (and also for Rozin and Kalat (1971)) is to predict ahead of time which associations are prepared and which unprepared in order to avoid circular reasoning. Simple operational definition does not remove the preparedness continuum from circularity.

1.4 Modification of General Process Theory

This group of explanations for taste-aversion learning proposed that minor modifications of existing theory were all that were necessary to account for stimulus selectivity and long delay in flavour-aversion learning. On this view, factors in the ontogenetic history of the organism may facilitate the formation of certain associations at the expense of others.

1.4.1 Stimulus Relevance and Concurrent Interference

Revusky (1977) proposed that flavours and illness are preferentially associated with each other because of stimulus relevance, "... events related to the feeding system tend to be selectively associated with each other." (p. 333). Stimulus relevance as described by Revusky (1971; see also Capretta, 1961) is the principle by which internal events involved in the maintenance of homeostasis are preferentially associated with other stimuli that are

involved in the same internal process and relatively unavailable for association with events that are involved in the maintenance of a constant external environment.

Revusky attacks the long delay problem by suggesting that organisms tend to associate an unconditioned stimulus (US) with the most recent and relevant conditioned stimulus (CS). That is, stimuli compete for association with reinforcers. Stimuli that occur in the interval between CS and US interfere with conditioning to the extent that they belong to the relevant class of stimuli for that particular reinforcer. The amount of interference depends on the strength and number of interfering associational events. Because novel tastes are not usually experienced between the flavour CS and the illness US, there is little concurrent interference to reduce effective conditioning. Other types of unconditioned stimuli (such as shock) are potentially associable with many external stimuli such as lights, tones and background cues. Thus, they are prone to much more interference and temporal contiguity becomes prerequisite for conditioning to occur.

Revusky is unable to account for the learning of illness-based aversions to visual cues in avians when long delays separate CS and US (Martin & Bellingham, 1979). It cannot be argued that there are few interferring visual events occurring during the delay in this situation.

1.4.2 Event Covariation

Testa and Ternes (1977) suggest that the selectivity of association of flavours and illness is due to certain common characteristics of spatial location and temporal patterns of intensity

shared by flavours and illness. When animals ingest food objects there is a complex of sensations in the mouth and stomach that persist for a period of time after termination of ingestion. The intensity of both these effects mounts rapidly and dissipates slowly. Testa and Ternes suggest that the physiological effects of a toxic agent have a parallel "shape" to the effects of ingested food objects. Food objects are associated with toxicosis over long delays because of this isomorphism in their temporal characteristics. Flavours, they suggest, are simply attributes or characteristics that are highly predictive of food objects and so flavours are associated with illness by way of the gastrointestinal aftereffects of food objects that bridge the delay and match the shape of unconditioned stimulus effects.

There is little direct evidence for the Testa and Ternes position to be found in the flavour-aversion literature, but there is some indication that Pavlovian higher order conditioning is facilitated both by spatial contiguity (Rescorla and Cunningham, 1979) and by similarity (Rescorla and Furrow, 1977) of the stimuli.

1.4.3 Developmental Considerations

Mackintosh's (1973) approach to the problem of selective association and long-delay learning stresses the importance of the associative history of the organism. Mackintosh proposed that "....the principle of relevance may be (in part) an instance of a much more general phenomenon of associative learning" (Mackintosh, 1973; p. 74). During ontogeny each individual gains experience with "natural contingencies but not unnatural ones" (Garcia & Hankins, 1977; p. 16). The suggestion is that animals may learn to associate certain classes

of stimuli with certain classes of reinforcers because of past experience with these stimuli and reinforcers and their pattern of covariation. If, in the past, a set of stimuli (X) have been highly correlated with a particular reinforcing consequence (R), then members of the set X will in the future more easily enter into an association with that reinforcer than an uncorrelated set of stimuli (Y). Members of the class of Y stimuli are "ignored" as predictors of R.

Basic to this line of argument is the assumption of a limited channel capacity of organisms. The notion of limited channel capacity implies that the animal cannot attend to all stimulus aspects of a situation at the same time and must, therefore, select particular features to which to attend. The active ignoring of non-valid stimuli reduces the number of stimuli to be attended to and selected out of the total stimulus array.

Recent experiments indicate that experiential factors during ontogeny may not play as large a role in selective association as Mackintosh has suggested. Rat pups as young as five days of age selectively associate tactile stimuli with shock and gustatory stimuli with illness (Gemberling, Domjan and Amsel, 1980). While Mackintosh's approach may help account for stimulus selection in taste-aversion learning, it does not directly address the issue of the formation of associations between flavours and toxicosis over long delays.

1.5 Mediational Mechanisms

The proposed mechanisms discussed below have in common the assumption that stimulus selectivity and long-delay learning in taste-aversion are artifacts mediated by some unknown peripheral

process. If this other process were controlled, then flavour-aversion results would look more like general process phenomena. In general, mediational mechanisms have been proposed to bridge the long delay and provide for contiguity between taste and toxin. It was believed that the problem of taste-toxin selectivity would also be obviated by evidence of contiguity between taste stimuli and gastrointestinal distress. If taste stimuli were experienced simultaneously with the effects of toxicosis then the contiguity principle alone could account for taste-toxin selectivity.

1.5.1 Residual Taste Mediation

One of the earliest accounts of long-delay taste-aversion learning was that the rat regurgitated the food at the onset of illness and temporal contiguity between CS and US was thereby achieved. Regurgitation of substances is highly unlikely to be involved in taste-aversion formation as rats lack the necessary sphincter control to allow for a regurgitation reflex (Garcia & Ervin, 1968). Other lines of evidence are also incompatible with the regurgitation hypothesis. Ephemeral substances are effective stimuli for illness-based aversion conditioning. Garcia, Green and McGowan (1969) found that a weak (0.5% w/v) solution of hydrochloric acid could become a reliable signal for illness even if no trace of the substance remained in the mouth or stomach at the time of illness. Animals are able to learn aversions to one of two concentrations of the same solution (Rozin, 1969), to differing temperatures of water (Nachman, Rauchenberger and Ashe, 1977), and to a flavour presented just prior to various masking flavours (Revusky & Bedarf, 1967). All of these

findings reduce the likelihood that regurgitation is involved in the delay gradient. Others (Bitterman, 1976) suggested that temporal contiguity between the flavour and the illness might be achieved if there was a prolonged aftertaste in the mouth. However any simple aftertaste explanation has difficulty accounting for conditioning when ephemeral substances and masking procedures are employed.

Finally, visual aversions in avians (Wilcoxon, 1977; Martin and Bellingham, 1979) have been produced with delays of up to six hours although no novel flavour is present to mediate conditioning.

1.5.2 Bloodstream Mediation

A more sophisticated aftertaste hypothesis has been proposed by Bradley and Mistretta (1971) who suggested that ingested substances enter the bloodstream and may be detected in the mouth for a period of time after ingestion. They provided evidence for such a mechanism by conditioning an aversion to a saccharin stimulus administered intravenously.

While Bradley and Mistretta may have demonstrated that rats can form aversions to flavours in the blood, they have not demonstrated that this is the actual mechanism by which rats associate flavours and malaise. The concentrations of saccharin injected in Bradley and Mistretta's experiments are much higher than concentrations encountered in most flavour-aversion experiments. It is unlikely that this mechanism is regularly employed by rats even though they have the capacity to do so in unusual circumstances.

1.5.3 Mediation by Extended Central Representation

The above arguments refute peripheral trace interpretations of

the flavour-aversion phenomenon. However, it is possible that flavours have extended traces in memory that decay less rapidly than traces for other stimuli such as lights and tones.

Krane and Wagner (1975) conditioned aversions to flavours employing shock as a reinforcer with delays as great as two hundred and ten seconds. They suggested that central representations of tastes in memory last longer than do representations of lights or other exteroceptive stimuli. If this is correct, then when taste stimuli are employed as CSs the onset of reinforcement must be delayed in order to avoid producing backward conditioning. Krane and Wagner argue that the temporal confound introduced by extended traces of flavour stimuli has not been controlled for in most studies demonstrating selective associability. While taste representations may extend for a longer period of time than representations for lights, it is unlikely that they would continue for a 12-hour interval (Smith & Roll, 1967), nor survive anaesthesia (Rozin and Ree, 1972).

1.6 Exteroceptive-Cue-Aversions

While there is little doubt that flavours are favoured over other stimuli as cues for illness, the following demonstrations of exteroceptive-cue-toxicosis associations in rats suggest that the selective relation between flavours and illness is not complete.

As early as 1957 Garcia and his colleagues demonstrated that rats could associate exteroceptive cues with illness (Garcia, Kimeldorf and Hunt, 1957). It took many training trials with high doses of X-ray irradiation to produce a transient avoidance of the chamber in which irradiation was experienced. Following this demonstration of

relatively weak conditioning to exteroceptive cues came several demonstrations of the rapid acquisition of robust aversions to gustatory cues when illness was the reinforcer (e.g. Garcia and Koelling, 1966). It is not surprising that the initial finding of exteroceptive-cue-aversions in rats was ignored for many years. More recently aversion conditioning to exteroceptive cues in rats has become a well established phenomenon, due in part to the development of more sensitive techniques for assessing associations. The following sections deal with the techniques employed to provide evidence of associations between exteroceptive cues and toxicosis.

1.6.1 Sensitivity of Measurement

Holland (1977) noted that the selection of a particular response as the index of association is a critical determinant of whether conditioning is observed. Holland found that when two stimuli, CS_A and CS_B were paired with a food reinforcer, only CS_A appeared to gain associative strength if the measure of association formation was the ability of the stimulus to evoke conditioned movement responses. However, when CS_B was compounded with a third stimulus, (CS_C) and this new compound stimulus was paired with reinforcement, there was evidence that CS_B had acquired associative strength in the pairing of CS_A and CS_B with the reinforcer. Holland concluded that in the original situation CS_B had been associated with the food reinforcer but that the index of association, conditioned movement, was not sensitive enough to demonstrate the presence of the association.

Results such as Holland's suggest that the ability of a stimulus to affect conditioning to a second stimulus provides a more

sensitive measure of association than a more direct measure response evocation (Holland and Rescorla, 1975; Holland, 1977). The following sections provide examples of the use of indirect measurement techniques for assessing exteroceptive-cue-toxicosis associations.

1.6.2 Blocking and Taste Aversion Learning

Blocking occurs when a stimulus that has been paired with a reinforcer prevents a second stimulus from acquiring conditioned properties when the two stimuli are presented in compound and followed by the same reinforcer (Kamin, 1969). According to one interpretation of the blocking phenomenon if a stimulus has come to predict the occurrence of reinforcement, then addition of a second stimulus to the first provides no further information to the animal about reinforcement and the second stimulus is effectively ignored.

Studies employing a blocking paradigm with rats have revealed the existence of illness-based aversions to background environmental stimuli (e.g. Rudy, Iwens and Best, 1977; Wilner, 1978; Batson and Best, 1979). In these experiments rats were exposed to a distinctive complex of environmental cues prior to being injected with an illness producing agent. Subsequently, a flavour-illness pairing was performed in the presence of the distinctive environmental cues and the aversion to the flavour stimulus was assessed. Attenuation of the flavour aversion was produced by the presence of the exteroceptive cues previously associated with toxicosis. The ability of exteroceptive cues to block conditioning to flavour cues implies that associative strength had accrued to the exteroceptive cues.

1.6.3 Other Techniques for Measuring Exteroceptive-Cue-Toxicosis Associations

Another commonly employed technique for assessing associations to exteroceptive cues is to measure the latency to approach or percent of time spent in the presence of exteroceptive stimulus previously paired with illness (Best, Best and Mickley, 1973; Henggeler, 1974; Best, Best and Henggeler, 1977; Martin and Ellinwood, 1974). Latency measures in all of these experiments have provided evidence of associations to exteroceptive cues that have been paired with toxicosis.

A variety of other techniques have been employed that also provide evidence of exteroceptive-cue-toxicosis associations. For example, background stimuli have been employed as secondary reinforcers in higher order conditioning preparations (Best et al., 1977). It has also been found that flavour-aversions extinguished in a different context from the original conditioning context undergo spontaneous recovery when the animals are returned to the original conditioning context (Archer et al., 1978). Further, differential bar-press responding in extinction has been observed in response to the presence or absence of environmental cues previously made aversive by lithium toxicosis (Morrison and Collyer, 1974) and lithium paired exteroceptive cues have been observed to either suppress (Domjan, 1973) or enhance (Domjan & Gillan, 1977) consumption of fluids.

1.7 Factors that Affect Exteroceptive-Cue-Aversions

While the phenomenon of aversion conditioning to exteroceptive cues is now well established, little is known about the mechanisms that

underly such conditioning. It is apparent, however, that the mechanisms underlying association of exteroceptive cues with toxicosis are different from those underlying association of flavours with toxicosis. Exteroceptive-cue-aversion demonstrations usually require many more conditioning trials, closer temporal continguity between the stimulus events, and more sensitive assessment techniques than do flavour aversions.

The following sections provide an analysis of the conditions under which exteroceptive-cue-toxicosis associations are likely to be formed. This analysis implicates attentional factors in the association of exteroceptive cues with toxicosis.

1.7.1 Novelty

Novel stimuli are more likely to be attended to than familiar stimuli. They provoke a greater orienting response (Sokolov, 1963) and more rapid conditioning in many learning preparations (Lubow, 1973; Siegel, 1974) than do familiar stimuli. Best (1975) has suggested that stimulus preexposure reduces the ability of the stimulus to elicit attention. In taste-aversion learning novelty is a more powerful predictor of associability than contiguity (Revusky & Bedarf, 1967).

Attempts to condition aversions to the external features of food containers also point to the importance of novelty. Mitchell, Kirschbaum and Perry, (1975) demonstrated that aversions to distinctive containers could only be produced if the container was novel relative to background stimuli. As in taste-aversion conditioning, relative novelty of the exteroceptive stimuli rather than contiguity was a better predictor of subsequent avoidance behavior.

A criticism that might be made of unsuccessful attempts to produce illness-based aversions to exteroceptive stimuli is that the target stimulus may have been no more novel than the background stimuli provided by the experimental apparatus. If an animal experiences illness after being exposed to a large number of novel exteroceptive stimuli, then it is highly unlikely that it will be responding to the stimulus that the experimenter intended.

1.7.2 Ingestional Interference

Best, Best and Mickley (1973), conditioned a motor avoidance to the black compartment of a shuttlebox by pairing exposure to the black box with immediate apomorphine injections. After two conditioning trials experimental animals spent significantly less time in the black compartment than unpoisoned controls. Best et al., found that the strength of the aversion was attenuated by the presence of fluids in the compartment during conditioning. Experimental animals that consumed nothing in the compartment prior to becoming ill formed stronger aversions than did animals who drank water or saccharin solutions prior to suffering toxicosis. The authors suggested that when a rat becomes ill it scans selectively in memory for events related to the feeding system. If no consummatory behavior has occurred in the interval prior to toxicosis, then associations between other novel stimuli and toxicosis might be facilitated. Best and his colleagues argued that the behavioral response that the animal engages in during conditioning influences cue processing. Stimuli such as smells and tastes are more likely to be processed while the animal is drinking, so one would not expect strong conditioning to environmental stimuli not attended to during the consummatory act.

Similarly, Shettleworth (1972) noted that allowing animals (in this case Gallus gallus) to engage in ingestive behaviors affected the stimuli associated with shock during avoidance training. Chicks allowed to ingest fluids during training associated visual cues with shock, while chicks not allowed to ingest anything during conditioning associated auditory cues with shock. Shettleworth's observation supports the contention that animals process certain types of stimuli in preference to others while engaging in consummatory behavior. Again the stimuli that are attended to during consummatory behavior appear to be those normally employed by the species to identify food objects.

1.7.3 Ingestional Mediation

Domjan (1973) was one of the first to suggest that ingestive experiences aid association to exteroceptive cues. He found that odour-aversion conditioning was more effective when subjects were allowed to ingest water during training than when ingestion was not permitted. His results indicated that although ingestive behavior is not necessary for the production of odour aversions, ingestion may facilitate or mediate conditioning to odour cues.

Experiments by Martin and Ellinwood (1974) and Morrison and Collyer (1974) further suggest that flavours mediate conditioning to environmental, non-ingestive stimuli. Martin and Ellinwood conditioned aversions to the grey compartment of a black and grey shuttlebox. They only obtained aversions to the shuttlebox when a novel flavour was experienced at the time of conditioning.

Morrison and Collyer (1974) reached a similar conclusion in a different situation. Conditioned suppression of a bar-press response

to a discriminative stimulus was only evidenced when light, flavour and illness occurred in rapid succession. When the light-flavour pairing was separated from the flavour-toxicosis pairing, no suppression of responding occurred to the light in subsequent extinction tests.

The suggestion that flavours directly mediate aversions to exteroceptive cues is further supported by observations of prey-lithium aversion formation in Buteo hawks (Brett, Hankins & Garcia, 1976). When visually distinctive prey items were marked with a novel flavour visual aversions were readily obtained. Prior to marking prey with a novel flavour, only a generalized suppression of consumption was evidenced after several pairings of prey and toxicosis.

1.7.4 Ingestional Facilitation

Two recent studies have provided evidence in rats of rapid aversion learning to exteroceptive cues. One surprising feature of these experiments is that they both depended upon the presence of a novel flavour to produce robust aversions to exteroceptive cues. Galef and Osborne (1979) found that rats poisoned shortly after ingesting visually distinctive food objects associated visual cues with toxicosis only if a novel flavour (quinine) was experienced at the time of exposure to the visual cue. Similarly, Rusiniak, Hankins, Garcia and Brett (1979) found that aversion conditioning to a novel, weak odour was potentiated by exposure to a novel flavour at the time of odour-aversion conditioning.

In both the Galef and Osborne (1979) and Rusiniak et al., (1979) experiments conditioning to the less salient exteroceptive cue was enhanced by compounding it with a more salient flavour cue. Little

or no aversion accrued to the exteroceptive cue when it alone was paired with illness. This facilitation of the weaker exteroceptive cue by the stronger flavour cue (referred to below as the flavour facilitation effect) would not be easily predicted from current theories of classical conditioning (Mackintosh, 1975; Rescorla and Wagner, 1972). These theories predict that a more salient cue should overshadow conditioning to a less salient cue when the two are compounded and followed by reinforcement.

Demonstrations of the facilitatory effect of novel flavours in exteroceptive-cue-aversion conditioning are inconsistent with results that ascribe an interfering role to novel flavours in such conditioning (Best et al., 1977). They are not inconsistent with suggestions that either novel flavours or ingestive experience are necessary to mediate conditioning to environmental cues (Domjan, 1972; Martin & Ellinwood, 1974; Morrison and Collyer, 1974).

Galef and Osborne (1979) suggested that the flavour facilitation effect is due to unconditioned effects novel flavours have on attention to other stimulus characteristics of ingesta. According to this view, when a rat encounters a novel flavour, the flavour acts as a surprising event that directs attention to other stimulus characteristics of the food object. That novel stimuli have an arousal function important in formation of stimulus-toxicosis associations has been noted previously by Rudy, Rosenberg and Sandell (1977). They found that animals exposed to novel exteroceptive stimulation prior to pairing a familiar flavour with toxicosis formed much stronger aversions to the flavour than animals which received no such exposure.

Rudy et al., (1977) suggested that exposure to novel exteroceptive stimulation activated an arousal system that modulated the formation of associations. For Galef and Osborne (1979) the arousal resulting from experiencing a novel flavour not only provides for association of that stimulus with toxicosis, but also facilitates association of other less salient but equally valid attributes of the food object with toxicosis.

Alternatively, Rusiniak et al., (1979) suggest that novel flavours exert their facilitatory effect by activating a taste-indexed memory system that marks exteroceptive cues for quick association with toxicosis. The need to mark exteroceptive cues becomes apparent when one considers that telereceptive sense organs are "busy" afferent channels continually receiving sensory inputs. If the odour or sight of the food object is not marked for association in some fashion, then interference from other sensory events in the same afferent channel might disrupt the formation of an aversion (also see Revusky, section 1.4.1). For example, many different odours might be experienced in between the target odour and toxicosis administration. This account requires that flavours be present at the time of exteroceptive-cue -conditioning to circumvent interference and to allow for association of the cue with toxicosis.

The following series of experiments examines the possibility that directing attention to non-gustatory cues in feeding situations is sufficient for association of such cues with toxicosis. If, as Galef and Osborne (1979) suggest, the primary role of flavours in facilitating exteroceptive-cue-toxicosis conditioning is to direct attention to non-gustatory attributes of ingesta, then any technique

that directs attention to exteroceptive stimuli should also be effective in producing illness-based aversions to exteroceptive cues.

CHAPTER 2

EXPERIMENT 1

2.1 The Flavour Facilitation Effect

Before initiating a study of the mechanisms underlying the flavor facilitation of visual-cue-toxicosis conditioning in rats it is important to demonstrate the repeatability of the phenomenon. The present experiment was undertaken to replicate Galef and Osborne's (1978) demonstration that in the presence of a novel flavor (quinine) rats can associate exteroceptive cues with toxicosis. While the present experiment is analogous to Galef and Osborne's initial demonstration of the flavour facilitation effect, it differs from it in one important feature.

Galef and Osborne measured exteroceptive-cue-toxicosis aversion formation by allowing subjects to choose between two simultaneously presented visual stimuli, one of which had been previously associated with toxicosis. They employed the order of selection of capsules as a measure of aversion learning. In the present experiment the latency to open individually presented visually distinctive capsules was used as a measure of aversion acquisition. Because single stimulus tests of the type used here are generally less sensitive than choice tests (Grote and Brown, 1971), it was decided to employ two conditioning trials in the present experiment, rather than pair visual cues and toxicosis only once as Galef and Osborne did.

2.2 Method

2.2.1 Subjects. Thirty experimentally naive male Long-Evans

rats, obtained from Canadian Breeding Farms, served as subjects. The subjects were maintained at 80 percent of their projected daily ad libitum weight for the duration of the experiment and weighed 150-200g at its initiation.

2.2.2 Apparatus. Figure 1 depicts the apparatus, a transparent Plexiglas start-box (28 x 18 x 13 cm) and goal-box (25 x 25 x 15 cm), joined by a guillotine door with two 6 x 5 cm apertures located in the wall of the goal-box opposite the start-box. A cubic metal food-bin, 7 cm long x 6 cm wide, x 5 cm deep could be inserted into each aperture or an aperture could be closed with a metal plate.

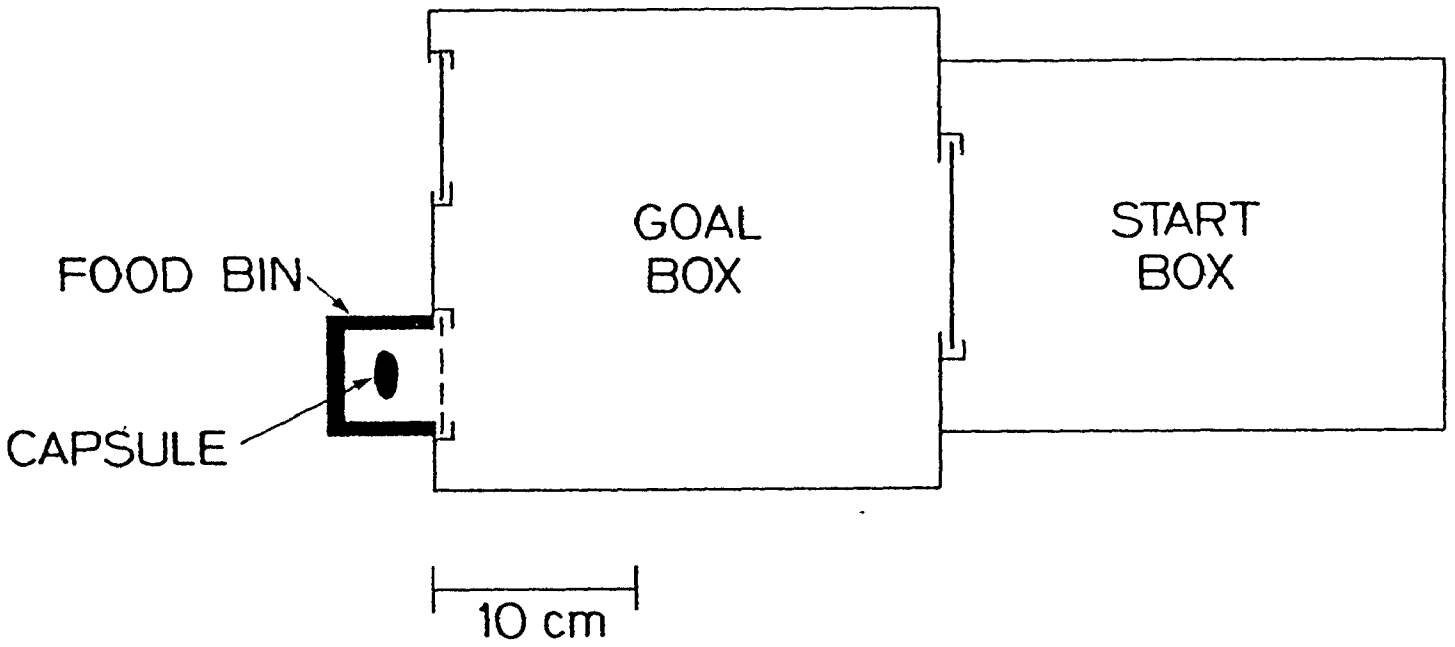
2.2.3 Procedure. Subjects were run in three replications each containing an approximately equal number of members from each of the groups described in section 2.2.6 below.

2.2.4 Habituation. All subjects were habituated to the experimental apparatus and testing room by 7 daily, 100 min sessions during which they received 20 min individual exposure to the apparatus and 80 min exposure to the experimental room.

2.2.5 Pretraining. On Day 1 of pretraining, all subjects were trained to feed from capsules by placing 10, number 2 white gelatin capsules (White Opaque, Parke-Davis Co., Ltd., Brockville, Ontario), each containing an average of .35 g of Purina Laboratory Chow, in each subject's cage for 60 min. Each subject completely consumed the contents of all capsules available to it.

On Days 2, 3, and 4 of pretraining each subject was trained, for 10 trials/day, to run from the start-box and retrieve single white capsules from a single food-bin in the goal-box. The food-bin

Figure 1. Experimental apparatus employed in all Experiments.


FOOD BIN
CAPSULE
GOAL
BOX
START
BOX
10 cm

containing the capsule was placed in a pseudo-random sequence[1] equally often to each subject's left and right as it entered the goal-box . On each pretraining trial a subject was allowed 60 sec to consume the contents of each capsule after it was opened. The intertrial interval, spent in the start-box, was 30 sec in duration.

2.2.6 Poison training. On Day 5 of the experiment subjects were randomly assigned to one of three groups for poison training. On both Days 5 and 6 subjects in all groups were given two trials on each of which they ate a visually distinctive capsule. Subjects in one group (group F5PP)[2] were given scarlet coloured, number 2 capsules (Scarlet Opaque, Parke-Davis) containing Purina Laboratory Chow adulterated 4 percent by weight with quinine hydrochloride to facilitate aversion conditioning to visual cues, confined to the start-box for 5 min following ingestion of the second capsule, and then injected with lithium chloride. Members of the second group (group F60PP) also received scarlet capsules with quinine adulterated contents, but these subjects were not injected with lithium chloride until 60 min after capsule ingestion. This group constitutes a specifically unpaired control for the non-associative effects of experiencing novel bitter capsules and toxicosis.

Members of the third group (group NF5PP) were treated in an identical fashion to members of group F5PP, except that the visually distinctive scarlet capsules they ingested on each of the two poisoning days contained unadulterated Purina Laboratory Chow. This group constitutes a poison alone group to control for the simple effects of experiencing toxicosis after being exposed to visually distinctive but familiar flavoured capsules.

2.2.7 Testing. All testing was conducted in a blind situation in which neither the experimenter nor his assistant was aware of the group assignment of subjects until all subjects in a replication had been tested.

On Day 7 of the experiment, all subjects were tested for an aversion to red capsules containing unadulterated Purina Laboratory Chow. Subjects were tested for 10 trials with single capsules located in the left and right food-bins in the same sequence as was used for presentation of pretraining capsules (see footnote 1). A subject was allowed a maximum of 60 sec per trial to ingest a capsule once it had been opened. A latency on any given trial of 300 sec or more to open a capsule was considered to be evidence of complete avoidance of that capsule. After completion of capsule ingestion or the elapsing of 300 sec since trial initiation, whichever occurred first, the subject was replaced in the start-box for 30 sec before the next trial was initiated.

The experimenter recorded each subject's latency to open each capsule on each of the 10 test trials and weighed each subject before and after each test session, allowing approximate assessment of the amount consumed by the subject during the 10 test trials.

2.2.8 Data analysis. Each subject was assigned a single score describing its performance during the 10 test trials. This score equalled the total number of seconds a subject spent retrieving and opening all 10 test capsules. In this and all subsequent experiments this total test latency measure was analyzed employing non-parametric procedures because of the nature of the underlying distributions of

scores. While one must be cautious in interpreting the results of non-parametric tests as indicators of differences in central tendency, they are adequate to determine if samples are taken from different distributions. Wherever possible other measures, descriptive or inferential, are supplied that provide converging evidence about the existence of an aversion. The .05 level of significance was employed for all experiments.

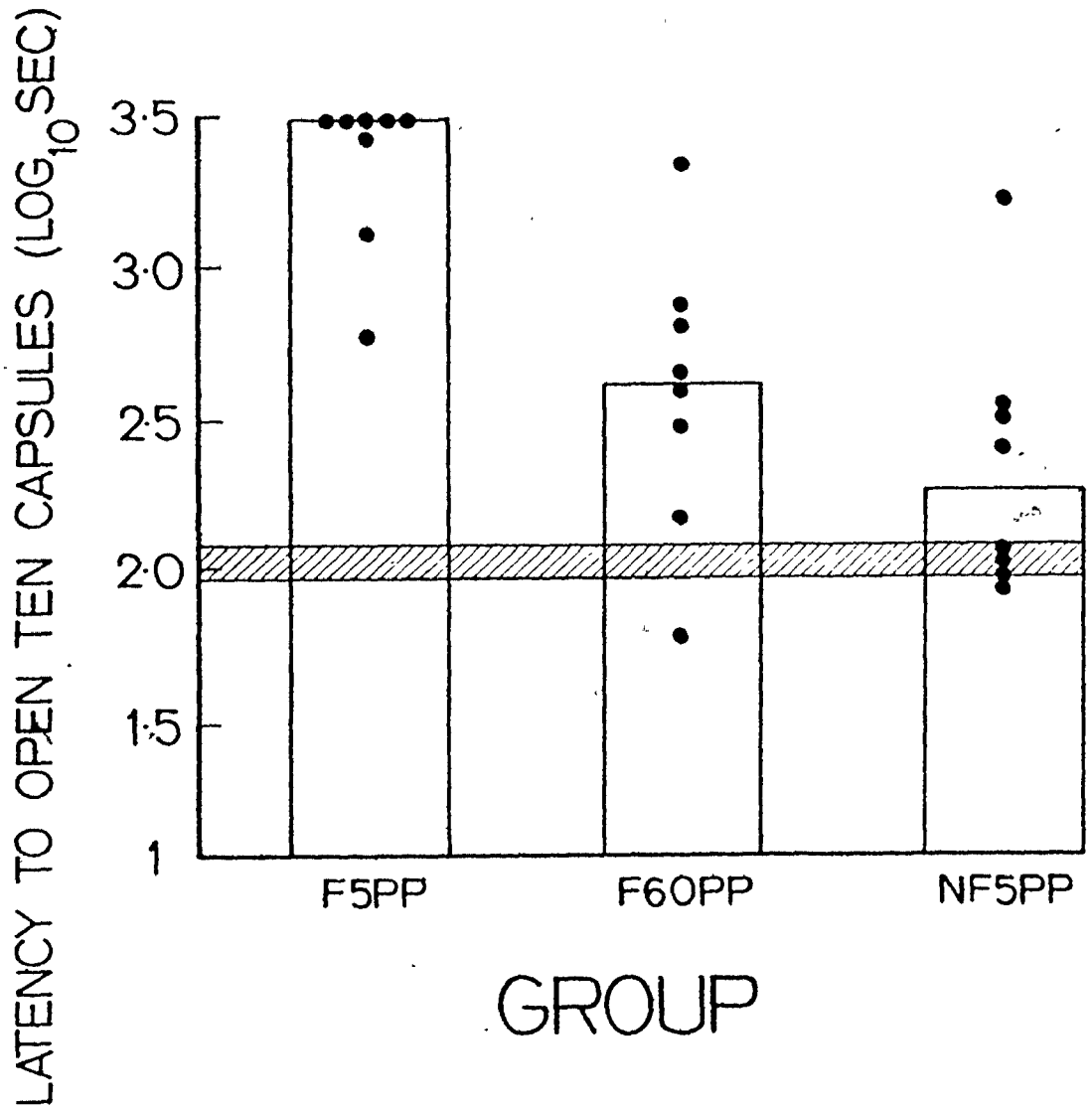
2.3 Results and Discussion

Four subjects were discarded for failing to learn to eat from the food-bin during pretraining. Two additional animals were discarded for failing to pick up quinine adulterated training capsule on the second day of poison training (one each from group F60PP and F5PP), leaving a total of 8 subjects in each group.

The main results of Experiment 1 are presented in Figure 2 which shows both individual and group median latencies to consume 10 test capsules. The horizontal bar across Figure 2 shows the range of group median latencies to ingest the 10 capsules on the last day of pretraining (Day 4), and provides a baseline for comparison across experiments. The raw data are presented in $\log_{10}$ sec format solely to facilitate graphic representation. All analyses were performed on the raw data (in seconds). This in no way changes the outcomes of the statistical tests because the rankings of scores are unchanged by the $\log_{10}$ transformation.

An analysis of total latencies of subjects in the three groups to open the 10 test capsules indicated that they were significantly different from each other (Kruskall-Wallace $\underline{H} = 13.59$, $\underline{p} < .02$,

Figure 2. Total latency to open 10 test capsules ($\log_{10}$ sec) for individual subjects in Experiment 1. The histograms represent the median latency of each group. The horizontal bar represents the range of the medians of the group total latency to open 10 capsules on the last day of pretraining. This bar serves as a baseline for comparison across experiments.


LATENCY TO OPEN TEN CAPSULES (LOG10SEC)
3·5
3·0
2·5
2·0
1·5
1
F5PP
F60PP
NF5PP
GROUP

two-tailed). Six subjects in group F5PP showed complete avoidance of test capsules on every trial, while no subject in either of groups F60PP or NF5PP exhibited complete avoidance of the visually distinctive test capsules.

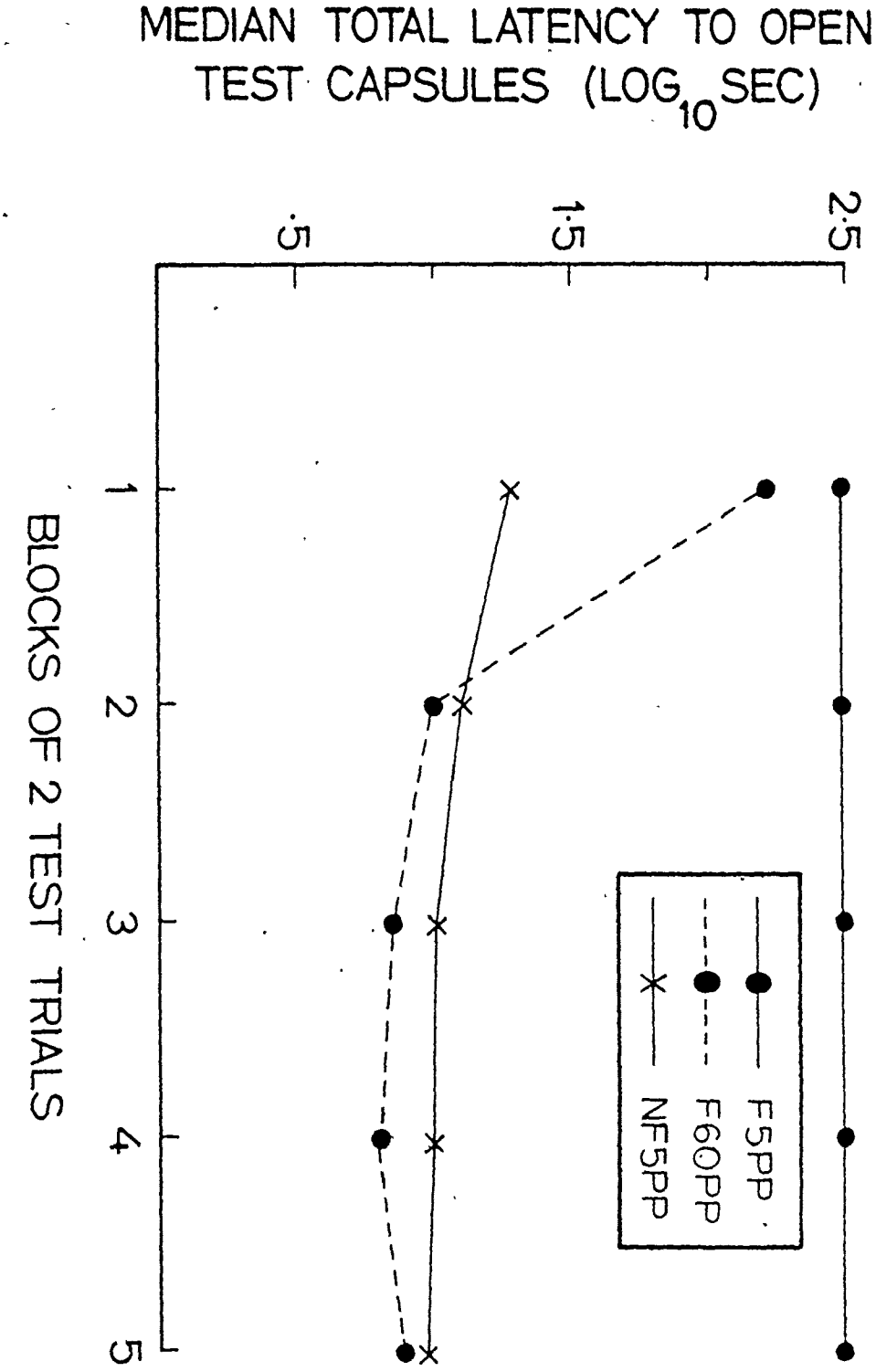
A modified Kruskall-Wallace, post-hoc comparison of total latency to open test capsules (Wilcoxon & Wilkox, 1964, p. 9) revealed that group F5PP was significantly different from both groups F60PP and NF5PP (respectively $p < .05$ and $p < .01$, two-tailed), which were not different from each other ($p > .1$, two-tailed).

Figure 3 presents the group median latencies to ingest capsules, in blocks of two testing trials. Group F60PP appears somewhat slower to ingest capsules on the first block of trials but this effect extinguished by the third test trial, and from that point their latencies were comparable to group NF5PP, which evidenced no disruption of performance on any block.

An analysis of weight changes over the test session revealed that the three groups consumed significantly different amounts of Purina chow during testing (Kruskall-Wallace $H = 9.0$, $p < .04$, two-tailed). Members of group F5PP were significantly different from each of group NF5PP and group F60PP (both p's $< .05$, two-tailed) which were not different from each other ($p > .1$, two-tailed). Seven subjects in group F5PP lost weight over the course of testing while only three of group NF5PP and two of group F60PP did so.

The present experiment replicates Galef and Osborne's findings: (1) that rats are able to form visual-cue-aversions over 5-min CS-US delays, if a novel quinine flavour is present to facilitate

Figure 3. Median total latency to open test capsules in blocks of two test trials for Experiment 1.


MEDIAN TOTAL LATENCY TO OPEN TEST CAPSULES (LOG10 SEC)
.5
1.5
2.5
BLOCKS OF 2 TEST TRIALS
1
2
3
4
5
F5PP
F60PP
NF5PP

conditioning, (2) that subjects poisoned shortly after consuming visually distinctive, unflavoured capsules do not form aversions to visual cues, and (3) that subjects poisoned 60 min after ingesting visually distinctive, bitter-tasting capsules show little evidence of an aversion to the visual cue. The transient disruption obtained on block one of testing for group F60PP was also observed in the Galef and Osborne (1978) situation. They attributed this disruption to the effects of experiencing an unpleasant bitter taste and not to an effect of experiencing toxicosis.

CHAPTER 3

EXPERIMENT 2

3.1 Attentional Factors

As discussed in section 1.7.4 above, two alternative interpretations of the flavour facilitation effect demonstrated in Experiment 1 have been advanced. (1) Galef and Osborne (1978) have suggested that the facilitatory role of flavours in exteroceptive-cue-aversion conditioning is due to their effect in directing attention to other stimulus attributes of ingesta. (2) Rusiniak *et al.* (1979) have suggested that the facilitatory role of flavours in exteroceptive-cue-aversion conditioning is due to activation of a taste-indexed memory system that marks the exteroceptive cue for association with delayed toxicosis.

Because the second hypothesis requires that a flavour be present at the time of conditioning to activate the special taste-indexed memory system while the first does not, they predict different outcomes in a variety of situations. If, for example, one were to direct subject attention to an exteroceptive cue and subsequently pair that cue with toxicosis, the first interpretation would predict that aversion conditioning should be facilitated. Because there is no novel flavour present at the time of aversion conditioning the second interpretation would suggest that there can be no activation of the taste-indexed memory system and, therefore, no exteroceptive-cue-conditioning should occur.

3.2. Method

The present experiment was performed to assess whether aversions could be conditioned to visually distinctive capsules without employing novel flavours to facilitate such conditioning.

In the present experiment subjects were trained to use a visual cue to choose between palatable and unpalatable foods prior to being exposed to a visually novel, but familiar tasting, food followed by toxicosis. If the attentional interpretation of the flavour facilitation effect is correct, then subjects pretrained to attend to visual properties of their food should be able to associate visual properties of food with toxicosis without the facilitatory aid of novel flavours.

Experiment 2 employed two groups, both of which were pretrained on a simultaneous visual discrimination. Following discrimination training, one of these groups was poisoned 5 min after presentation of a visually novel, familiar-tasting stimulus and the other 60 min after presentation of the same stimulus. Both the Galef and Osborne (1978) experiments and Experiment 1 above suggest that a 60-min delay precludes conditioning to exteroceptive cues. Thus, subjects in the group poisoned 60 min after presentation of visually distinctive capsules serve as one of several possible controls for non-associative effects of following a novel visual cue with toxicosis.

3.2.1 Subjects. Naive male rats (150-200g) of the Long Evans strain (N=24), maintained at 80 percent of their projected daily ad libitum weight, served as subjects.

3.2.2 Apparatus. The apparatus was identical to that employed in Experiment 1 (see section 2.2.2.).

3.2.3 Procedure. The present experiment was performed in three replications each containing an approximately equal number of subjects from both groups.

3.2.4 Habituation. The subjects were habituated to the experimental situation as described in section 2.3.1 of the Method of Experiment 1.

3.2.5 Pretraining. On Day 1, all subjects were allowed access to 10 unflavoured gelatin capsules containing .35 g of Purina Laboratory Chow. Half the subjects received light-coloured white capsules and half dark-coloured scarlet capsules during pretraining.

On Day 2 of pretraining all subjects were trained to run from the start-box and retrieve, from a food-bin, capsules identical to those to which they had been exposed on Day 1. The food-bin was assigned to left and right positions in a pseudo-random sequence (footnote 1).

3.2.6 Discrimination training. On Day 3 each subject was given a series of trials on each of which it was offered a choice between a capsule similar to that which it had been pretrained to eat, and a novel coloured capsule (either light or dark, as appropriate) containing Purina Laboratory Chow adulterated 4 percent by weight with quinine hydrochloride. During discrimination training, two identical food-bins were mounted in the far wall of the goal-box and the subject was allowed to choose between simultaneously-presented visually-distinctive capsules.

As before, subjects were allowed 60 sec to consume the contents of a capsule before being returned to the start-box for a 30 sec intertrial interval. Subjects were allowed a maximum of 21 trials on Day 3 to attain a criterion of 90 percent correct choices (i.e. ingesting a capsule containing regular Purina Laboratory Chow prior to contacting an adulterated capsule) in any block of 10 trials. If a subject failed to attain criterion on Day 3, it was given a second day of discrimination training on Day 4 identical to the first.

3.2.7 Poison training. Twenty-four hr after attaining the discrimination criterion, subjects were randomly assigned to one of two groups for poison training. Capsules used during poison training were visually distinct from pretraining capsules. Pretraining capsules were either light or dark while poison training capsules were 1/2 light and 1/2 dark, (each capsule had a white end and a scarlet end) and all contained unadulterated Purina Laboratory Chow.

Subjects were given a single intraperitoneal injection (2 ml/100g body weight) of .12 M LiCl solution, either 5 min or 60 min after retrieving the second of two visually distinctive training capsules, one capsule from the left and one from the right food-bin. Each subject in the 5-min delay group (group D5P)[3] spent the delay interval in the start-box. Each subject in the 60-min delay group (group D60P) spent the first 5 min in the start-box and the remaining 55 min in its home cage.

3.2.8 Testing. Twenty-four hr following poison training, subjects were tested for an aversion to ingesting 1/2 light, 1/2 dark capsules containing unadulterated Purina Laboratory Chow. As in

Experiment 1, subjects were allowed 10 test trials and a maximum of 300 sec to ingest a capsule (see section 2.2.7).

3.3 Results and Discussion

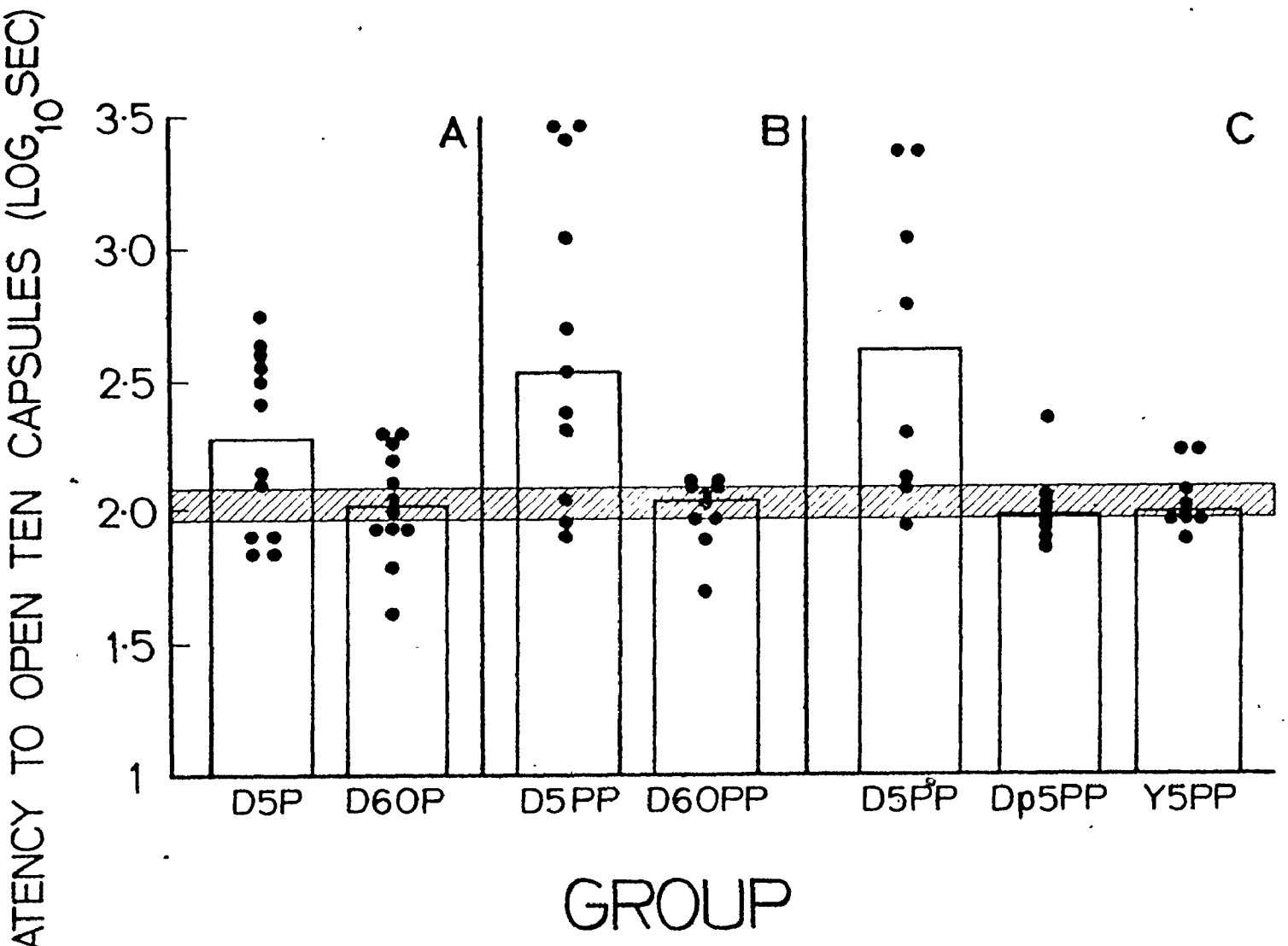
Experimental subjects (group D5P) did not differ from control subjects (group D60P) on the number of trials to criterion during discrimination training ($\overline{X}_{D5P}$ = 15.3; $\overline{X}_{D60P}$ = 16.3).

The main results of the present experiment are presented in Panel A of Figure 4 which illustrates individual subject and group median total latencies to ingest 10 test capsules. Although six subjects in group D5P took longer to ingest capsules than any subject in group D60P, this result is not significant (Kruskall-Wallace $\underline{H}$ = 1.76, .2 < $\underline{p}$ < .4, two-tailed).

An examination of Panel A of Figure 4 reveals that the scores of subjects in Group D5P are bimodally distributed. If one separates each group into high and low scorers, by dividing them at their respective medians, then high-scorers in group D5P were significantly different from high-scorers in group D60P (Mann-Whitney Test, $\underline{U}$ = 0, $\underline{p}$ < .002, two-tailed). Low scorers in each group were not different from each other. While this post-hoc test cannot be used as support for the initial hypothesis, it does suggest that there may be an effect of discrimination training on exteroceptive-cue-aversion conditioning worth investigating in more detail.

At least three hypotheses can be proposed to explain the bimodal distribution of scores in the present experiment. First, some of the subjects may not have been attending to visual cues at the time of aversion conditioning. Although solution of the visual

Figure 4. Total latency to open 10 test capsules ($\log_{10}$ sec) for individual subjects in Experiment 2 (Panel A), Experiment 3 (Panel B) and Experiment 4 (Panel C). The histograms represent the median latency of each group and the horizontal bar is the baseline derived from Experiment 1.


LATENCY TO OPEN TEN CAPSULES (LOG10SEC)
3·5
3·0
2·5
2·0
1·5
1
A
B
C
D5P
D60P
D5PP
D60PP
D5PP
Dp5PP
Y5PP
GROUP

discrimination insured that subjects were attending to the visual characteristics of their ingesta during discrimination training, the 24-hr delay interpolated between discrimination training and poison training may have resulted in some subjects not attending to visual cues at the time of aversion conditioning. Second, not all subjects were visibly ill after toxin injection, and it is possible that some of the injections may have been positioned inaccurately. Third, it is possible that this type of conditioning requires more pairings of the stimulus with the reinforcer to produce evidence of an association.

EXPERIMENT 3

3.4 Two Conditioning Trials

The present experiment replicates Experiment 2 but employs two pairings of the novel visual stimuli with toxicosis during poison training to insure that all subjects experience toxicosis after being exposed to visually novel capsules.

3.5 Method

3.5.1 Subjects, apparatus, procedure and habituation. All details of subjects (N=21), apparatus, procedure and habituation were identical to those of Experiment 2.

3.5.2 Pretraining. Subjects were pretrained, as described in section 3.2.5 above, to ingest light-coloured capsules from a food-bin in the goal-box.

3.5.3 Discrimination training. All animals received two consecutive days, 20 trials/day, of discrimination training whether or not they had attained the 90 percent criterion on the first day of discrimination training.

3.5.4 Poison training. Each animal received poison training (see section 3.2.7) on two successive days.

3.5.5 Testing. In the previous experiment some experimental subjects were observed to reject test capsules (e.g. to not eat or to spit out their contents). These rejection responses were systematically recorded in the present experiment in addition to recording the total latency to ingest test capsules.

3.6 Results and Discussion

The experimental group (group D5PP, $n = 11$) did not differ from the control group (group D60PP, $n = 10$) on the number of trials to discrimination criterion ($X_{D5PP} = 20.5$; $X_{D60PP} = 20.4$).

The main results of the present experiment are presented in Panel B of Figure 4 which shows individual and group median total latencies to open 10 test capsules. On this measure, group D5PP was significantly different from group D60PP (Kruskall Wallace $H = 6.08$, $p < .04$, two-tailed).

Further evidence that experimental subjects had formed aversions to visually distinctive capsules derives from observations of behavior made during the blind testing session. Animals that have ingested unpalatable or aversive substances may rub their mouths along the floor of the cage, urinate on their food, spill their food and spit it out, or make rapid brushing movements with their fore-paws to remove traces of the ingesta from the fur around their mouths (Grill and Norgen, 1978). Nine members of group D5PP made one or more of the rejection responses described above during testing, while only three members of group D60PP were observed to do so. (Fishers-Exact test, $p =$

.05, two-tailed). Many of these rejection responses were made as the subject approached the visually distinctive capsule prior to picking up the capsule. Subjects in the experimental group (D5PP) acted "as if" the visually distinctive capsules actually "tasted" bad, while those in the control group (D60PP) did not.

The results of the present experiment are consistent with the hypothesis that the facilitatory role of flavours in exteroceptive-cue-aversion conditioning results from their unconditioned effect, directing attention to other stimulus characteristics of ingesta. Discrimination training had an effect similar to that of presenting novel flavours at the time of exteroceptive-cue-toxicosis conditioning in facilitating visual-cue-toxicosis conditioning.

EXPERIMENT 4

3.7 Sensitization Control and Yoked Control Groups

In the previous experiment the strength of aversion to visual cues decreased as the delay between CS presentation and US onset increased from 5 min to 60 min. This delay of reinforcement gradient is suggestive of an associative process, in that one would not expect a non-associative process to respond to an associative manipulation such as increasing the CS-US delay interval. Further evidence that an associative process is involved in the aversion to visual cues derives from the observation that two conditioning trials (Experiment 3) produced stronger aversions to visual cues than one conditioning trial (Experiment 2). It is still possible, however, to interpret the results of Experiment 3 without reference to the existence of an association between the visual cue and the illness reinforcer.

The novel visual appearance of the poison training capsule may itself produce reflexive responses that are enhanced by exposure to the unconditioned stimulus, but this enhanced neophobia may only occur if the novel stimulus is presented 5 min (but not 60 min) prior to toxicosis induction. If this were the case, then a control group poisoned 5 min after presentation of one visually novel stimulus but tested with a different visually novel stimulus would provide evidence of the associative nature of the effect observed at 5 min. If this procedure also produced avoidance of the test stimulus, then the observed effect would be attributable to a non-associative, emotional response that any novel stimulus would evoke. The present experiment, therefore, includes a group which received novel pellets of purina Laboratory chow during poison training but which were tested with a different novel capsule to assess the role played by enhanced neophobia in the expression of the aversion.

A second control group was included in the present experiment to assess the contribution of discrimination pretraining to the formation of aversions to visual cues. In Experiment 3 the obtained visual-cue-aversion might have resulted simply from experiencing novel quinine-flavoured, visually-distinctive capsules during the discrimination phase. That is, it is possible that subjects receiving no discrimination pretraining might also form visual-cue-aversions over a 5-min CS-US delay. The present experiment, therefore, includes a control group, yoked to the experimental group in terms of its trial by trial experience with palatable and unpalatable capsules during the discrimination phase of the experiment, but lacking experience of a visual cue predicting palatability during that phase.

3.8 Method

3.8.1 Subjects, apparatus, habituation and pretraining. All details of subjects (N=24), apparatus, habituation and pretraining were identical to those of Experiment 2 (see sections 3.2.1 to 3.2.5).

3.8.2 Procedure. There were three groups in the present experiment. The first (group D5PP, $\underline{n}$ = 8) was treated identically to group D5PP of the previous experiment. Members of the second group (group Dp5PP, $\underline{n}$ = 8)[4] were treated identically to subjects in group D5PP except that during poison training sessions subjects in group Dp5PP ate .35 g of unencapsulated Purina Laboratory Chow hardened into a solid pellet. Both of these groups were poisoned on 2 successive days 5 min after ingesting the appropriate food object (see section 3.2.7). Any evidence of an aversion to ingesting 1/2 light, 1/2 dark capsules in group D_p5PP would suggest that such an aversion results from a non-associative, sensitization-like process.

Members of the third group (group Y5PP; $\underline{n}$ = 8) were yoked to the eight subjects of Group D5PP of the present experiment in terms of their trial by trial discrimination training with palatable and unpalatable capsules of Purina Laboratory Chow. Subjects in group Y5PP were also exposed to visually distinctive capsules during discrimination training, however, capsule colour was not correlated with capsule flavour. On fifty percent of the trials subjects picked up red capsules and on fifty percent of the trials white capsules. Capsule colour on each trial was determined by the pseudo-random sequence given in footnote 1. This yoking procedure equated as closely as possible the probability of experiencing quinine in a red capsule to

that of experiencing quinine in a white capsule. It also equated the probability of experiencing Purina Laboratory Chow in red capsules and in white capsules. Poison training for group Y5PP proceeded in an identical fashion to that of group D5PP. Subjects in both groups received lithium chloride injections 5 min after ingesting 1/2 light, 1/2 dark capsules that contained regular Purina Laboratory Chow.

3.9 Results and Discussion

The main results of the present experiment are presented in Panel C of Figure 4 which shows both group median and individual total latencies to open 10 test capsules. The first two histograms in Panel C of Figure 4 clearly indicate that, of the subjects pretrained to attend to the visual characteristics of their food, only subjects poisoned 5 min after ingesting 1/2 light, 1/2 dark capsules (Group D5PP) avoided such capsules (Kruskall-Wallace $H = 6.35$, $p < .04$, two-tailed). Subjects poisoned 5 min after ingesting unencapsulated pellets of Purina Laboratory Chow (Group Dp5PP) exhibited no aversion to ingesting 1/2 light, 1/2 dark capsules.

Behavioral observations revealed that six members of group D5PP exhibited rejection responses during testing, while none of group Dp5PP were observed to exhibit such behaviours (Fishers-Exact, $p = .01$, two-tailed).

These data indicate that the avoidance of visually distinctive capsules by subjects pretrained to attend to the visual characteristics of their food is due to an association between the distinctive visual characteristics of capsules experienced prior to toxicosis and subsequent gastrointestinal distress and not to the non-associative effects of experiencing novel food objects during poison training.

The third histogram in Panel C of Figure 4 illustrates both group median and individual total latencies to open 10 test capsules of subjects in group Y5PP. An examination of the figure reveals that animals in the yoked control group (Group Y5PP) did not exhibit elevated latencies to open capsules. A Wilcoxon Matched-Pairs-Signed-Ranks Test (Siegel, 1956) revealed that group D5PP of the present experiment was significantly different from group Y5PP ($T = 1$, $p < .02$, two-tailed). These data indicate that the correlation between capsule flavour and capsule color during discrimination training is a potent factor in facilitating subsequent aversion conditioning to visual cues. Simple experience with novel flavours and novel visual stimuli, uncorrelated with each other, was not sufficient to facilitate subsequent stimulus-toxicosis conditioning. The results of the present experiment provides further support for the hypothesis that attentional factors are important in the production of visual-cue-toxicosis associations in flavour-facilitation experiments.

CHAPTER 4

EXPERIMENT 5

4.1 Long-Delay Visual-Cue-Aversions

The experiments reported in Chapter 3 demonstrate that rats pretrained to attend to visual cues are able to form visual-cue-toxicosis associations in the absence of flavour mediation. These aversions are not observed when the delay between experiencing the visual cue and toxicosis is of 60-min duration. In contrast, flavour-toxicosis aversions may be obtained with delays of many hours between stimulus presentation and a single administration of toxin (e.g. Smith and Roll, 1967). The experiments reported in the present chapter describe three attempts to produce long-delay, visual-cue-aversion learning in rats using discrimination pretraining to potentiate the formation of visual-cue-toxicosis associations.

4.2 Study 1 - Overtraining and Interference

In the present study two manipulations were introduced to facilitate the formation of visual-cue-aversions over long delays. The first manipulation employed was intended to reduce interference from visual stimuli, other than the CS, occurring during the CS-US delay. As discussed in section 1.4.1, Revusky (1977) has argued that the strength of association between a target CS and a reinforcer is a function of the interference from other relevant stimuli that the subject experiences during the CS-US delay period. It was reasoned that if all other sources of visual stimulation were eliminated during the CS-US delay then rats might develop aversions to visual cues over

moderate delays between stimulus presentation and reinforcer administration. The second manipulation employed in the present study to increase the probability of long-delay learning involved increasing the amount of discrimination training to which subjects were exposed. Perhaps, as discussed in section 3.3, not all of the subjects were attending to visual cues at the time of visual-cue-toxicosis conditioning. If so, then subjects receiving additional discrimination training prior to aversion conditioning might be able to form visual-cue-aversions over a 30-min CS-US delay because of enhanced attention to visual properties of ingesta.

4.3 Method

Of the three groups in the present study one received the usual 2 days of discrimination training prior to aversion conditioning with a 30-min CS-US delay, the second was treated identically to the first but spent the 30-min CS-US delay in total darkness while the third received a total of 5 days visual discrimination training, prior to aversion conditioning with a 30-min CS-US delay.

4.3.1 Subjects. Experimentally naive rats (150-200g) of the Long Evans strain (N=24), maintained at 80 percent of their projected daily ad libitum weights, served as subjects.

4.3.2 Apparatus. The apparatus was identical to that used in all previous experiments (see Figure 1).

4.3.3 Habituation. Subjects received the same 7 days of habituation to the apparatus as described previously (see section 2.2.4).

4.3.4 Pretraining. Pretraining was identical to that employed in all previous experiments (see section 2.3.2). Subjects were allowed

to ingest 10 capsules of unadulterated Purina Laboratory Chow on Day 1 and on Day 2 they were trained for 10 consecutive trials to run out and retrieve unadulterated capsules from a food-bin in the goal-box.

4.3.5 Discrimination training. On Days 3 and 4 each subject received discrimination training identical to that which subjects received in Experiments 3 and 4 of the previous chapter (section 3.5). On each of Days 5, 6, and 7 the overtraining group (Group OTD30PP)[5] received 20 additional trials of discrimination training. The onset of discrimination training was delayed for 3 days for the non-overtrained groups such that all subjects completed discrimination training on the same day, allowing poison training and testing to be performed at the same time for all groups.

4.3.6 Poison training. Poison training for each subject commenced 24 hr after its last day of discrimination training. The overtraining group (OTD30PP) were poisoned on 2 successive days, 30 min after ingesting visually distinctive 1/2 light, 1/2 dark unadulterated capsules. The 30-min delay control group (D30PP) were also poisoned 30 min after ingesting visually distinctive 1/2 light, 1/2 dark capsules but had not experienced any additional discrimination training. The non-overtrained, lights-out-group (LOD30PP) received poison training identical to that received by members of group D30PP but spent the 30-min delay in complete darkness. Group D30PP therefore serves as a baseline condition to assess the effect of the two manipulations of overtraining and reducing visual interference.

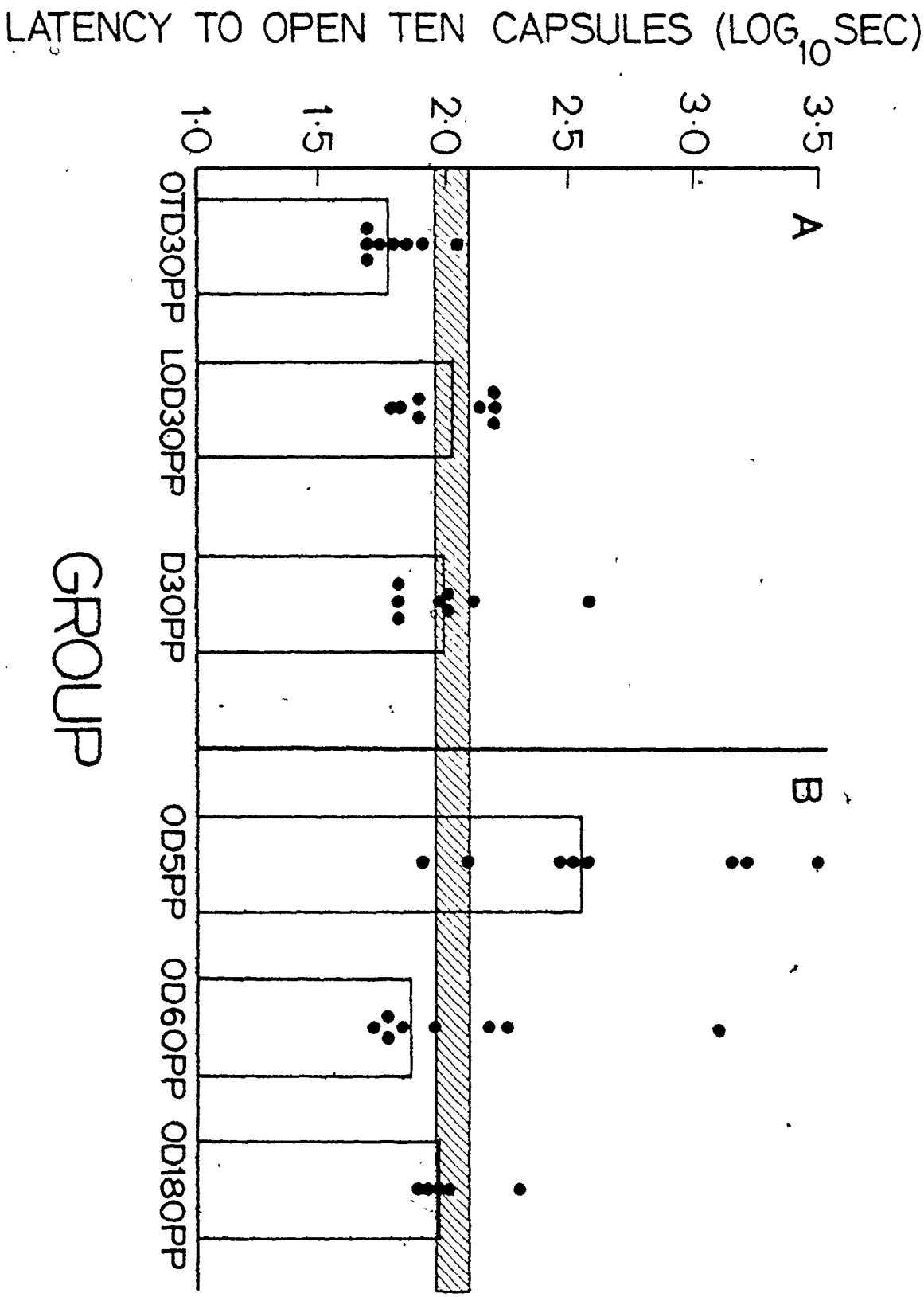
4.3.7 Testing. Testing was conducted exactly as described in section 3.2.8.

4.4 Results and Discussion

The main results of the present study are presented in Panel A of Figure 5 which shows both group median and individual total latencies to open 10 test capsules. Examination of this figure reveals that, if anything, increased discrimination training reduced capsule opening latencies on the aversion test. There were, however, no signficant differences among the three groups, (Kruskall-Wallace H = 6.8, $.05 < p < .1$, two-tailed). Group D30PP showed no evidence of conditioning when compared to baseline and neither increasing discrimination training (group OTD30PP)nor turning out the lights during the CS-US interval (group LOD30PP) facilitated aversion conditioning to visual cues over 30-min CS-US delays. Apparently a 30-min delay between the presentation of the novel visual stimulus and administration of the toxic agent is too long to support exteroceptive-cue-conditioning.

It may be the case that aversion conditioning to exteroceptive cues only occurs at intervals of a few minutes duration. Alternatively the manipulations employed in this experiment may not have been those appropriate to produce long-delay learning. One problem with the present experiment is that, although discrimination overtraining may enhance attention to visual cues, it also allows subjects to learn to run faster over the course of training. The next experiment provided subjects with extensive visual discrimination training from weaning to maturity without concomitantly shortening response latencies in the experimental apparatus.

Figure 5. Total latency to open 10 test capsules ($\log_{10}$ sec) for individual subjects in Experiment 5-Study 1 (Panel A) and Experiment 5-Study 2 (Panel B). The histograms represent the median latency of each group. The horizontal bar is the baseline derived from Experiment 1.


LATENCY TO OPEN TEN CAPSULES (LOG10 SEC)
1·0
1·5
2·0
2·5
3·0
3·5
A
B
GROUP
OTD30PP
LOD30PP
D30PP
OD5PP
OD60PP
OD180PP

4.5 Study 2 - Developmental Considerations

The previous study failed to produce conditioned visual-cue-aversions over moderate, 30-min delays. Mackintosh (1973) has argued that stimulus specificity and long-delay learning might be functions of animals' experience with naturally occurring contingencies during ontogeny (see section 1.4.3). It may be the case that the two manipulations employed in the previous study were simply not sufficient to override subjects' extensive experience of gustatory cue post-ingestional-consequence correlations and visual cue post-ingestional-consequence lack of correlation. The following experiment constitutes a simple test of this idea.

It was hypothesized that if rats were presented from weaning with a choice between palatable and unpalatable diets marked with distinctive visual characteristics then the selective bias of association that is obtained in toxicosis conditioning experiments might be reduced and visual-cue-toxicosis associations might be formed over long delays. This manipulation has the added advantage of not shortening response latencies of subjects in the discrimination apparatus that occurred in the previous study.

4.6 Method

4.6.1 Subjects. 22, 19 day old, male Long-Evans rats from the McMaster colony served as subjects. One subject died during the course of the experiment.

4.6.2 Apparatus. In the present study subjects were presented, from weaning to maturity, with a choice between a light yellow-coloured palatable diet and a dark brown-coloured unpalatable diet. Both diets

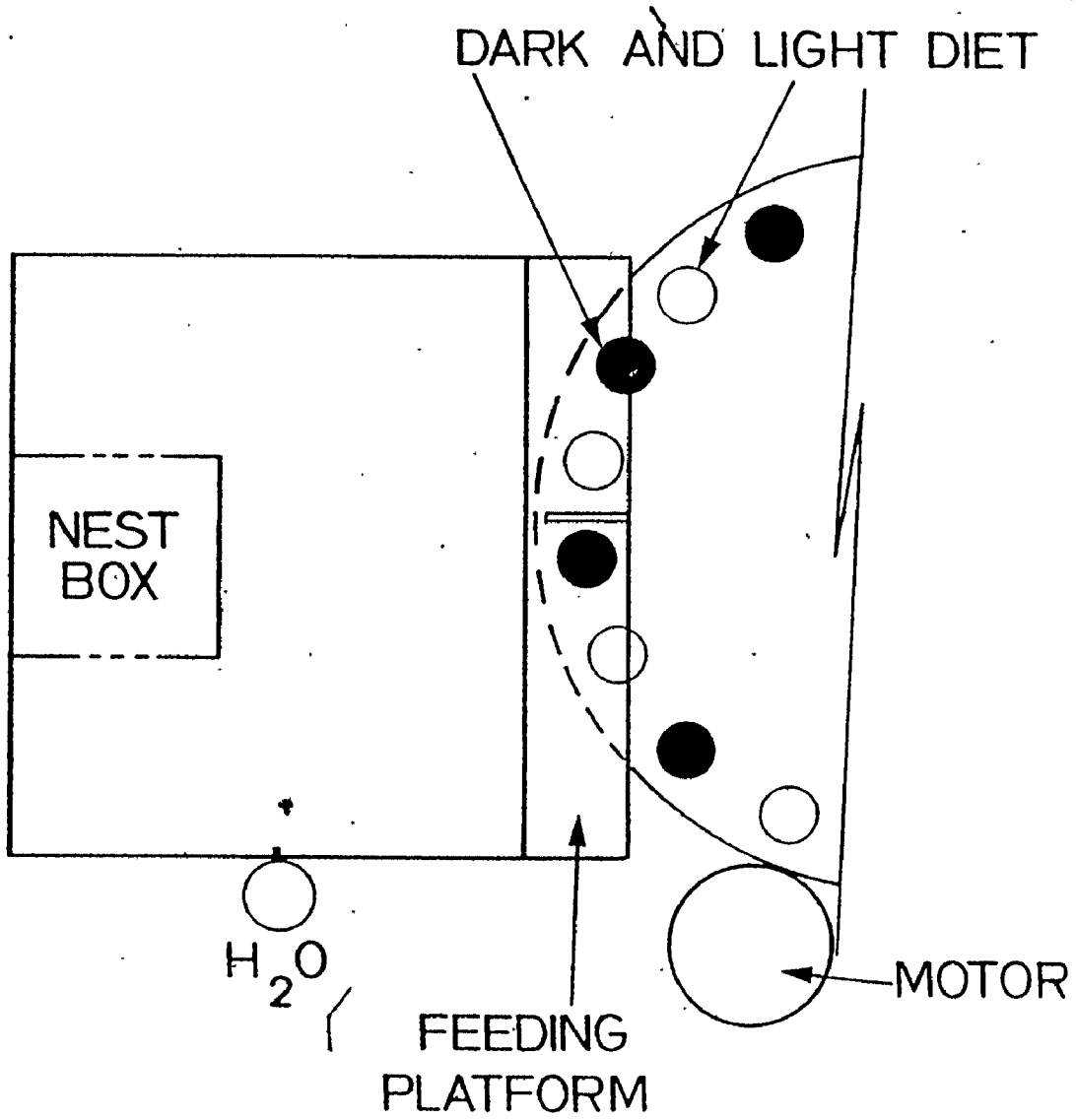
were compounded of sugar based Teklad diet, made visually distinctive by the addition of light yellow or dark brown (equal parts green and red) food dye (Club House Food Colour Preparation, 2 ounces per 500 g of diet). The dark diet was adulterated with 2 percent by weight quinine hydrochloride.

Diets were placed in 12 small, 6g containers, presented to the subjects in a light/dark alternating sequence on a revolving wheel that changed the position of the diets every 5 min (see Figure 6). Access to containers was by means of four, 5-cm diameter circular holes in the floor of a raised feeding platform in the subjects' cage.

4.6.3 Procedure. The present study was conducted in three separate replications. Initially 4, 19-day-old subjects were placed in a communal living cage (1 x 1 m) and the diet wheel was activated. For the first 5 days, pellets of Purina Laboratory Chow were provided until subjects learned to eat from the wheel (usually by Day 3). The only food available to subjects from Day 5 until the beginning of capsule discrimination training (at 42 days of age) was the light-coloured palatable or the dark-coloured unpalatable diets contained in the wheel. Diet containers were refilled at 10:00 a.m., 1:00 p.m. and 4:00 p.m.

A test of the diet discrimination was performed on Day 14 of the first replication by removing the dark adulterated diet and replacing it for 1 hr with dark unadulterated diet. During this period none of the dark-coloured diet but almost all of the light-coloured diet was consumed suggesting that subjects were employing visual cues to select diets.

Figure 6. The home cage and feeding apparatus in which subjects in Experiment 5-Study 2 were raised from weaning to maturity with a choice between light, palatable and dark, unpalatable diets. The rotating wheel presented subjects with a new choice of diets every 5 min.


DARK AND LIGHT DIET
NEST BOX
H_2O
FEEDING PLATFORM
MOTOR

4.6.4 Habituation. Subjects in the present study were pre-exposed for 7 days to the discrimination apparatus (Figure 1) exactly as described in section 3.2.4, after which a 22 hr deprivation schedule was initiated by inactivating and covering the home-cage wheel feeder. Access to powdered Purina Laboratory Chow was allowed for 2 hr between 1:00 p.m. and 3:00 p.m.

4.6.5 Pretraining. Subjects in the present study were pretrained to run out and eat capsules from food-bins as described in section 3.2.5.

4.6.6 Discrimination training. Subjects in the present study were trained for two consecutive days in an identical fashion to subjects in Experiment 3 (section 3.5.3) to select for ingestion light-coloured capsules containing unadulterated Purina Laboratory Chow and to avoid ingesting adulterated, dark-coloured capsules.

4.6.7 Poison training. Poison training was identical to that described in Experiment 3 except that a third group of subjects poisoned 180 min after ingesting novel 1/2 light, 1/2 dark capsules of unadulterated Purina Laboratory Chow was included. In the present experiment group designations are prefixed with the letter "O", which stands for ontogeny and are constituted as follows; group OD5PP ($\underline{n}$=8), group OD60PP ($\underline{n}$=8) and group OD180PP ($\underline{n}$=5)[5].

4.6.8 Testing. Testing was conducted exactly as described in section 3.2.8

4.7 Results and Discussion

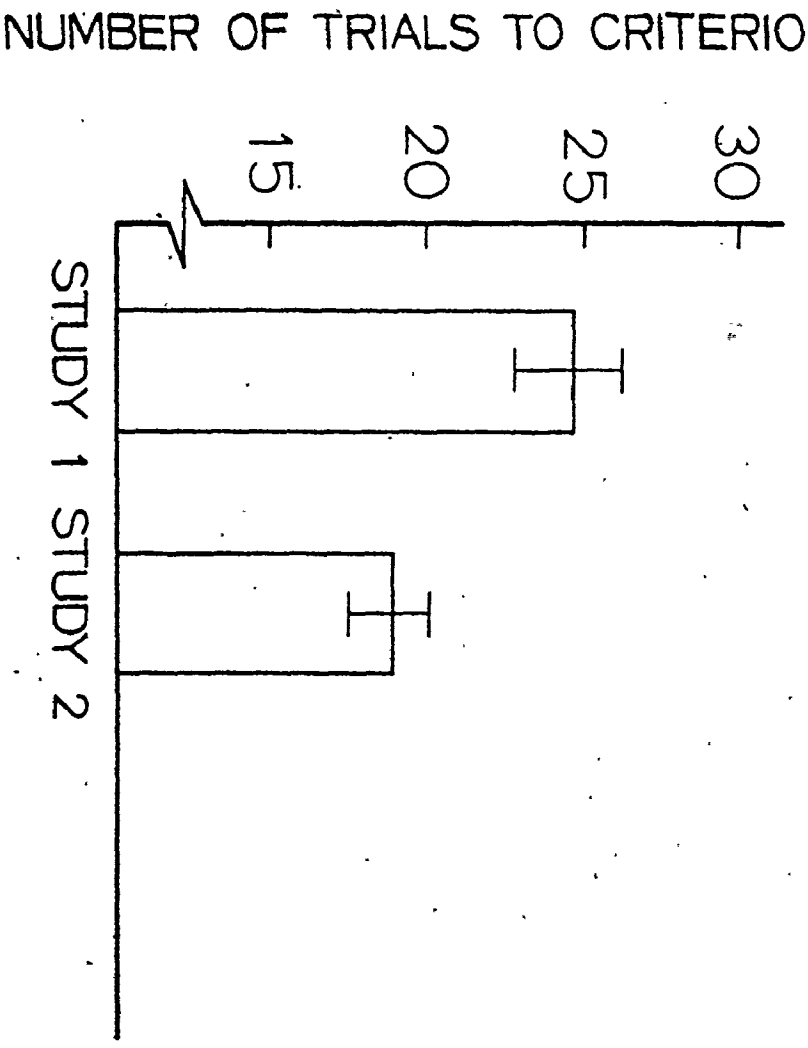
The main results of the present study are contained in panel B of Figure 5 which shows both group median and individual total

latencies to open 10 test capsules. Examination of the figure reveals no evidence of conditioning over long CS-US delays. Group OD5PP (n = 8) appears to simply replicate the results of previous D5PP groups. Because the two long-delay groups did not differ from each other (Kruskall-Wallace H = .49, $p > .1$) they were combined into a single group for comparison with the 5-min delay group. Subjects in group OD5PP (n = 8) were significantly different from subjects conditioned at long delays (n = 13) (Kruskall-Wallace H = 11.3, $p < .002$, two-tailed) on the total latency measure.

Examination of Figure 7, which presents the mean number of trials to criterion during the discrimination training phase of the experiment, reveals that subjects in the present study acquired the capsule discrimination significantly more rapidly than subjects in the previous study. (Kruskall-Wallace H = 8.997, $p < .02$; two-tailed). Taken together these results suggest that there was an effect of experience with varied diets during ontogeny on acquisition of visual discriminations but not on acquisition of long-delay visual aversions.

In conclusion, none of the manipulations performed in the present experiment produced exteroceptive-cue-aversions over long delays. Accounts that stress the importance of interference during the CS-US delay or accounts that place prime importance on the ontogenetic experience of the experimental organism do not appear to adequately account for the ability of flavours, but not visual cues, to become associated with toxicosis over long delays.

Figure 7. Mean number of trials to criterion during the acquisition of the visual capsule discrimination of Experiment 5-Study 1 (n = 24) and Study 2 (n = 21). Flags indicate plus and minus one standard error of the mean.


NUMBER OF TRIALS TO CRITERION
15
20
25
30
STUDY 1
STUDY 2

CHAPTER 5

EXPERIMENT 6

5.1 The Relation of the Stimulus to the Food Object

Testa and Ternes (1977) have suggested that only stimuli that are, or are made to be, attributes of a food object will be readily associable with toxicosis (see section 1.4.2). Similarly, Galef and Osborne (1979) suggested that novel flavours direct attention to other stimulus attributes of the ingesta. These accounts suggest that a decrement in aversion conditioning should be observed when target stimuli are not localized on the food object itself. For example, the more diffuse visual characteristics of food-bins should not be as easily associated with toxicosis as the localized visual attributes of food objects themselves.

The present experiment investigated the problem of the relationship between target stimuli and food objects. First, subjects were pretrained to attend to visual characteristics of either food-bins (Study 1) or feeding-chambers (Study 2) from which they received food capsules. Following pretraining, subjects were injected with lithium chloride either 5 or 60 min after having retrieved food from a novel chamber or bin to determine if subjects could associate such stimuli with toxicosis. Second, one would predict on the basis of the Testa and Ternes (1977) hypothesis that aversions to food capsules would be stronger than aversions to either food-bins or food-chambers. A comparison of aversion conditioning to food capsules (Experiment 3), food-bins (study 1, present Experiment) and food-chambers (Study 2,

present Experiment) was performed to assess whether the relative strength of conditioning in each situation conformed to the directional hypothesis provided by Testa and Ternes (1977).

5.2 Study 1 -Aversion Conditioning to Food-Bins

In the present study rats were pretrained using a simultaneous visual discrimination, to attend to the visual properties of food-bins from which they received visually non-distinctive capsules of Purina Laboratory Chow. They were subsequently made ill after exposure to a novel food-bin.

5.3 Method.

5.3.1 Subjects, apparatus, habituation and pretraining. Long-Evans rats (N = 16, 150-200g) were, habituated and pretrained as described in sections 2.2.4 and 2.2.5 above.

5.3.2 Discrimination training. All details of discrimination training are the same as those given in section 3.2.6 except that, whereas previously (e.g. Experiments 3, 4 and 5) capsule colour was correlated with capsule flavour, in the present study food-bin colour was correlated with capsule flavour and capsule colour remained constant. Subjects were allowed to choose between a black food-bin that contained white capsules filled with unadulterated Purina Laboratory Chow and a white food-bin that contained white capsules filled with Purina Chow adulterated 4 percent by weight with quinine hydrochloride. Black and white food-bins were located in the left and right positions in a pseudo-random sequence (footnote 1). Subjects were trained on 2 consecutive days to a criterion of 90 percent correct choices on any block of 10 trials. As before, a correct choice was

defined as ingesting the palatable capsule prior to contacting the unpalatable capsule.

5.3.3 Poisoning training. On the 2 poison training days, white capsules of unadulterated Purina Chow were presented in a novel, vertically black and white striped food-bin. Toxin administration occurred either 5 min (group FB5PP)[6] or 60 min (group FB60PP) after ingesting the second of two capsules that had been presented in the novel food-bin, once on the left and once on the right.

5.3.4 Testing. Testing consisted of presenting white capsules of regular Purina Laboratory Chow in the novel striped food-bin, one at a time for 10 trials. The same position sequence as in all previous tests was employed (footnote 1). The total latency for subjects to pick up and open 10 test capsules was recorded.

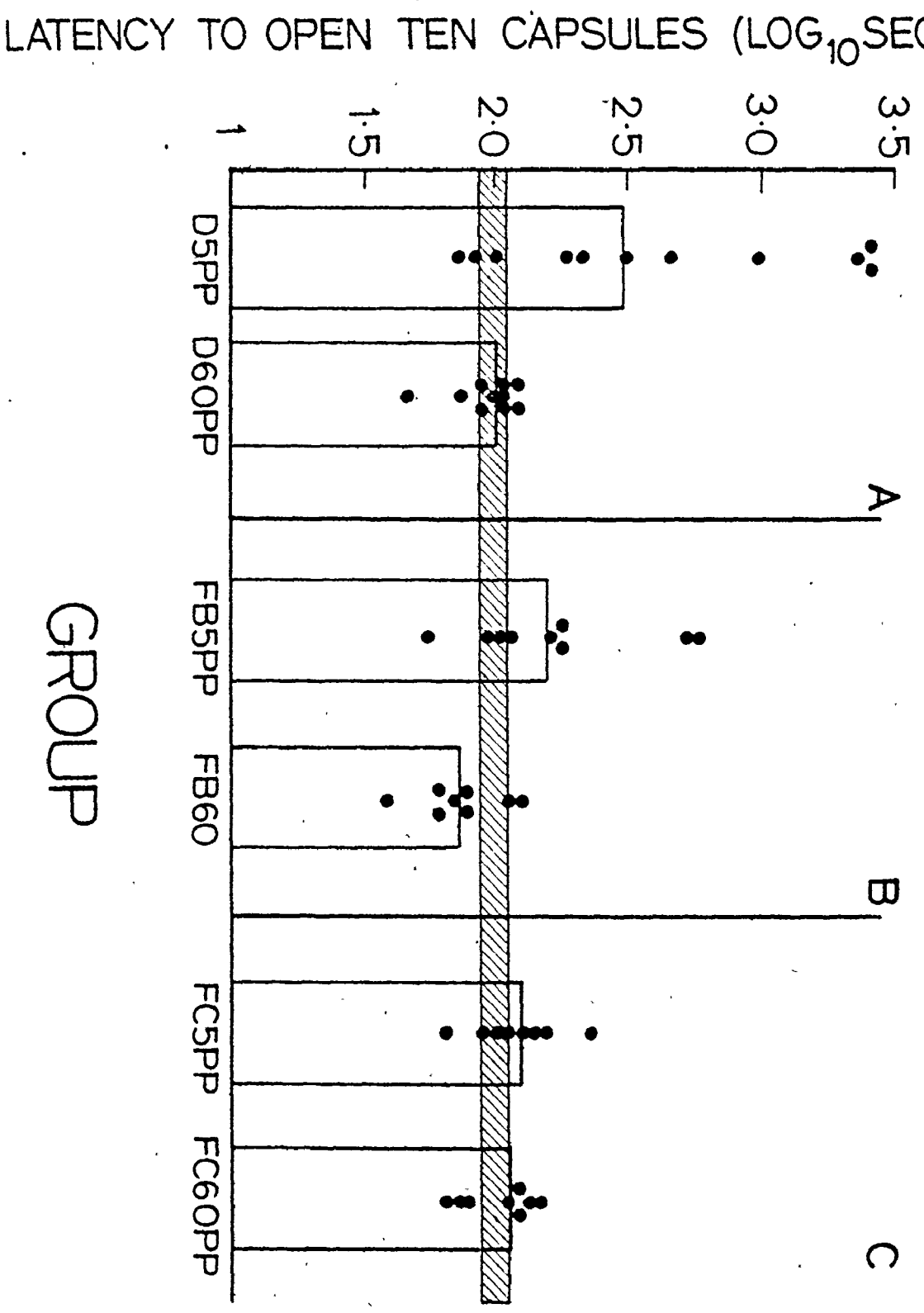
5.4 Results

Experimental and control subjects did not differ on the number of trials to criterion on the discrimination ($\overline{X}_{FB5PP} = 23.3$; $\overline{X}_{FB60PP} = 24.6$).

The main results of the present experiment are shown in Panel B of Figure 8 which presents both individual and group median total latencies to ingest 10 test capsules from the novel food-bin. Members of group FB5PP were significantly different from members of group FB60PP on this measure (Kruskall-Wallace $H = 5.78$; $p < .04$, two-tailed).

An examination of panels A and B of Figure 8 suggests that the size of the effect appears to be smaller in the present experiment, (Panel B) than in Experiment 3 (Panel A).

Figure 8. Total latency to open 10 test capsules ($\log_{10}$ sec) for individual subjects of Experiment 3 (Panel A) of Experiment 7 - Study 1 (Panel B) and Experiment 7 - Study 2 (Panel C). The histograms represent the median latency of each group. The horizontal bar is the baseline derived from Experiment 1.


LATENCY TO OPEN TEN CAPSULES (LOG10SEC)
1
1·5
2·0
2·5
3·0
3·5
D5PP
D60PP
FB5PP
FB60
FC5PP
FC60PP
A
B
C
GROUP

5.5 Study 2 - Aversion Conditioning to Food-Chambers

Study 1 indicated that subjects pretrained to attend to the visual characteristics of food-bins were able to form associations between novel food-bins and toxicosis. In the present study the major change from the previous study was that the food-bins were replaced by individual food-chambers which subjects could enter completely.

5.6 Method

This study is exactly analogous to the previous study except that large food-chambers were employed rather than food-bins.

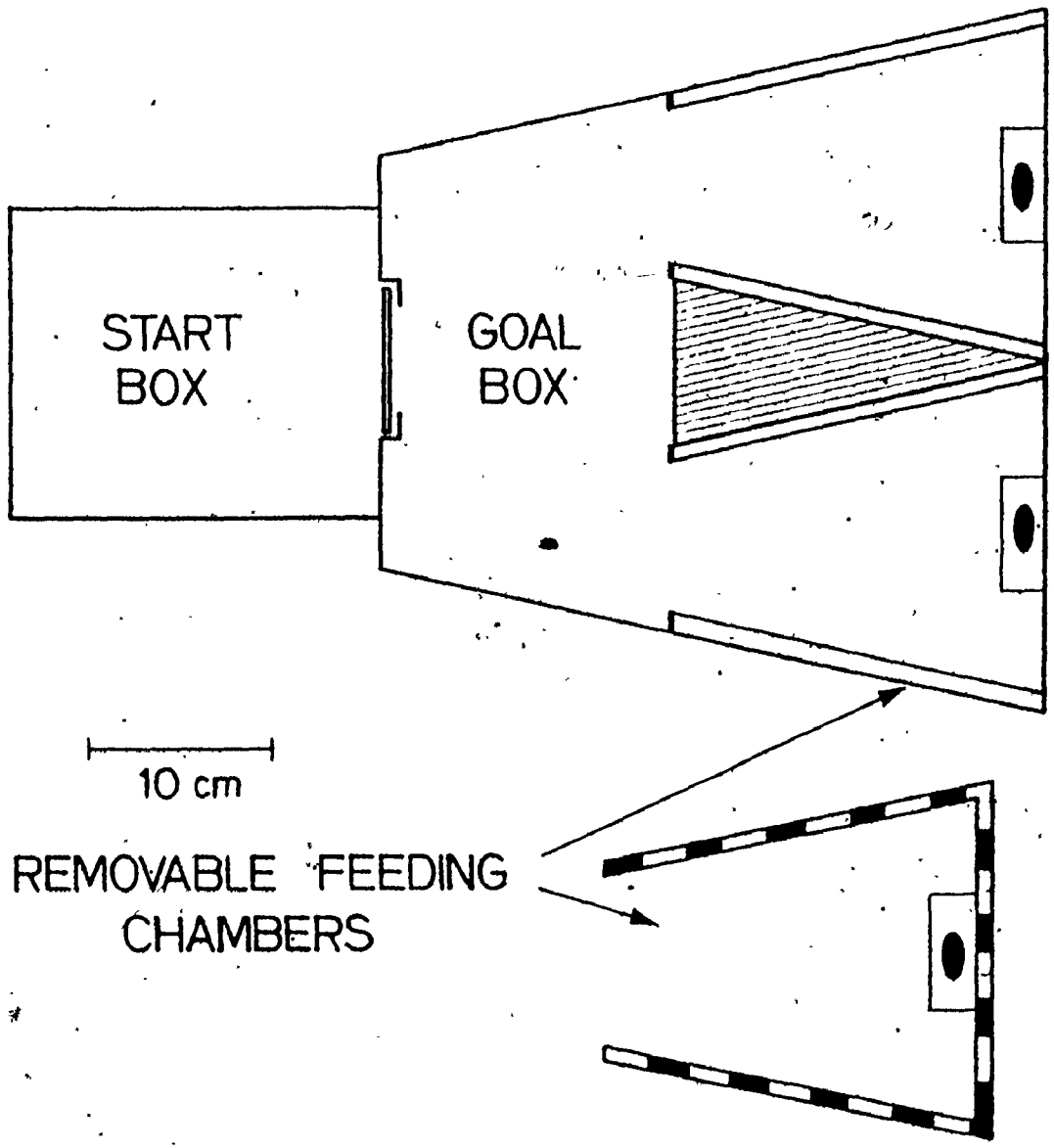
5.6.1 Subjects. Long-Evans rats (N = 16, 150-200g) served as subjects.

5.6.2. Apparatus. The experimental apparatus was rebuilt to accommodate two large wedge-shaped chambers (see Figure 9), which measured 12 cm wide at the rear, narrowed to a 6 cm opening at the front and were 14 cm high and 20 cm long. Located in the centre of the back wall of each chamber was a 5 cm by 2 cm ledge that allowed presentation of a single capsule. These food-chambers could be coloured by cardboard inserts, either white, black or striped black and white with vertical 2-cm diameter stripes.

5.6.3 Habituation. Subjects were habituated to the apparatus as before, by 7 daily group exploration sessions (see section 2.2).

5.6.4 Pretraining. On Day 1, subjects were pretrained to run out and retrieve unadulterated capsules from one of two identical chambers (both black or both white) for 10 trials. Capsule position was determined by the pseudo-random sequence given in footnote 1.

Figure 9. Experimental apparatus employed in Experiment 7 - Study 2. The food-chamber discrimination apparatus.


START
BOX
GOAL
BOX
10 cm
REMOVABLE FEEDING
CHAMBERS

5.6.5 Discrimination training. On each of Days 2 and 3 subjects were trained to a 90 percent correct criterion to enter one visually distinctive chamber to obtain capsules of Purina Laboratory Chow and to avoid entering the other visually distinctive chamber containing capsules of Purina Laboratory Chow adulterated 4 percent by weight with quinine hydrochloride. A correct trial was defined as one in which the subject ate the unadulterated capsule without entering (both front paws over) the food-chamber containing the quinine adulterated capsule. Capsule colour remained constant in any given replication (either white or scarlet) and only food-chamber colour varied and was correlated with capsule flavour. Food-chamber colour was counterbalanced between replications to control for subject preferences for black or white chambers.

After each trial the floor and walls of the entire goal area were wiped clean with 95% ethanol to eliminate odour trails and traces of food.

All other features of the food-chamber discrimination were identical to all previous discrimination procedures as described in sections 3.2.6 and 3.5 (i.e. black and white food-chambers were located an equal number of times in the left and right positions, subjects were allowed 60 sec to ingest an open capsule and a 30 sec intertrial interval was employed).

5.6.6 Poison Training. Poison training in the present study was exactly analogous to poison training in Study 1 above except that a novel, black and white striped food-chamber was employed instead of a novel black and white striped food-bin. Half the subjects were

poisoned 5 min after eating unadulterated capsules in the novel food-chamber (Group FC5PP)[6] and half were poisoned with a delay of 60 min (Group FC60PP).

5.6.7 Testing. Subjects were tested, as before, for an aversion to the novel visual stimulation provided by the striped food-chamber for 10 consecutive trials (section 3.2.8).

5.7 Results and Discussion

Group FC5PP did not differ from group FC60PP on number of trials to discrimination criterion (X_{FC5PP} = 15.6; X_{FC60PP} = 18.8; Kruskall-Wallace, $H < 1$, N.S.). Nor did the colour of the food chamber affect the trials to criterion measure (white, positive goal box, X = 17.5; black positive goal box, X = 16.9, Kruskall-Wallace, $H < 1$, N.S.)

The main results of the present experiment are shown in Panel C of Figure 8 which presents individual and group median total latencies to ingest 10 test capsules. Members of group FC5PP were not significantly different from members of group FC60PP. (Kruskall-Wallace Test, $H < 1$, N.S.).

Panel A of Figure 8 presents individual and group median total latencies to ingest 10 test capsules for subjects in Experiment 3. These subjects were treated identically to subjects in the present two studies except that the discrimination and conditioning stimuli were the visual characteristics of the food object rather than the visual characteristics of food-bins or food-chambers.

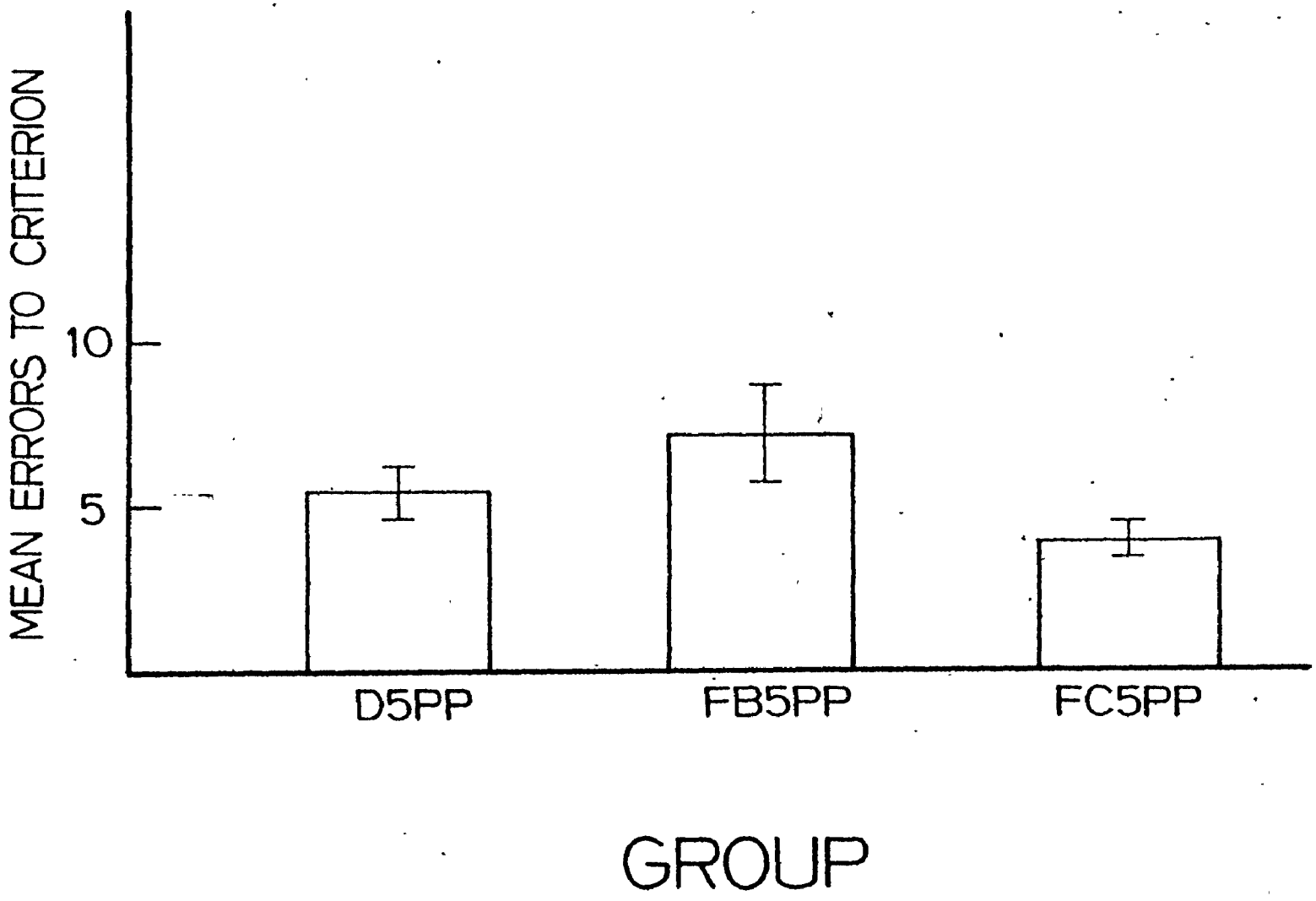
In addition to the within experiment significant differences between 5-min experimental groups and their 60-min controls (Experiment 3 and Study 1 - Experiment 5) a comparison of the latency scores of the

three different 5-min delay groups revealed that they were significantly different from each other (Extention of the Median Test, $\underline{X}^2 = 6.884$, $\underline{p} = .035$, one-tailed). Individual comparisons indicated that subjects poisoned 5 min after experiencing visually distinctive capsules took longer to ingest capsules on the test than subjects poisoned 5 min after experiencing visually distinctive food-chambers ($\underline{X}^2 = 5.84$, $\underline{p} < .02$; one-tailed), or subjects poisoned 5 min after experiencing visually distinctive food-bins ($\underline{X}^2 = 5.05$, $\underline{p} = .027$, one-tailed).

Taken together these results suggest that there are limits to the type of visual stimuli that rats can associate with toxicosis after being pretrained to attend to such stimuli. While it is unarguably the case that the conditioning stimuli employed in these three situations vary along many different dimensions, the relative strength of conditioning in each situation suggests that stimuli localized on the food object, for example capsule colour, are more easily associated with toxicosis than are stimuli not localized on the food object. This gradient of associability with toxicosis of stimuli in terms of their relation to the ingesta is consistent with both the Testa and Ternes (1977) and Galef and Osborne (1979) suggestion of the importance of stimulus attributes of food objects. It seems that rats are more likely to treat certain stimuli as attributes of food objects and these stimuli are more easily associated with toxicosis.

Figure 10 presents the errors to criterion made by subjects in the 5-min delay groups during discrimination training. Analysis indicates that the groups were not significantly different from each

Figure 10. Mean number of errors to criterion during the acquisition of the three different types of visual discrimination: Represented are a capsule discrimination (Experiment 3) the food-bin discrimination (Experiment 7 - Study 1) and the food-chamber discrimination (Experiment 7 - Study 2). Flags indicate plus and minus one standard error of the mean.


MEAN ERRORS TO CRITERION
10
5
D5PP
FB5PP
FC5PP
GROUP

other on this measure (Extension of the Median Test, $\underline{X}^2 < 1$, n.s.). One cannot argue that the failure to produce robust illness-based aversions to food-chambers or to food-bins is a function of the discriminability of the stimuli because, if anything, subjects in the food-chamber discrimination made less errors than subjects in the other two groups. This suggests that the stimuli employed in all three studies were discriminable to the subjects but that discriminability alone does not insure that a stimulus will be available for association with toxicosis.

CHAPTER 6

SUMMARY AND GENERAL DISCUSSION

6.1. The Flavour Facilitation Effect - Chapter 2

The results of Experiment 1 demonstrated that rats can form visual-cue-toxicosis associations with as few as two pairings of visual cue and reinforcer. Contrary to expectations based on arguments that flavours or ingestive experiences interfere with conditioning to exteroceptive cues (Best et al., 1977; Shettleworth, 1972), the presence of a novel flavour facilitated conditioning to the exteroceptive cue.

This facilitatory effect of flavours on exteroceptive-cue-aversion conditioning is also unexpected given current models of classical conditioning (Mackintosh, 1975; Rescorla and Wagner, 1972) which suggest that the more salient member of a stimulus compound should overshadow the less salient member in association formation. The reverse of overshadowing was obtained. While both the Mackintosh and the Rescorla and Wagner models suggest that overshadowing is a multiple-trial process, recent evidence suggests that overshadowing can be obtained in only one trial (Revusky, 1971). Thus, it is unlikely that the minimal number of pairings of the compound stimulus with reinforcement was responsible for the failure to obtain overshadowing in this experiment.

6.2 The Attentional Mechanism - Chapter 3

The results of Experiments 2, 3, and 4 provide evidence of a mechanism by which flavours may facilitate conditioning to

exteroceptive cues. Aversions to visual cues can be produced in the absence of flavour mediation if subjects are trained to attend to the visual characteristics of their ingesta prior to experiencing visual-cue-toxicosis pairings. Thus, the results of the experiments reported in Chapter 3 are consistent with the hypothesis that novel flavours direct attention to other stimulus characteristics of ingesta and that this focussing of attention allows for association of visual stimuli with the reinforcer.

Comparison of the results of Experiments 1 and 3 indicate that aversions to visual-cues produced by pretraining attention to them are not as robust as aversions produced by compounding visual cues with novel flavours prior to toxicosis conditioning. There are a number of possible explanations for this difference in the extent of the facilitation effect. In particular, lengthening the interval between the attentional manipulation and poison training might result in some animals not attending to visual cues at the time of aversion conditioning. For example, in Experiment 1 group F5PP experienced the novel flavour 5 min prior to lithium administration and strong aversions were produced. If bitter flavours direct attention to the other stimulus attributes of ingesta, then it is probable that most of the subjects in this condition would be attending to the appropriate stimuli at the time of conditioning. In Experiments 2, 3, and 4, there was a 24-hr delay between discrimination training and poison training and this delay may have made it more difficult to obtain aversions to visual cues. If discrimination training and poison training were carried out in close temporal proximity to each other, then stronger

aversions to visual cues might be obtained. Unfortunately, carrying out both procedures in close temporal proximity to each other might result in some lingering residue of quinine taste mediating aversion formation. It would then be impossible to decide between taste-indexing and attentional interpretations.

6.3 Long-Delay Visual-Cue Aversion - Chapter 4

The results of Experiment 5 suggest that, under the present set of procedures, visual-cue-aversions can only be formed over short, 5-min delays between presentation of the visual-cue and administration of the toxic agent. While it was demonstrated (Study 2) that extended ontogenetic experience employing visual cues to select food facilitated visual discrimination acquisition, no comparable facilitation of long-delay visual-cue-aversion acquisition was observed. In both Chapters 3 and 4, visual-cue-aversions were obtained only when a 5-min delay interposed between stimulus presentation and reinforcer administration. This delay is considerably greater than that tolerated by rats in light-shock conditioning preparations (Kimble, 1961) but is not of the same order of magnitude as delays commonly employed in flavour-toxicosis conditioning preparations (e.g. Smith and Roll, 1967).

The results of Experiment 5 suggest that neither concurrent interference (Revusky, 1977) nor ontogenetic experience (Mackintosh, 1973) can account for the ability of flavour-toxicosis, but not visual-cue-toxicosis, associations to be formed over long delays.

6.4 The Relation of the Stimulus to the Food Object - Chapter 5

The results of Experiment 6 suggest that aversion conditioning

to non-ingesta related visual cues is not as strong as aversion conditioning to ingesta related visual cues. Aversion conditioning to visually distinctive food capsules was stronger than was aversion conditioning to visually distinctive food-bins (Study 1), and there was no evidence at all of aversion conditioning to visually distinctive food-chambers (Study 2). It cannot be argued that this reduction in the strength of aversion conditioning in Studies 1 and 2 is due to problems with discrimination pretraining because subjects rapidly learned to discriminate between distinctive food-bins and between distinctive food-chambers.

The results of Experiment 6 suggest that not all exteroceptive cues are equally associable with toxicosis. Exteroceptive cues exhibited a graded propensity to be associated with toxicosis and this propensity was affected by the relationship between the visual stimulus and the food object. Apparently, rats are more likely to treat certain stimuli as attributes of food objects and these stimuli are more readily associable with toxicosis.

Adaptive-evolutionary accounts that dichotomize stimuli into those that are and those that are not associable with toxicosis (section 1.3.1) or accounts that suggest that all exteroceptive cues are contraprepared to be associated with toxicosis (section 1.3.4) cannot account for the present finding of graded exteroceptive-cue-toxicosis conditioning.

It appears that rats exhibit an intermodal-hierarchy of responsiveness to the stimuli experienced prior to toxicosis. Flavours are favoured over odours which, in turn, are more associable than

visual stimuli with illness (Kalat and Rozin, 1970). However, within each stimulus modality further orderings may be observed that correspond to the relation of the stimulus to the food object.

The effect of pretraining attention to visual cues prior to visual-cue-aversion conditioning may be to elevate the position of visual stimuli in the modality hierarchy such that visual stimuli which would not normally enter into an association with toxicosis (group NF5PP of Experiment 1 and group Y5PP of Experiment 4) become effective signals for gastrointestinal distress as a result of visual discrimination pretraining (groups D5PP of Experiments 3, 4 and 5).

6.5 Conclusions

The results of recent experiments by Durlach and Rescorla (1980) suggest that associations between stimulus elements of a compound CS itself, may provide a mechanism by which flavours exert their paradoxical facilitatory effect on conditioning to exteroceptive cues. Durlach and Rescorla demonstrated that associations between the odour and flavour elements of a compound stimulus were produced by pre-exposure to the compound and that aversion to the odour component was enhanced and maintained by a learned aversion to the flavour component. While the mechanism of within-compound association described by Durlach and Rescorla might operate in situations in which odours and flavours are experienced simultaneously, prior to the onset of illness, no such within-compound associations could be produced in the experiments reported in Chapters 3, 4 and 5 above. Only a single stimulus, the visual-cue, was presented to the subjects prior to the onset of reinforcement. In this situation it seems likely that an

association between the CS and the US rather than between CS components accounts for the expressed aversion. The within-compound associative mechanism proposed by Durlach and Rescorla (1980) may operate in addition to the attentional mechanism in situations where more than one cue is presented to the animal prior to toxicosis conditioning.

Recently, Palmereno, Rusiniak and Garcia (1980) performed an odour-flavor potentiation experiment which they interpreted in terms of a special interaction between the two chemical senses of olfaction and gustation. The potentiation of conditioning to visual cues by flavours in Experiment 1 and by discrimination training in Experiments 3, 4, 5 and 6 is not amenable to interpretation in terms of a chemical system interaction. However, the effect obtained by Palmereno et al., (1980) appears to be different from that obtained in the present experiments. Pomereno et al., were able to produce evidence of significant aversions to odours over delays as long as 2 hr, while visual-cue-toxicosis associations do not appear to be able to bridge delays of more than a few minutes. It is not clear whether this difference in delay tolerance reflects the operation of different mechanisms underlying odour-flavour and visual-cue-flavour potentiation or whether the two stimulus modalities reach different asymptotes of potentiated conditioning because they start out at different baselines. It is well known that, in rats, aversion conditioning to odours is intermediate in strength to aversion conditioning to flavours or visual cues (Kalat and Rozin, 1970).

The results of the present series of experiments suggest that, although rats may have pre-existing biases to associate certain cues

with certain consequences such biases are not immutable. For rats, flavours appear to be favoured over other stimuli as cues for illness-aversion learning, but simple peripheral, attentional manipulations yield significant conditioning to other stimulus attributes of ingesta. In accord with Mackintosh's (1973b) view, we suggest that rats and possibly other omnivore-generalists are able to learn about a variety of relations between stimuli and reinforcers, stimuli and other stimuli, and stimuli and responses especially when such stimuli have been employed successfully in previous learning episodes.

The experiments of this thesis have delineated further the conditions under which certain stimuli may be associated with reinforcers. The associability of a stimulus varies as a function of at least four factors. First, from stimulus selectivity demonstrations in taste-aversion learning the salience of a stimulus is known to vary as a function of the type of reinforcer. Tastes presented alone are more rapidly associated with illness then they are with shock. Second, Galef and Osborne's (1978) work and the results of the present series of experiments both suggest that the salience of a stimulus fluctuates not only as a function of the reinforcer but also as a function of other stimuli present during conditioning. Flavours facilitate aversion conditioning to visual cues. Third, it appears that in situations employing delayed illness as a reinforcer, stimulus attributes of the food object are more readily associated with the reinforcer than stimuli that are not attributes of the food object. Lithium paired visually distinctive capsules are avoided more than

lithium paired visually distinctive food-chambers. Finally, the animal's past experience with employing various types of stimuli in feeding situations may serve to facilitate aversion conditioning to those stimuli. Visual discrimination pretraining facilitates aversion conditioning to visual cues.

Other classical conditioning phenomena, for example, overshadowing, sensory preconditioning and higher order conditioning are independent of reinforcer modality and can be produced when either appetitive or aversive reinforcers are employed. To date, the flavour facilitation effect has only been observed with respect to toxicosis. It is hoped that the flavour facilitation effect will be observed in appetitive learning situations. In the event that such demonstrations are not forthcoming flavour potentiation would remain another anomaly peculiar to taste-aversion learning. If demonstrations of appetitive flavour facilitation are provided in the future then the present investigations will have set limits upon the generality of overshadowing and demonstrated the importance of stimulus sequencing on attention in classical conditioning situations.

References

Archer, T., Sjoden, P., Nilsson, L., and Carter, N. Role of exteroceptive background context in taste-aversion conditioning and extinction. Animal Learning and Behavior, 1978, 7, 17-22.

Batson, J.D., and Best, P.J. Drug-preexposure effects in flavour-aversion learning: Associative interference by conditioned environmental stimuli. Journal of Experimental Psychology: Animal Behaviour Processes, 1979, 5, 273-284.

Best, M.R. Conditioned and latent inhibition in taste-aversion learning: Clarifying the role of learned safety. Journal of Experimental Psychology: Animal Behavior Processes, 1975, 1, 97-113.

Best, P.J., Best, M.R., and Henggeler, S. The contribution of environmental non-ingestive cues in conditioning with aversive internal consequences. In L.M. Barker, M.R. Best, M. Domjan, (Eds.), Learning Mechanisms in Food Selection. Baylor University Press, 1977, 371-394.

Best, P.J., Best, M.R., and Mickley, G.A. Conditioned aversion to distinct environmental stimuli resulting from gastrointestinal distress. Journal of Comparative and Physiological Psychology, 1973, 85, 250-257.

Bitterman, M.E. Reply to Garcia, Hankins, and Rusiniak. Science, 1976, 192, 266-267.

Bradley, R.M., and Mistretta, C.M. Intravascular taste in rats as demonstrated by a conditioned aversion to sodium saccharin. Journal of Comparative and Physiological Psychology, 1971, 75, 186-189.

Braveman, N.S. Relative salience of gustatory and visual cues in the formation of poison based food aversions by guinea-pigs (Cavia porcellus). Behavioral Biology, 1975, 14, 189-199.

Brett, L., Hankins, K., and Garcia, J. Prey-lithium aversions. III: Buteo hawks. Behavioral Biology, 1976, 17, 87-98.

Capretta, P.J. An experimental modification of food preference in chickens. Journal of Comparative and Physiological Psychology, 1961, 54, 238-242.

Domjan, M.E. Ingestional aversion learning: Unique and General processes. To appear in J.S. Rosenblatt, R.A. Hinde, C.Beer, and M. Busnel (Eds.), Advances in the study of behavior. Vol. 11. New York: Academic Press.

Domjan, M. Role of ingestion in odor-toxicosis learning in the rat. Journal of Comparative and Physiological Psychology, 1973, 84, 507-521.

Domjan, M.E. Role of Ingestion in Aversion Learning. Ph.D. Thesis: McMaster University, 1973.

Domjan, M., and Gillan, D.G. Aftereffects of lithium conditioned stimuli on consummatory behavior. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3, 322-334.

Domjan, M., and Wilson, N.E. Specificity of cue to consequence in aversion learning in the rat. Psychonomic Science, 1972, 2[illegible]

Durlach, P., and Rescorla, R.E. Potentiation rather than overshadowing in flavour-aversion learning: An analysis in terms of within-compound associations. Journal of Experimental Psychology: Animal Behaviour Processes, 1980, 6, 155-174.

Estes, W.K. The statistical approach to learning theory. In S. Koch (Ed.), Psychology: A Study of Science. New York: McGraw-Hill, 1959.

Galef, B.G., and Osborne, B. Novel taste-facilitation of the association of visual cues with toxicosis in rats. Journal of Comparative and Physiological Psychology, 1978, 92, 907-911.

Garcia, J., and Ervin, R.R. A neuropsychological approach to the appropriateness of signals and specificity of reinforcers. Communications in Behavioural Biology, 1968, 1, part A, 389-415.

Garcia, J., Ervin, F.R., and Koelling, R.A. Learning with prolonged delay of reinforcement. Psychonomic Science, 1966, 5, 121-122.

Garcia, J., Green, K.F., and McGowan, B.K. X-ray as an olfactory stimulus. In C.F. Pfaffman (Ed.), Olfaction and Taste III. New York, Rockefeller University Press, 1969, 299-309.

Garcia, J., and Hankins, W.G. On the origin of food aversion paradigms. In L.M. Barker, M.R. Best, and M. Domjan, (Eds.), Learning Mechanisms in Food Selection. Baylor University Press, 1977, 3-22.

Garcia, J., Kimeldorft, D.J., and Hunt, E.L. Spatial avoidance in the rat as a result of exposure to ionizing radiation. British Journal of Radiology, 1957, 30, 318-321.

Garcia, J., and Koelling, R.A. Relation of cue to consequence in avoidance learning. Psychonomic Science, 1966, 4, 123.

Gellerman, L.W. Chance orders of alternating stimuli in visual discrimination experiments. Journal of Genetic Psychology, 1933, 42, 206-208.

Gemberling, G.A., Domjan, M., and Amsel, A. Aversion learning in 5-day-old rats: Taste-toxicosis and texture-shock associations. Journal of Comparative and Physiological Psychology, 1980, submitted.

Gillan, D.J. Learned suppression of ingestion: Role of discriminative stimuli ingestive responses and aversive tastes. Journal of Experimental Psychology: Animal Behaviour Processes, 1979, 3, 258-272.

Grill, H.J., and Norgren, R. The taste reactivity test I: Mimetic responses to gustatory stimuli in neurologically normal rats. Brain Research, 1978, 143, 263-279.

Grote, F.W., Jr., and Brown, R.T. Conditioned taste-aversions: Two-stimulus tests are more sensitive than one-stimulus tests. Behavior Research Methods and Instrumentation, 1971, 3, 311-312.

Henggeler, S. Conditioned aversions to external stimuli resulting from delayed malaise. Paper presented at the proceedings of the Forty-fifth annual meeting of the Eastern Psychological Association, Philadelphia, 1974.

Holland, P.C. Conditioned stimulus as a determiner of the form of Pavlovian conditioned response. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3, 77-104.

Holland, P.C., and Rescorla, R.A. Second-order conditioning with food unconditioned stimulus. Journal of Experimental Psychology: Animal Behavior Processes, 1975, 88, 459-467.

Kalat, J.W., and Rozin, P. "Salience": A factor which can override temporal contiguity in taste-aversion learning. Journal of Comparative and Physiological Psychology, 1970, 71, 192-197.

Kamin, L.J. Predictability, surprise, attention and conditioning. In B.A. Campbell and R.M. Church (Eds.) Punishment and Aversive Behavior. New York: Appleton-Century-Crofts, 1969.

Kimble, G.A. Hilgard and Marquis' Conditioning and Learning. New York: Appleton-Century-Crofts, 1961.

Krane, R.V., and Wagner, A.R. Taste-aversion learning with a delayed-shock US: Implications for the "generality of the laws of learning". Journal of Comparative and Physiological Psychology, 1975, 88, 882-889.

Lubow, R.E. Latent inhibition. Psychological Bulletin, 1973, 79, 398-407.

Mackintosh, N.J. Stimulus selection: Learning to ignore stimuli that predict no change in reinforcement. In R.A. Hinde and J. Stevenson-Hinde (Eds.), Constraints on Learning. New York: Academic Press, 1973.

Mackintosh, N.J. The Psychology of Animal Learning. New York: Academic Press, 1973(b).

Mackintosh, N.J. A theory of attention: Variations in the associability of stimuli with reinforcement. Psychological Review, 1975, 82, 276-298.

Martin, G.P. and Bellingham, W.P. Learning of visual food aversions by chickens (Gallus gallus) over long delays. Behavioral and Neural Biology, 1979, 25, 58-68.

Martin, J.C., and Ellinwood, E.H., Jr. Conditioned aversion in spatial paradigms following methamphetamine injections. Psychopharmacologia, 1974, 36, 323-325.

Maclaurin, W.A., and Scarborough, R.B. Extension of the interstimulus interval in saccharin avoidance conditioning. Radiation Research, 1963, 20, 317-324.

Morrison, G., and Collyer, R. Taste-mediated conditioned aversion to an exteroceptive stimulus following LiCl poisoning. Journal of Comparative and Physiological Psychology, 1974, 86, 51-55.

Nachman, M., Rauchenburger, J., and Ashe, J.H. Studies of learned aversions using non-gustatory stimuli. In L.M. Barker, M.R. Best and M. Domjan (Eds.), Learning Mechanisms in Food Selection. Baylor University Press, Waco: 1977.

Pavlov, I.P. Conditioned Reflexes. Oxford University Press: Oxford, 1927.

Palmereno, C.C. Rusiniak, K.W., and Garcia, J. Flavor-illness aversions: The peculiar roles of odor and taste in memory for poison. Science, 1980, 208, 753-755.

Rescorla, R.A., and Wagner, A.R. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and non-reinforcement. In A.H. Black and W.F. Prokasy (Eds.), Classical Conditioning II: Current Research and Theory. New York: Appleton-Century-Crofts, 1972.

Rescorla, R.A., and Furrow, D.R. Stimulus similarity as a determinant of Pavlovian conditioning. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3, 203-215.

Rescorla, R.A., and Cunningham, C.L. Spatial contiguity facilitates Pavlovian second order conditioning. Journal of Experimental Psychology: Animal Behavior Processes, 1979, 5, 152-161.

Revusky, S.H. The concurrent interference approach to delay learning. In L.M. Barker, M.R. Best, and M. Domjan, (Eds.), Learning Mechanisms in Food Selection. Baylor University Press, 1977, 229-254.

Revusky, S., and Bedarf, E.W. Association of illness with ingestion of novel foods. Science, 1967, 155, 219-220.

Revusky, S.H. The role of interference in association over a delay. In V. Honig and P.H.R. James (Eds.), Animal Memory, New York: Academic Press, 1971.

Rozin, P. Central or peripheral mediation of learning with long CS-US intervals in the feeding system. Journal of Comparative and Physiological Psychology, 1969, 67, 421-429.

Rozin, P., and Kalat, Specific hungers and poison avoidance as adaptive specializations of learning. Psychological Review, 1971, 78, 459-486.

Rozin, P., and Ree, P. Long extension of effective CS-US interval by anesthesia between CS and US. Journal of Comparative and Physiological Psychology, 1972, 80, 43-48.

Rudy, J.W., Iwens, J., and Best, P.J. Pairing novel exteroceptive cues and illness reduces illness induced taste aversions. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3, 14-25.

Rudy, J., Rosenberg, L., and Sandell, J. Disruption of the taste familiarity effect by novel exteroceptive stimulation. Journal of Experimental Psychology: Animal Behavior Processes, 1977, 3, 26-36.

Rusiniak, K.W., Hankins, W.G., Garcia, J., and Brett, L.P. Flavor illness aversions: Potentiation of odor by taste in rats. Behavioral Biology, 1979, in press.

Selgiman, M.E.P. On the generality of the laws of learning. Psychological Review, 1970, 77, 400-418.

Shettleworth, S.J. Stimulus relevance in the control of drinking and conditioned fear responses in domestic chicks (Gallus gallus). Journal of Comparative and Physiological Psychology, 1972, 80, 175-198.

Siegel, S. Non-parametric statistics for the behavioral sciences. New York: McGraw-Hill, 1956.

Siegel, S. Flavour preexposure and 'learned safety'. Journal of Comparative and Physiological Psychology, 1974, 87, 1073-1082.

Skinner, B.F. The Behavior of Organisms. New York: Appleton-Century-Crofts,

Smith, J.C., and Roll, D.L. Trace conditioning with X-rays as an aversive stimulus. Psychonomic Science, 1967, 9, 11-12.

Sokolov, E.N. Perception and the conditioned reflex. Oxford: Pergamon Press, 1963.

Thorndike, E.L. Fundamentals of Learning. New York: Teachers College, 1932.

Testa, T.J., and Ternes, J.W. Specificity of conditioning mechanisms in the modification of food preferences. In L.M. Barker, M.R. Best, and M. Domjan, (Eds.), Learning Mechanisms in Food Selection. Baylor University Press, 1977, 229-254.

Wilcoxon, F., and Wilkox, R.A. Some Rapid and Approximate Statistical Procedures. Pearl River: Lederle Laboratories, 1964.

Wilcoxon, H.C. Long delay learning of ingestive aversions in quail. In L.M. Barker, M.R. Best, and M. Domjan, (Eds.), Learning Mechanisms in Food Selection. Baylor University Press, 1977, 419-454.

Wilner, J.A. Blocking of a taste aversion by prior pairings of exteroceptive stimuli with illness. Learning and Motivation, 1978, 9, 125-140.

Footnotes

1. The following series was obtained from an article by L.W. Gellerman (1933). This sequence was constructed to insure that there were an equal number of lefts and rights, that there were no more than three lefts or rights in a row and to insure that either a single or double alternation strategy would obtain a chance score of 50%. The sequence is as follows:

L R R L R R L L L R

When employing more than ten trials, as in discrimination training where twenty trials were commonly employed, the above series was repeated a second time.

2. In the group designations of Experiment 1 the appearance of an "F" indicates that poison training capsules contained Purina Laboratory Chow distinctively flavoured with 4 percent by weight quinine hydrochloride and NF indicates that poison training capsules contained familiar flavoured Purina Laboratory Chow. The numbers 5 or 60, refer to the delay interval that subjects encountered between presentation of the last training capsule on any poison training day and toxicosis administration which was either of 5 min or 60 min duration. All subjects spent the initial 5 min of the delay interval in the start-box and the remaining 55 min (for 60 min delay subjects) were spent in the subject's home-cage. Each letter "P" indicates a single intraperitoneal injection of a .12 molar solution of lithium chloride (a toxin) in an amount calculated to 2 percent of the subject's own body weight.

3. In the group designations of Experiment 2 and all subsequent experiments the letter "D" indicates that subjects were pretrained to attend to the visual appearance of food capsules by discrimination procedures. As described in Footnote 2 above the numbers refer to the CS-US delay interval and each letter "P" indicates a poison training experience.

4. In the group designations of Experiment 4 the appearance of a small "p" indicates that the subjects were poisoned after ingesting unencapsulated pellets of Purina Laboratory Chow. The appearance of the letter "Y" indicates that the subjects were yoked to subjects in group D5PP in terms of their trial by trial experience with palatable and unpalatable food capsules. All other symbols have the meanings described in footnotes 2 and 3 above.

5. In the group designations of Experiment 5, "OT" indicates that subjects were overtrained on the visual discrimination and "LO" indicates that subjects spent the CS-US delay in total darkness. All other symbols have the meanings described in footnotes 2 and 3 above.

6. In the group designations of Experiment 6, "FB" indicates that the subjects were pretrained to attend to the visual appearance of food-bins while "FC" indicates that subjects were pretrained to attend to the visual appearance of feeding-chambers. All other symbols have the meanings described in footnotes 2 and 3 above.