The Determinants of Exploration and Neophobia

DAVID T. COREY

Environmental Medicine Unit, St. Joseph's Hospital, and Department of Psychology
McMaster University, Hamilton, Ontario, Canada

(Received 16 August 1978)

COREY, D. T. The determinants of exploration and neophobia. NEUROSCI. BIOBEHAV. REV. 2(4) 235--253, 1978. — The literature dealing with the factors that determine approach and avoidance responses to novelty is reviewed and evaluated and suggestions for further clarifying research are incorporated. Only those studies that measure exploration in a choice-type task are included because of the interpretive difficulties associated with forced-exploration tasks (e.g., the open-field). The determinants that are reviewed include changes in stimulus novelty and changes in responsiveness independent of stimulus novelty. The latter factors include physiological variables such as lesions and drugs. The juxtaposition of some recent data with older findings has helped to reveal similarities that may reflect the presence of similar underlying mechanisms. The status of the concepts of optimal arousal level and adaptation level is briefly discussed and it is concluded that they are incapable of encompassing the range of data available. In addition, some methodological issues are considered and it is concluded that concentration on the results of choice-type tasks has helped resolve some of the inconsistencies and ambiguities that had arisen through the use of forced-exploration tasks. The necessary requirements for the demonstration of flavor neophobia are also discussed.

Exploration Neophobia Stimulus novelty Neotic behavior

AS THE INTRODUCTION to a paper in 1950, Berlyne [11] observed that psychology had had "surprisingly little to say about stimuli which influence behavior simply because they are new". Almost 30 years later, one could hardly voice the same complaint. The intervening years have seen an intensive examination of a wide range of novelty-related responses in a number of species. The significant role of stimulus novelty has been persuasively demonstrated in a number of areas such as learning [118,149], social interactions [78,120], and dietary selection [6]. The purpose of this paper is to review a selected portion of the stimulus novelty literature that has accumulated since 1950 in order to reveal some trends and commonalities encountered in different species and across a range of stimulus modalities. Some theoretical considerations will also be discussed.

Most earlier reviews of novelty-related behavior (e.g., [72]) primarily accessed data dealing with approach responses but, in recent years, there has been an increasing amount of research on novelty-avoidance responses. Flavor neophobia, for example, has received increased attention because of the role that it plays in taste aversion learning. Therefore, this paper is concerned with a wider range of behaviors and stimulus modalities than have been considered before and a conceptual framework capable of encompassing this range of phenomena is required. The term neotic (I am indebted to N. Wiener for coining this word as well as pointing out its usefulness.) behavior is offered to describe the entire range of responses to novel stimuli including exploration, neophobia, aggression, and orientation. Within the present terminology, exploration and neophobia can be referred to as neotic approach and avoidance, respectively, and this review will be limited to only these two neotic responses. Neotic approach and avoidance will be referred to, collectively, as "neotic preference." This term can be employed here since, in a choice-type task, the organism can either prefer the novel (approach) or prefer the familiar (avoidance).

The determinants of neotic preference can be conveniently organized into two main categories. First, are those manipulations which influence the novelty of a stimulus (i.e., the organism's past experience), while the second are extra-stimulus factors that influence the responsivity of the animal to a stimulus (e.g., drugs). However, before continuing, it is necessary to discuss the sorts of procedures which provide data that can be easily interpreted in terms of neotic preference.

Exploration: The Measurement Problem

The presence of exploratory-type behavior (especially in

1An earlier version of this paper was submitted to the Department of Psychology of York University in partial fulfillment of the Ph.D. degree. I wish to thank N. Wiener, R. Deutsch and L. Boulter for their helpful comments on this version. The unpublished research cited in this paper was funded by National Research Council Grant No. APA 301 to N. Wiener. Requests for reprints should be sent to: Dr. David T. Corey, Environmental Medicine Unit, St. Joseph's Hospital—McMaster University, Fontbonne Building, 301 James Street S., Hamilton, Ontario L8P 3B6, Canada.
FAMILIARIZATION

Approach

Neotie behavior is almost invariably identified by the response decrement that occurs with repeated or continuous exposure to a stimulus. The most widely investigated neotie response is approach, which encompasses visual and locomotor exploration including the concomitant investigatory and manipulatory behaviors. The approach tendency declines with continued stimulus exposure and, if the stimulus has little intrinsic value to the organism, it eventually fails to evoke a response [11, 12, 134, 147, 201]. The decline follows a negatively accelerated function such that the initial moments of contact have a proportionately greater impact on subsequent behavior.

Given the above criteria, a neotie approach is also exemplified by operant behaviors that produce a temporary change in the environment (sensory reinforcement). Rodents and monkeys will bar press for sensory change and this responding declines with continued exposure [72, 113, 145, 157, 185], although exceptions have been noted [29, 65].

Avoidance

While many authors (e.g., [73]) have emphasized the attractive, curiosity-inducing properties of novelty, there are also many conditions under which an animal, if given the opportunity, will avoid or withdraw from novel stimuli. Neotie avoidance is observed when a rat is permitted to emerge from its home-cage or a familiar area into a strange runway or chamber [18, 107, 134, 203]. Blanchard et al. [18] gave rats a choice between remaining in their home cage or entering a U-shaped alley. One group had previously been forcibly exposed to the alley for 10 min while a second group had been provided with 10 min of irrelevant exploration. The “irrelevant exploration” group entered the alley after 153 sec while the pre-exposed animals entered in only 10 sec. Montgomery [133] also reported that rats confronted with a similar situation will tend to “look away” from the doorway and retreat to the rear of the cage, but the animals become bolder with continued direct exposure to the situation, will venture into the alleyway, and explore it with increasing vigor. This exploratory behavior also declines with familiarization. This pattern of avoidance, approach and disinterest (given that the stimulus is intrinsically neutral) is also observed with humans ([13], p. 205) and with non-human pri-mates, especially when a novel object is introduced into their living area [199, 200]. Humans also tend to rate stimulus objects as more pleasant as they become more familiar; pleasantness ratings increase as a function of exposure frequency [180, 217]. These findings provide excellent evidence that the novelty of a stimulus determines to a large extent whether an organism approaches or avoids it.
Flavor neophobia. Many animals, upon encountering a novel food, will exhibit an initial hesitancy to consume that food. This avoidance will occur even though the food, when familiar, is highly palatable [37] indicating that the avoidance is due to the novelty of the food. Although flavor neophobia has been most extensively studied in the rat [7, 32, 54] it has also been observed in other species such as dogs [121], codfish [119], rhesus monkeys [190], and humans [188]. Domjan [54] has investigated flavor neophobia in rats in some detail and has tested a number of explanations for its dissipation. He demonstrated that the simple passage of time, without exposure, was not sufficient for neophobia reduction. Moreover, the enhancement of intake was not due to associations between the novel flavor and thirst reduction (cf. [148]). Therefore, the intake of a novel food appears to be directly related to the amount of prior exposure to that food and its concomitant increase in familiarity.

Olfaction appears to play a major role in the neophobic response but not to the odors of foods that have odors. Rats with olfactory bulb ablation and peripherally anosmic rats responded to novel apple juice without any neophobia but they responded to a non-odorous flavor (saccharin) with a near-normal neophobic response as determined by latency to drink and the frequency of drinking pauses [89]. These data suggest that flavor neophobia might occur in response to both olfactory and gustatory stimuli but the way in which these components interact is not known. For example, it is not clear why the gustatory stimuli provided by apple juice should not produce neophobia whereas the gustatory stimuli provided by saccharin do produce neophobia. There are also some preliminary indications that exposure to the odor of a food alone is sufficient to reduce the intensity of the neophobic response to that food when it is later encountered [26, 114]. However, these experiments were conducted with very young rats and further experiments are needed to confirm this effect in adult rats. If the latter effect is obtained then it would have important implications for the mechanisms of neophobia and its dissipation. For example, it would indicate that the animal need not associate ingestion of the flavor with its consequences (or absence thereof) in order to enhance its later consumption (cf. [156]). Perhaps simple familiarity with the flavor or its odor is sufficient to reduce neophobia.

It should be pointed out that the rats' avoidance of a novel food is not absolute, i.e., they will consume appreciable amounts of a new food even when satiated [96, 142, 144, 184] or when a familiar substitute is simultaneously available [42, 139]. The amounts consumed (2 or 3 ml) are more than sufficient to allow the animal to taste the flavor. This tendency to sample new foods [7, 154] probably allows the animal to gain some familiarity with the food, while at the same time keeping the quantity below potentially dangerous levels. Unfortunately, the role of olfaction plays here is unclear, although most of the above studies employed relatively non-odorous substances such as saccharin.

Container neophobia. Consummatory behavior is also influenced by novelty when a rat is offered a familiar food in a novel container [8, 35, 44, 128, 131, 171]. The presence of the new container produces a temporary depression in intake which in wild strains can be very profound, resulting in a total cessation of eating for 2 or 3 days [8, 44]. If a familiar food is simultaneously available from a familiar and a novel source (choice test), the animals will consume most of their food from the familiar source. Mitchell [128] has demonstrated that this choice test is a more sensitive and reliable measure of container neophobia than non-choice measures of consumption or latency to eat. With familiarization consumption from the novel source gradually increases until both containers are about equally used.

Container neophobia is only one of a number of environmental changes which can temporarily depress eating. Moving the usual food source to a new location will depress eating in wild strains of rats although not to the same extent as the introduction of a new container [44, 171]. A stronger reaction is produced by the introduction of a new object into the environment [8, 35, 171]. This "new object reaction" can result in a total or partial cessation of eating for several days depending upon the object's proximity to the food source. For example, Barnett [8] simply placed a tin cup in the home cages of wild rats and found that their food consumption dropped about 35% over a 24 hr period but returned to normal the next day. Cowan [45] has provided evidence that the drop in consumption is not the result of a general disruption of eating but is due rather to a specific avoidance of the novel objects. Wild rats with two food sources simply increased their consumption from the alternate source when novel objects were placed near the first. Placing a hungry rat in an entirely new environment with familiar food available also disrupts its "readiness to eat" [19, 22, 23, 33, 204]. Readiness to eat (given that other factors such as hunger are held constant) is directly related to the amount of prior exposure to the test chamber [19, 23, 204] and even 5 min of preexposure is sufficient to significantly increase readiness to eat [19].

The investigations of "container neophobia" and "new object reaction" developed independently of the "readiness to eat" literature and, consequently, different hypotheses have been offered to explain these nearly identical phenomena. Most researchers viewed the former two effects as resulting from neotic avoidance or fear while the latter was seen as resulting from competing exploration (e.g., [19, 23]). As support for this position Bolles and Rapp [23] point out that 90% of the activity prior to eating is "exploratory" in nature. However, since the "exploratory" behaviors occurred in a forced-exposure situation, it is difficult to conclude that they indicated neotic approach. Instead, the rearing and locomotion might have represented attempts to escape the apparatus. One way of clarifying the relative contributions of approach and avoidance responses would be to employ a choice task in which the animal could escape from the novel chamber. If the rats chose to leave the novel chamber one could more readily interpret the "readiness to eat" phenomenon as resulting from neotic avoidance. This finding would place the interpretation of the "readiness to eat" phenomenon more in line with that of the "container neophobia" and the "new object reaction" phenomena.

STIMULUS DISCREPANCY

Since novelty is here considered to be a function of the degree of contrast between present perception and past experience, it is possible to expose an animal to stimuli of varying degrees of novelty if its experiential history is known. There are several unknowns which determine the novelty of the stimulus (such as stimulus generalization) so it is difficult to predict, in advance, the neotic response that will be elicited by a given stimulus. However, it is often possible to organize a series of stimuli such that one can predict whether one stimulus will be more or less novel (discrepant) than another.
Menzel, Davenport and Rogers [126] tested the responses of young chimpanzees to objects of varying degrees of novelty. They had been familiarized to a standard wood block, and wooden objects differing in size, shape and color, or any combination of these characteristics, were presented to them. The time spent in contact with an object was directly related to the number of novel cues it provided.

Readiness to eat is also influenced by the number of modifications to the immediate surroundings. Chance and Mead [33] removed rats from their home cages for a short period and modified the cage in a number of ways (e.g., new sawdust, extra food containers, new flooring). When the animals were returned their latency to eat varied positively with the number of modifications.

For animals reared on water, solutions in increasing concentrations will be more distinct in taste from water and thus should be more novel. The intensity of the neophobic response should vary accordingly. For example, rats initially find 0.1% saccharin to be more acceptable than 1% saccharin [139, 184] but the relative aversiveness of the 1% solution is not due solely to palatability differences since it is equally acceptable after several exposures. Rather, it appears that the animals are more neophobic to the higher concentration.

Domjan and Gillan [57] have investigated these neophobic responses over a wide range of concentrations. Independent groups of rats were given daily exposures to 5 different concentrations of saccharin (0.1%, 0.5%, 1%, 2%, 3%) followed by equal access to water. On the first exposure, acceptability was inversely related to concentration but, by the fourth exposure, the animals consumed equal amounts of the 0.15% to 1% solutions while the higher concentrations were less acceptable. It appears that the increased avoidance of saccharin solutions varying from 0.15% to 1% is due to increasing novelty whereas the higher concentrations (2% and 3%) are avoided on the basis of both novelty and palatability.

On the basis of the preceding data it is apparent that the discrepancy of a stimulus from past experience determines the form of the neotic response. Discrepancy can also play an important role in the contrast between a novel stimulus and the context in which it is found. Novel objects encountered in new environments are often investigated with little hesitation [12, 44, 215] while the same stimuli in familiar contexts are initially avoided [44, 161, 215]. Cowan [44] investigated this neophobic phenomenon in some detail in a wild strain of Rattus rattus who were placed in a strange living area with access to 4 adjoining arms (a ‘+’ maze). There were novel objects present in one of the arms and, when the animals were first placed in the apparatus, this arm was visited with the same frequency and duration as the rest. The objects were removed and the rats were then given 2 or 4 hr of access to this arm per day for 7 days, and on the seventh day different objects were placed in the arm. The objects reduced visits to that arm by the 2 hr-access group and completely eliminated visits by the 4 hr-access group. Therefore the response to the novel objects was a function of the degree of familiarity of the context in which they were placed; when the context was novel they were approached but, when familiar, they were strongly avoided. Hebb [93] also noted that chimpanzees were most fearful of objects that combined familiar and novel elements (e.g., a keeper without a lab coat, a detached monkey head). These data suggest that the contrast between the novel and familiar elements of stimulus complex is an important determinant of neotic behavior, and one which requires more thorough investigation.

One possible interpretation of context discrepancy is that, in a completely novel situation the animal has no safe, familiar place to which to retreat and is therefore unable to withdraw, while in a familiar environment, the animal is able to avoid and does so (cf. [205]). This view is consistent with the finding that rats in a strange situation tend to seek the proximity of familiar objects [169] but this explanation cannot encompass Hebb's [93] data. Another interpretation of the phenomenon is that the presence of novel stimuli within a familiar context is discrepant with the past constancy of the familiar context. That is, the animal has acquired some expectations about the familiar context and the change is discrepant from these expectations. The resultant ‘surprise’ produces a more powerful reaction, akin to that produced by greater novelty. This interpretation derives some support from the finding that animals who are accustomed to changeable conditions come to accept novel stimuli quite casually (see Diverse Experience). Possibly these animals are not surprised by novelty because their past experience leads them to expect nothing else. Additional work is needed to test this hypothesis and to outline the conditions under which it applies, but its strength is found in its ability to explain some neotic phenomena. For example, it is known that the reinforcement value of sensory change is positively related to the amount of preexposure to the test apparatus in the absence of the sensory change [113]. Leaton et al. [113] assumed that preexposure to the apparatus allowed for the habituation of exploration which would have otherwise interfered with bar pressing. The expectancy view would suggest that the increased reinforcement value is the result of the surprise produced by the change in the stimulus complex, i.e., during preexposure the animal develops certain expectancies of the apparatus which are violated by the introduction of the sensory change contingency and the sensory change is, therefore, more discrepant than if it occurs as soon as the animal enters the apparatus.

**STIMULUS ABSENCE**

A neotic response, once habituated, can often be partially reinstated if the stimulus is withdrawn for a period of time and then re-presented. The intensity of the response is usually weaker and the response again habituates, usually more quickly than on the original encounter. The recovery of neotic behavior has indicated to some authors that, while the stimulus is absent, it is gradually forgotten and, therefore, is relatively more novel when re-encountered (see [94], p. 277 ff.). The reinstatement of neotic behavior with stimulus absence has been widely documented in rats [12, 19, 133, 134, 145, 204]; monkeys [28, 147]; and humans [181].

Readiness to eat is also influenced by the lapse of time since the animal last encountered the environmental situation. Chance and Mead [33] investigated the willingness of hungry (24 hr deprived) rats to begin eating when returned to their home cages after various periods of absence. Those returned after 10 min were less hesitant to begin eating than those absent for one day. Similarly, rats absent for one day ate more readily than those absent for 3 days, but the difference between 3 and 5 days absence was not significant. Blanchard et al. [19] similarly tested hungry rats after 30 min, 1 day, 3 days or 9 days absence. Latency to eat and eating time were recorded and, although they obtained a trend of increasing latency, their results did not reach statistical significance. The discrepancy in the results of the two studies may be partially due to the different food deprivation conditions employed. Blanchard et al. [19] maintained their
animals at 90% of ad lib weight plus they were tested while 24 hr deprived. Chance and Mead's animals were deprived for only the 24 hr period prior to the test. Since readiness to eat is strongly influenced by weight loss [22], the stimulus absence effect may have been partially overridden by the rats' hunger. This suggestion is consistent with the mean eating latencies in the two experiments: Chance and Mead—184.1 sec; Blanchard et al.—42.9 sec.

The recovery of neotic behavior with stimulus absence can also occur over time intervals shorter than hours or days. Montgomery [132, 133] observed rats exploring mazes of varying configurations and recorded the patterns of movement. The animals consistently approached and explored areas of the maze that had been visited least recently. It has been suggested that this tendency underlies the phenomenon of spontaneous alternation [48, 132, 133]. That is, in a 'Y' or 'T' maze situation the animal enters the arm least recently visited because it is more novel and therefore more attractive. As the subsequent treatment is the opposite condition exists and so on. Moreover, this hypothesis predicts that as the intertrial interval is increased the alternation tendency will decrease, because the last-visited arm is regaining some of its attractiveness. This prediction has been supported [48, 49].

The phenomenon of spontaneous alternation reflects a general tendency of several species to repeatedly visit portions of their territory on a more or less regular basis [10]. This tendency has been measured in a residential maze which consists of a central nest-box with four adjoining arms (a "+" maze). Since some arms contain food or water they are regularly visited, but the remaining empty arms are also visited consistently and at a constant rate [44]. This regular "patrolling" is systematic, that is, the animals "tend to move from one arm to a different one each time they pass through the nest box" [10]. Thus, they exhibit spontaneous alternation.

Apparently, short-term stimulus absence does not reinstate flavor neophobia as it does other neotic responses. Instead, as measured by either enhanced consumption or preference, flavor neophobia dissipates with time following the initial exposure to a food [87, 138]. Even a 17 day period interpolated between the second and third exposures to a flavor produces only a very slight, and nonsignificant return of neophobia [54]. However, neophobia does recover over a longer, 75-day interval [55]. The fact that neophobia continues to dissipate following exposure suggests that a learning or habituation process is continuing in the absence of stimulus. It is tempting to attribute this effect to a long-term gustatory memory, except that delay can also result in a further dissipation of neophobia in a non-gustatory modality [180]. These results suggest that during stimulus absence, learning, as well as forgetting, can occur.

Even though flavor neophobia does not appear to be markedly influenced by stimulus absence, responses to less novel foods are appreciably influenced by withdrawal. Several authors have reported that if a particular food is withdrawn for several days (the rat is maintained ad lib in the interim), consumption of that food will be markedly enhanced upon its return. The enhancement has been noted with a number of edible substances including saccharin [81, 196], chocolate [31], alcohol [175], and food pellets, as well as non-nutritive solids such as erasers and crayons [206]. In some experiments consumption increased by a factor of three or more over the pre-withdrawal levels. Monkeys are similarly influenced by the absence of a food [199] and humans rate familiar tastes as more pleasant after a week's absence [181]. This effect probably accounts for the increased appetite and consumption commonly noted in humans when dietary change is provided. It also suggests that responses to foods of varying degrees of novelty are similar to those to non-gustatory stimuli. That is, highly novel foods may be avoided but, less novel foods may be approached and preferred.

If the effects of food withdrawal are due to the partially recovered novelty of the food because of forgetting, then we should expect a stronger effect with longer periods of absence (up to a point) and continued exposure to the substance upon its return should result in a reduction of consumption to baseline or near-baseline levels. The first prediction has been supported by Sinclair, Walker and Jordan [176] who reported that the withdrawal effect increased with longer periods up to 75 days. The second prediction is borne out by most studies [173, 175, 176, 181, 195, 196, 206]. Also consistent with the second prediction is the finding that the greatest consumption occurs within the first hour of the flavor's return [173, 176]. This consumption can approach 25% of the animals' total daily intake.

The preceding data only deals with the effect of one period of withdrawal. A number of studies have also investigated repeated periods of presentation and withdrawal. Typically, an animal is maintained ad lib on food and water while a third substance is intermittently presented and removed for one or two day periods [196]. The periodic presentation procedure results in consumption levels that are much higher than those found with constant access. The effect was first reported, using ethanol, by Sinclair and Senter [174], who suggested that the enhanced consumption illustrated the presence of an alcohol "need". However the effect is not confined to alcohol since periodic presentation will also elevate the consumption of non-preferred solutions of salt, citric acid [195], quinine, and saccharin [196]. One again, intake is found to be greater with longer periods of absence (Cott, personal communication) and it rapidly declines to baseline levels with continuous exposure [143]. It is also noted that the most prodigious intake occurs immediately after the substance is returned [196].

The periodic presentation paradigm is analogous to a forced-choice trial in a spontaneous alternation task. In a forced-choice trial the subject is allowed to enter only one arm of a maze and is then confined there for a period of time. On a subsequent free-choice trial, it will strongly prefer the other arm [49]. Periodic presentation confines the animal to two edible substances (food and water) and then temporarily allows a third option. The strong, temporary preference for the new option is reminiscent of the effects of a forced-choice trial and suggests the possibility that similar determinants are at work. The presence of spontaneous alternation in the gustatory modality has been clearly demonstrated by Holman [98] and Morrison [136]. They exposed rats to a distinctly flavored familiar fluid and then allowed them to choose between that and a second, equally palatable, novel flavor. The rats exhibited a clear, temporary preference for the second alternative; an effect that occurred with a number of flavors and procedures. This data was viewed by Morrison [136] as evidence that "palatability declines as a function of amount tasted," a position substantively similar to more general theory known as "stimulus satiation" [83]. Pinel and Huang [143] also offer a similar hypothesis based on the periodic presentation data. They hypothesize a "taste-related inhibitory factor which develops with consumption of
a flavored substance and dissipates over periods when the substance is not consumed” (p. 695). These views emphasize the aversive effects of increasing familiarity in contrast to the attractive properties of novelty. Unfortunately, the available evidence is not sufficient to allow one to distinguish between these views. Perhaps a tenable position might be to emphasize an organism’s need for optimal levels of stimulation [65] and view a changing food source as one source of that stimulation: Perhaps the returned food is attractive because it provides the organism with a source of sensory stimulation. This view would predict that one could reduce the impact of periodically presenting a food if the organism’s level of stimulation was already at optimal levels. This could be accomplished if the animal were placed in a highly variable environment. In any case, the withdrawal of foods appears to produce the same effects and to be influenced by the same factors as stimulus absence in other modalities. These similarities suggest that a specialized mechanism such as that offered by Pinel and Huang [143] need not be hypothesized until the broader perspective is taken into account and more general hypotheses considered. Finally, the data suggests that the pattern of neotic behavior as a function of decreasing novelty (avoidance, approach, disinterest) occurs with gustatory stimuli as well as non-gustatory stimuli.

RESPONSE VARIABLES

This portion of the paper is concerned with those variables that are usually considered to modify neotic responsiveness independently of stimulus novelty. These variables can be grouped into four general categories: (1) prior stimulation, (2) developmental and experiential factors, (3) organismic factors, and (4) physiological factors. Each of these general categories includes a number of specific variables which will be reviewed separately.

PRIOR STIMULATION

Ambient Stimulation

The quantity of sensory stimulation that an organism has encountered over a period of time has a significant influence on its subsequent response to a novel stimulus. A period of sensory deprivation will enhance the reinforcement value of stimulus change, as measured by response rate [28,75]. Moreover, Berlyne, Koenig and Hirota [15] have demonstrated that relatively high ambient levels of sensory stimulation modify the reinforcement value of sensory change in the opposite direction to that of sensory deprivation. They trained rats to barpress for either a familiar or a novel stimulus. However, some of the animals were inadvertently housed in a noisy room next to some print-out counters while the rest were housed in a quiet and relatively isolated room. This maintenance factor turned out to be an important one. The novel stimulus was less reinforcing for the “noisy-room” group, indicating that the high stimulation levels reduced the reinforcement value of novelty. This finding, as well as the sensory deprivation data, is consistent with the view that organisms attempt to regulate their stimulation input towards intermediate levels.

Short-term Stimulation

The effects of short-term stimulation on immediately subsequent neotic behavior are not as consistent as those of ambient stimulation. Leventhal and Killackey [115] exposed rats for 10 sec to a flashing light and an intermittent buzzer before allowing them to choose between a novel and a familiar compartment. The rats thus treated selected the novel compartment with the same high preference as those without the treatment, even though the stimulation apparently stressed the animals as determined by defecation and latency to respond. On the other hand, Haywood and Wachs [92], employing a similar procedure, found that 15 sec exposure to white noise at an intensity “just less than that required to produce audiogenic seizures” reduced neotic approach. However, it should be pointed out that their animals did not avoid the novel chamber. Rather, they entered the two chambers on an equal basis, in comparison to the control group’s high preference for novelty. This result raises the possibility that the animals had not changed their neotic preference at all but were behaving on a random basis due to the disruptive effects of the noise.

Sheldon [169] has provided a unique demonstration of the effects of prior exposure to a novel environment on subsequent neotic preference. She exposed rats for 1 hr to a novel environment consisting of a “primate cage filled with assorted novel objects, odors, a hamster, and 6 strange same-sex rats.” Immediately following this treatment, the rats were allowed to approach a novel and a familiar object on a Y-maze. This treatment reduced neotic preference from a usual 75% to 50%. Unfortunately, this experiment is also not exempt from the “random behavior” argument, since the animals displayed no clear preference for the novel or familiar alternative.

Shock

A number of studies have demonstrated that neotic approach is reduced in rats that have been subjected to electric shock immediately prior to a choice test [2, 3, 92, 170]. However, in most of these experiments, the animals did not actually avoid the novel choice but chose the two sides on an approximately equal basis. Again, the possibility is raised that the behavior was essentially random. Aitken and Sheldon [3] and Aitken [2] approached this problem by observing the animals’ behavior after they made their initial choice. In both experiments, most of the shocked rats who had initially entered the novel chamber left it, and entered the familiar side, while the unshocked rats persisted in their original choice. In the 2 min interval following the initial choice, the shocked rats spent 77% of their time in the familiar compartment. These results have led Aitken [2] to suggest that the shock disrupts the initial choice but also induces the animal to avoid the novel chamber after the initial choice has been made. However, that the initial choice is not disrupted in all situations is evidenced by two reports that shocked rats initially avoid a novel compartment [170,190]. Shock can produce a striking preference reversal. Thompson and Higgins [190] reported that 76.7% of their unshocked rats preferred a novel maze arm while 80% of the shocked rats preferred the familiar. Apparently, then, prior shock can induce neotic avoidance as measured either by initial choice behavior or the subsequent retreat from a novel compartment.

One interpretation of the neotic effects of shock might be that the painful, aversive nature of the treatment induces the animal to temporarily avoid any additional stimulation. But it is instructive that the immediate, physiological after-effects of a shock need not be present. Haywood and Wachs [92] found that placing a rat in a start box in which shock had been previously received was sufficient to reduce neotic
approach to the same extent as though shock had actually been given. Expectation of shock alone was sufficient to reduce neotic approach.

The conclusion that shock reduces exploratory tendencies has been questioned by data and a theoretical formulation offered by Halliday [(88), see review in (159)]. He suggested that exploration was actually induced by fear and, in support, presented data that was interpreted as evidence that shock increased exploration. The experimental apparatus was a Y-maze consisting of two plain-colored arms and one striped arm. Rats were preexposed to the maze on 3 successive days and, prior to the fourth trial, were shocked in a separate box. On the fourth and subsequent trials the shocked rats exhibited an enhanced preference for the striped arm. This finding, which has been essentially replicated by Williams [210] and Wong and Bowles [216], was interpreted as evidence that the shock induces enhanced exploration of the striped (more complex) arm. Control procedures instituted by Halliday [(88) and Williams [210] have eliminated the possibility that the behavior is due to stimulus generalization between the shock-box and any part of the maze. However, an alternative hypothesis, based on altered neotic preference, can be offered. An examination of the published data reveals that the rats display a slight to moderate preference for the striped arm during their preexposure trials. Since familiarity is a function of the amount of direct exposure to a stimulus, it can be assumed that the striped arm is therefore more familiar after preexposure. Accordingly, after the shock, they display an enhanced preference for the most familiar portion of the maze; a conclusion in complete agreement with the previously cited data. Confirmation of this interpretation is found in the data provided by Wong and Bowles [216]. During preexposure their subjects had a choice among 3 maze arms and one of the groups (non-handled) spent 46% of their time in the striped arm while the other group (handled) stayed there 31% of the time. Therefore the maze arms were equally familiar to the “handled” animals while the striped arm was more familiar to the “non-handled” group. As expected, the shock induced an enhanced preference for the most familiar (striped) arm in the “non-handled” group but not for the “handled” group. In conclusion, there is good evidence that shock induces neotic avoidance, and the data which has been offered to demonstrate that shock enhances exploration can also be reinterpreted in terms of neotic avoidance.

ORGANISMIC FACTORS

Hunger and Thirst

The evidence that hunger and thirst increase locomotor activity in the rat has been available for many years [47] but, as previously discussed, it is difficult to infer neotic preference from this measure. The inference is made more difficult by the evidence that activity induced by external stimulation is also greatly enhanced by deprivation [187]. The use of exploration measures that are unconfounded by activity levels is therefore required here and a number of authors have employed choice tests, which meet this criterion. The most common finding is that hungry rats prefer novel stimulation to a greater degree than do sated rats [66, 70, 103, 151, 218] and neotic approach is also positively related to the severity of deprivation [70]. Water deprivation also results in increased neotic approach [151]. When the influence of hunger and thirst on bar-pressing for sensory reinforcement is assessed it is again important that the possibility of stimulation-induced activity be controlled. Fortunately, a two-lever apparatus (one bar non-functional) provides a measure of sensory reinforcement unconfounded by activity level since random activity should not be preferentially directed towards the functioning bar unless that behavior is also reinforcing (cf. [106]). Extinction measures also provide estimates of reinforcement value independent of performance levels. Fortunately there are a number of studies that meet these criteria and the majority of these report that stimulus change is more reinforcing for food deprived and water deprived rats [36, 185, 186]. The reinforcement value of sensory change also varies positively with increasing deprivation and this relationship holds over a wide range of deprivation conditions ranging from one day to 10 days constant deprivation [186]. However, not all studies find that food deprivation enhances the value of sensory reinforcement. Smith and Donahoe [177] report that hunger reduces bar-pressing for light onset and Chapman and Levy [34] report that hungry rats run more slowly to a goal box offering novel stimulation than do sated rats. However, the latter study can be reinterpreted by suggesting that their animals may also have been investigating the runway in more detail, a response which would naturally hamper runway performance.

The conclusion that hunger increases exploratory behavior is not at all surprising when one considers the immense survival value that exploration must confer in the discovery of new food sources. Certainly, even thoughventuring into unknown territory may be dangerous, a starving animal has little to lose by doing so. Perhaps, in some sense, hunger-induced exploration is food-seeking behavior and one would expect the exploration to cease once food is discovered. At the very least, we would predict that, given a choice between a known food source and a new territory, a hungry animal should select the food. But this rather commonsensical view is directly contradicted by the available evidence: hungry rats will explore new pathways in preference to travelling a known route to food [40, 74]. This preference is found even with ample training and reinforcement [74] but begins to fade with high levels of deprivation [40]. Apparently, then, food detection and consumption are not the immediate goals of hunger-induced exploration. Olton, Walker, Gage and Johnston [140] have investigated the food-searching strategies of hungry rats in a seminaturalistic environment and their data provide a possible answer to this seeming anomaly. The rats had 3 possible food locations available, of which only one contained food at any one time. Once an animal located food, it tended to return to this source but it also searched other possible locations. But once it discovered that a particular location was empty it very seldom returned there. Apparently, the strategy is that once a food source is located and ‘secured,’ the vicinity will also be searched for additional supplies. Possibly this strategy evolved because the rats’ food sources tend to be located in clusters. Unfortunately, though, this sort of analysis does not suggest a possible mechanism through which hunger should enhance exploration although the data appear to contradict most theories based on “optimal arousal state” (see [65]). For example, Berryle [13,14] explicitly predicts that hungry animals should be less exploratory.

Sex

Several studies report that female rodents tend to emerge
from their home cages faster than males [127,212] and that they more readily approach and explore novel stimuli [151; see review 5]. Female rats will also spend more time in a novel compartment in a choice test [160]. However, Hughes [99,103] has repeatedly found no sex differences in neoceptive preference. Even so, Hughes does note that the two sexes engage in distinctly different patterns of behavior while in the novel compartment. Males spend more time grooming, eating, drinking, and freezing, and females engage in more exploratory-type activities (rearing, sniffing, locomotion). Rearing frequency tends to be the major sexual difference [99,103] but it should be pointed out that the females may do this more readily simply because they are smaller and lighter than their male peers. Differences in body size might also partially explain why males spend more time in maintenance activities such as grooming and eating.

One clue to the reasons for the discrepant findings is provided by reports of a sex × rearing condition interaction in rats [197]. Sex also appears to interact with the stimulus complexity of the testing situation [197]. A recent finding by Russell [161] may also provide a partial resolution. He found that female rats explore more than males if a short-term exposure to novelty is provided but, with more exposure time, the males gradually increase their exploration levels and surpass the females. Thus the 2 sexes ultimately engage in equivalent amounts of exploration if the test period is long enough. Unfortunately, the status of Russell's [161] finding in terms of neoceptive preference is unclear since, when the females did explore more, their neoceptive preference was not actually greater than that of the males. Rather, they explored both the familiar and novel alternatives more than did the males. Further clarification on this finding and on Russell's [161] test apparatus is required.

Archer [5] has recently suggested that rodent sex differences in emotionality may be due to hormonal influences. For example, the female rodents' emotional responsiveness may change with estrogen levels such that they display enhanced neoceptive approach during estrus.

Domestication

The domestication of rodents has resulted in a number of profound behavioral changes such as increased docility [21], and greatly reduced neophobia [9]. This latter effect has been observed in mice [125, 146, 215] and in rats [45, 78, 128, 155]. In fact, Barnett and Cowan [10] have suggested that rodent sex differences in neophobia may be due to the relative insensitivity of the container as it gains more experience. This scenario predicts a pattern of neoceptive behavior which would progress from hesitancy and avoidance in infancy, through curiosity and play in childhood, to disinterest in old age. Aside from the support that this view receives from our conventional knowledge, there are some experimental studies which are consistent with it. For example, 6-week-old human infants prefer to look at familiar objects, whereas at 8 weeks they prefer the novel stimulus [200]. Young (1–2 year old) chimpanzees respond to a new object placed in their cage with cautious observation while older chimps quickly approach and vigorously manipulate the same objects [202]. Year-old rats are much less interested in novel objects than are younger rats [77]. On the other hand, responses to strangers by human infants do not follow a similar developmental trend. They begin with positive responses (e.g., observing and smiling) and are replaced by negative affect, such as looking away and crying, at about 6–8 months of age [25,86]. As the child grows older the negative response tendency also dissipates and is replaced by curiosity and approach. This developmental sequence is not consistent with a simple progression of neoceptive preference and may well reflect the interaction
of additional factors such as the development of attachment to the mother, etc.

The above examples only begin to convey the complexities of development which can make a simple interpretation of the data very hazardous. For example, Mason, Harlow and Ruping [122] report that infant rhesus display an increasing tendency to manipulate various objects up to about 90 days of age. However, this developmental change can either be viewed as an increasing preference for novelty or as maturation of the appropriate manipulatory abilities. Similarly, Egger, Livesey and Dawson [63] have investigated the marked developmental change in spontaneous alternation which occurs in rats. Sixteen-day-old pups alternate at a rate of 20%, 24-day-olds at 50%, and 100-day-olds at around 90%. It would appear that the 16-day-olds are actively avoiding the more novel side, but this interpretation is directly contradicted by the finding that increasing the novelty of the second arm increases preference for that arm to 50% for these rats [62]. Based on further pharmacological data, Egger et al. [63] suggest that the tendency to perseverate in the 16-day-old rats is due to the immaturity of the cholinergic inhibitory systems. That is, they perseverate because they fail to habituate to the cues from the first arm.

Human and non-human primates tend to leave the mother on more frequent and extensive forays as they grow older [150]. Although Rheingold and Eckerman concluded that the increased exploration is not due to the maturation of locomotor abilities, it is difficult to determine whether the observed trend indicates an increased preference for novelty or a decreased need for the mother's presence (see Role of Attachment).

The preceding examples indicate the complexities inherent in development which make the interpretation of changes in neotic preference very difficult. The manifestation of the appropriate neotic behavior is dependent on the maturation of the appropriate responses, control systems, and discrimination abilities. Moreover, the development of social attachment and the quantity and quality of experiences continually interact with, and modify, neotic behavior. The contributions of these factors are examined in more detail in the following sections.

Role of Attachment

The presence of an attachment figure (i.e., a mother or substitute) in the immediate vicinity of a young animal helps to encourage active exploration. Infant rhesus monkeys who have been reared with cloth-covered surrogate mothers retreat to the mother and cling when a novel "fear stimulus" is introduced into the home cage. After a period of clinging, the infant will visually explore the object and a brave one might even approach and manipulate it [90]. Similar behaviors occur if the infant is placed in an open field with a number of objects present and the surrogate available: The infant uses the mother as a secure base of operations and may even bring objects towards the mother for closer inspection. The response of the same monkeys with the surrogate absent is that of abject terror, characterized by self-clutching, vocalization, and rocking. The play and exploratory behavior of human infants is also enhanced by the presence of the mother [1, 141]. The mother's absence in a strange environment inhibits locomotor, visual, and manipulatory exploration, and increases crying. Again, the infants engage in "secure-base" behavior by occasional tactile and/or visual contacts with the mother. Rats pups are also attracted to adult conspecifics and to their residual olfactory cues and they tend to eat and explore in the immediate vicinity of these stimuli [79, 80].

The characteristics that comprise an effective attachment object have been investigated to some extent. Familiarity with the object is a necessary pre-condition (at least in primates): the presence of an unfamiliar cloth surrogate served only to enhance the emotional reactions of infant monkeys who were not raised with it [90]. Familiarization alone, however, is clearly not sufficient. Infant monkeys raised with wire-covered surrogates do not engage in "secure-base" behaviors, nor is their emotionality decreased in the presence of that surrogate. Likewise, the presence of a favorite toy does not enhance play behavior in human children [141]. If the familiar object also provides the primate with "contact-comfort" it can function as an effective attachment object. Cloth-covered dummies are effective for rhesus infants [90] and blankets are adequate for children [141]. In fact, Passman and Weisberg found that blankets can be as effective as mothers in promoting play in blanket-attached children.

The role of the attachment object appears to be that of fear reduction. In strange or threatening circumstances the infant seeks out the object and this contact calms the animal, allowing it to explore the fear-inducing stimulus under conditions of relative security. Presumably as the infant gains experience, its environment becomes less novel and threatening and it is more willing to leave the mother and explore by itself [150]. It has also been suggested that early, forced separation from the mother retards the organism's ability to overcome its fear of novelty (e.g., [25]).

Early Stimulation

It is well known that the availability of certain kinds and amounts of environmental stimulation profoundly influences the later behavior of a developing organism. The most commonly manipulated sources of early stimulation have been handling, shock, social interaction and visual variety. Animals who have been "stimulated" by comparatively more exposure to these environmental sources of input tend to be less emotional and more exploratory as adults. Open-field measures of the infantile stimulation effect have typically produced unreliable results (cf. [211]) but choice measures have proved to be consistent and interpretable. Rats who are "stimulated" in infancy are more willing to emerge from their home cage [50, 117, 127, 212] and more likely to enter and explore a novel environment [209]. Similarly, "stimulated" rats spend more time in association with novel objects [51, 197, 211]; but see [117].

It has recently been reported that early handling increases consumption of novel sucrose solutions and milk, but since this consumption difference persisted for at least 10 exposures it is difficult to interpret the difference in terms of altered flavor neophobia [198]. However, this interpretation would be consistent with the preceding data.

Turpin [191] reported that rats reared in social isolation since weaning prefer a familiar environment while group-reared rats prefer a novel environment. Similarly, socially-reared rats are more exploratory on a hole-board apparatus [69]. However, Sahakian, Robbins and Iversen [165] found the opposite effect; isolates displayed an enhanced neotic preference. Social isolates and rats reared in visually restricted environments also display enhanced container
neophobia [38,135] and dark-reared rats are less willing to eat in novel environments [182].

Most of the cited experiments have manipulated the presence or absence of a particular kind of stimulation but the relationship between early stimulation and later behavior may be better clarified by examining a number of stimulation levels as Hughes [100] has done. He raised rats under either visual deprivation or enrichment and half of each group were either handled daily or undisturbed. They were then tested and, as expected, the handled rats in the deprived condition were more exploratory than the non-handled rats. However, in the enrichment condition, the non-handled rats were the more exploratory. Thus the combination of both treatments reversed the usual finding, suggesting a possible inverted U-shaped relationship between early stimulation and later neotic approach. This finding emphasizes the usefulness of manipulating a number of levels of stimulation rather than simple presence or absence.

Sackett [163] explored the effects of three rearing conditions on neotic behavior. He raised rats in either a black or a white cage under three lighting conditions; constant dark, constant light, or a light-dark cycle. As adults, they were given a choice between black or white chambers under lit conditions on two trials. The dark-reared rats preferred the black box on both trials (i.e., the intensity most similar to their rearing condition), the light-reared animals preferred the novel color on both trials, and the light-dark-reared rats preferred the familiar color on the first trial but shifted to the novel one on the second. Since the amount of time the animals spent in lighted conditions should provide differential availability of visual stimulation, it is evident that the animals reared with the most stimulation (constant light) preferred the novel box while those with the lowest level preferred the most familiar condition. Sackett [164] also examined the novelty preference of rhesus monkeys who had been reared under various conditions: (1) feral, (2) with mother and peers, (3) in wire cage (opportunity to see and hear other monkeys, but no physical contact), (4) 6 months of isolation (complete social and partial sensory isolation for the first 6 months of life) and (5) 12 months of isolation. At 4-5 years of age the monkeys were placed in a chamber and after 5 min were allowed access to a second, attached, chamber where a dark square was projected on one of the walls. Sackett [164] measured the latency to enter the novel chamber and the time spent visually and tactually exploring the projection screen. The feral and mother-peer groups were equivalent on both measures and were more exploratory than the wirecage and 6 month isolates, while the latter 2 groups did not differ. The 12 month isolates displayed enhanced neotic avoidance. There was also a strong sex x rearing condition interaction such that the males were more disturbed by rearing deprivation. A similar interaction is also found with rats [197].

The preceding studies demonstrate that neotic preference is strongly influenced by the quantity of early environmental stimulation. There is little evidence that the quality or modality of the stimulation is important, i.e., early handling or shock appear to have effects indistinguishable from the effects of early social stimulation, etc. Hence, there is little necessity, as yet, to hypothesize specific mechanisms for each type of stimulation (cf. [191]).

Diverse Experience

The possibility that diverse dietary experience could influence later dietary habits was raised by Kuo [112]. In a number of pilot experiments he raised dogs, cats, and birds on either one food or a number of foods. When older, the animals raised on a single food exhibited a strong food neophobia while the animals with a diverse dietary history accepted new foods with less hesitation. These findings have been extended by Capretta, Petersik and Stewart [31]. They exposed immature rats to 3 novel flavors (vanilla, black walnut and rum extracts) for 4 days each (diverse group), while control groups were exposed to only tap water or only one of the flavors. All groups were then given an ad lib choice between a novel chocolate flavor and tap water for 18 days. A second, identical, experiment was conducted with mature rats as subjects. The immature diverse group preferred the chocolate flavor significantly more than the immature control groups, but the preference of the mature diverse rats was not similarly affected by the treatment. The authors concluded that the immature animals were less neophobic as a result of the diversity of their prior experience, but there are some possible objections to this interpretation. The first is that one of the “diverse” flavors could somewhat resemble the chocolate flavor and, therefore, it would be less novel because of this stimulus generalization. This suggestion is made more plausible by the apparent generalization between such distinctly different flavors as casein hydrolysate and saccharin [53], and saccharin and salt (Corey, Wiener and Duncan, unpublished data). In the Capretta et al. [31] experiment there is some evidence of generalization between vanilla and chocolate since the vanilla-only group preferred the chocolate more than the water-only group. However, as Capretta et al. [31] point out, if stimulus generalization is to be accepted as a reasonable explanation then the mature rats should have also displayed the diversity effect. Therefore it is not clear what role generalization plays in the behavior of the immature rats. A more thorough understanding of generalization between tastes would certainly be helpful.

A second objection concerns the specificity of the dietary diversity effect to novel foods. Donovick, Burright and Bentzen [58] exposed young rats to 6 different novel foods (e.g., sunflower seeds, 8% sucrose) for a period of 10 days. After this treatment, the rats drank more of novel quinine and saccharin solutions much as Capretta et al. [31] reported. However, they also consumed more tap water, a familiar taste. This finding questions the neotic specificity of Capretta et al. effect. Moreover, the data presented by Capretta et al. are not consistent with a neotic interpretation. The initial chocolate preference was the same for all groups and the group differences only emerged over several days and then remained stable for 18 days. This pattern is unlike that of modified neophobia; the difference should be large initially and then converge over a number of days. An alternative explanation might be that early experience with only one diet produces an imprinting-like attachment to that diet. This attachment could then be disrupted if a large number of foods are experienced (e.g., [27]).

On the other hand, other experiments on “dietary diversity” have produced results that are specific to novel foods and appear to produce lessened neophobia. These experiments differ in two noteworthy aspects from the previous studies: (1) the duration of the exposure to each of the flavors during diversity treatment is less (20-60 min each vs 4 to 10 days) and (2) the effect is found both with mature and immature rats (Braveman and Jarvis, unpublished manuscript; Corey et al., unpublished data). The basic procedure is very similar to that of Capretta et al. [31]. It consists of
EXPLORATION AND NEOPHOBIA

presenting rats with 3 or 4 different novel flavors for a short (e.g., 60 min) period on successive days and then testing their responses to a novel test flavor. Control groups are either exposed to tap water only or to one of the treatment flavors and are then tested with the same novel flavor. The diverse group typically consumes more at test, and the conclusion that this is due to reduced neophobia is supported by two findings: (1) the consumption difference disappears after 2 or 3 exposures to the test flavor as the control group begins to consume more and (2) all groups consume equivalent quantities of familiar fluids at test (Corey, et al.).

Again the problem of stimulus generalization must be met. Braveman and Jarvis found that the diverse treatment did not attenuate the associability of the test flavor with illness although the neophobic response was reduced. Since familiar tastes are much less associable with illness than are novel tastes [149], this finding provides good evidence that the test solution is not any less novel through stimulus generalization.

If stimulus generalization is not a suitable explanation of the effect of dietary diversity then we are left with the question of what does constitute a good explanation. Several possibilities are immediately apparent. First, the animal may learn that the class of stimuli which constitutes novel foods is not dangerous (cf. [16]). Secondly, the animals might come to expect another novel flavor because of their previous experience and, therefore, react less strongly to its arrival. This view is consistent with the behavior of wild rats in constantly changing environments (see below). Finally, the mechanism of the effect may be similar to that of the "early stimulation" effect; that is, the organism may become adapted to a certain level of variability or stimulation and seek to maintain that level (see [95]). Further work is needed to test these possibilities and examine some of the implications of the dietary diversity treatment for "early stimulation".

I should also point out that the effects of diverse experience are not confined to diets. Chimpanzees who are exposed to a series of different novel objects become less cautious and increasingly willing to play with each new object [128,201]. Wild rats who live in a constantly changing environment (a garbage dump) exhibit very little avoidance of new objects, in sharp contrast to the extreme avoidance exhibited by their counterparts who live in more stable environments [20]. Sheldon [169] exposed hooded rats to 14 different novel objects in a series of trials. On the first trial only 30% of the rats approached the novel object, but with each trial this avoidance gradually reversed until they displayed a 75% preference for a novel object on the 14th trial. These results, taken together, indicate that diverse experience is an important determinant of neotic behavior. Possibly the animals' past experience leads them to expect change and more change is therefore accepted casually. Unfortunately, though, it is not possible to determine the potential role of stimulus generalization in the preceding instances.

Perhaps the clearest way to circumvent the confounding problem of stimulus generalization is to investigate inter-modal transfer of prior diversity. Two recent experiments have indicated that inter-modal transfer may occur. Young rats, exposed to variable auditory stimulation, later exhibited a tendency to provide themselves with more variable tactual stimulation [95]. Similarly, exposure to a variety of odors results in an increased willingness to consume novel fluids [96]. Unfortunately, though, the latter paper failed to demonstrate that the consumption difference was limited to the particular flavors when novel only. More research is needed on the inter-modal transfer of prior diversity.

PHYSIOLOGICAL FACTORS

Lesion Effects

Considering the pervasive role of the limbic system in motivation, it is not surprising that lesions in a number of limbic sites dramatically influence neotic behavior. The data reviewed here include lesions of the hippocampus, the amygdala and the septum.

One of the more striking changes produced by temporal lobe ablations in monkeys is that concerning neotic behavior. These animals repeatedly manipulate, smell, and "taste" novel objects and they display little avoidance of normally fear-inducing stimuli [108]. These changes appear to be due, primarily, to amygdaloid damage (see [85]). Rats with amygdaloid damage also display a similar pattern of behavior [167]. Unfortunately, these alterations in neotic behavior have not been investigated in more detail with choice-type tasks. For example, rats with amygdaloid lesions tend to be more active in open fields [43] and in their home cages when confronted by novel lights or odors [208]. However, when tested in a choice-type task the amygdala-lesioned rats display the same level of neotic approach as do intact rats [41, 43, 123]. In fact, they can be more ambulatory and yet display unaltered levels of neotic approach at the same time [41]. Therefore the increased activity may not represent altered neotic approach, but the reasons for the increased activity are not clear.

The most consistent neotic effect produced by amygdaloid damage is that lesions centered in the basolateral complex markedly reduce flavor neophobia in rats. This effect is seen both when absolute consumption [41,137] and preference measures of neophobia are employed [24, 41, 154]. Moreover, the altered consumption is not produced by (e.g.) altered taste reactivity, since it only occurs when the flavor is novel [41,137]. Surprisingly, though, the reduced neophobia is only found with certain flavors; it is seen with saccharin, casein and a 0.02% quinine but not with coffee or vinegar solutions [41]. Although this finding is somewhat confusing, it does rule out a number of explanations for the altered neophobia produced by the lesions. For example, Nachman and Ashe [137] suggested that the lesioned rats are unable to perceive novelty, but, since they respond appropriately to at least some novel flavors, it is clear that their perception of novelty per se is not deficient. Rather, it was suggested [41] that they have a deficient arousal or activation response to novelty such that when a stimulus is weakly arousing they have a residual capacity to respond appropriately, but when the stimulus is intensely arousing, their relative deficiency becomes apparent. This hypothesis would predict that the effect of the amygdala lesion would become apparent only when a sufficiently intense arousal response was normally elicited. This position is consistent with the previously reported data on flavor neophobia; that is, the differential neophobia is only seen with the more salient and/or novel flavors. The effect of amygdaloid lesions are also seen with other arousing stimuli such as looming objects [17,41] and predators [17]. In addition, since wild rat strains are much more arousable than domesticated strains, we should expect to see that amygdala lesions have a more profound effect on their neotic behavior. As expected, amygdala
lesions reduce the container neophobia of wild strains [78] but not domesticated strains [41] and the wild rats tend to be much less refractory to human handling after amygdaloid lesions [78] while domesticated rats are not altered in this response following amygdaloid lesions [43].

Septal lesions also produce changes in neotic behavior although the data is not always as consistent as that derived from amygdaloid lesions. Septal rats seem to avoid novel stimulation. They are slower to emerge into a novel environment and, once in it, will make fewer contacts with novel objects [58,59]. Septal rats are more hesitant to move when a change is introduced into a familiar environment [43] and they also perseverate in a spontaneous alternation task in bright light [37]. But some studies report opposite findings. For example, Clody and Carlton [37] obtained faster emergence in septals, although this behavior could also be viewed as escape-motivated since the animals were leaving a novel enclosure. However, this interpretation cannot be applied to the procedure employed by Thomas, Moore, Harvey and Hunt [189], who found faster home-cage emergence in septals. Differences in lighting conditions may contribute to some of the discrepant findings since septals are over-reactive to light [76]. For example, Clody and Carlton [37] found that septals alternate at near chance levels in the dark but perseverate in lighted conditions. The pre-surgical experience of the animals can also play a crucial role in the lesion effects since early environmental or dietary diversity ameliorates the effect of septal lesions on neotic behavior [58,59]. The septal rat's tendency to avoid novelty is consistent with its general hyperreactivity to a wide array of stimuli, including lights, shocks, tastes and touch [76]. It would be instructive to investigate the response of septals to novel foods and feeding conditions in addition to a wider range of environmental stimuli.

Hippocampal lesions alter behavior on "exploration" tasks in a number of ways; open-field activity is increased but, on the other hand, spontaneous alternation is reduced to near-chance levels [60,124,153]. Once again there is a discrepancy between the open-field data and direct measures of neotic approach from a choice situation. Hippocampally-ablated gerbils display enhanced locomotor activity but when confronted by novel objects in their home cage they are less investigatory as measured by biting and manipulating responses [84]. In any case, the open-field differences may not reflect changes in neotic behavior per se. Rather, the rate of habituation is much slower in hippocampally-lesioned rats (see [105]). It is clear how this factor would increase open-field activity over a fixed time interval and Stevens [182] has demonstrated how slower habituation alters spontaneous alternation. He confined independent groups of lesioned and intact rats to their initial choice arm for either 50 sec or 50 min. The intact rats alternated under both conditions but the hippocampals only alternated after the 50 min confinement, suggesting that this additional time was needed for them to habituate to the arm.

There are two studies which suggest that neotic approach per se may also be altered in hippocampal rats. Normal rats will attempt to escape from an open-field by jumping onto the edge of the wall (if conditions allow) but rats with hippocampal lesions do not attempt this [183]. Hippocampally-lesioned rats, given a choice between novel and familiar tastes, also exhibit a greatly reduced flavor neophobia compared to controls [109]. The reason for these neotic preference changes is not clear, although an inability to perceive novelty is one possible explanation (see [39]).

**Drug Effects**

A wide array of drugs have been found to modify neotic preference. They can be conveniently grouped into three categories on the basis of their primary behavioral and central nervous system action: stimulants, depressants, and toxic agents. The first group includes amphetamine, methamphetamine, methylphenidate, caffeine and ephedrine.

Amphetamine has a well known stimulant action on rearing and locomotion (e.g., [97, 116, 152]). These behaviors might be taken as evidence of increased exploratory tendencies except that when amphetamine-treated rats are given an opportunity to explore novel stimuli they invariably explore less than non-drugged rats [116, 152, 213]. Moreover, the increased rearing and ambulation can occur in a familiar area at the same time that the animals are avoiding a novel chamber [102]. These results indicate that the enhanced rearing and ambulation reflect drug-induced spontaneous activity rather than exploratory behavior. Several other paradigms have been employed to sample the neotic behavior of amphetamine-treated rodents. Animals so treated display decreased investigation of empty "troughs" in a maze [110], as well as fewer and shorter "head-dips" on a hole-board apparatus [71,193]. Amphetamine also produces increased avoidance of strange conspecifics in adult [172] and 30-day-old rats [30]. A fairly consistent dose-response relationship is often observed, such that larger doses further increase neotic avoidance [30, 71, 193] although Hughes and Grieg [102] reported an inverted U-shaped relationship.

Methamphetamine has effects very similar to those of amphetamine (e.g., [102]) and Berlyne [14,15] has extensively investigated its action on the reinforcement value of sensory change. By training rats to bar press while drugged and testing their responding in extinction while non-drugged, Berlyne was able to distinguish the reinforcement value of sensory change from performance changes induced by the drug. In the first experiment [15] rats bar pressed for either a novel or a familiar stimulus. The novel stimulus was more reinforcing for the non-drugged animals but the familiar stimulus was more reinforcing for drugged rats. A similar pattern of results was obtained when light-change versus no-light-change was compared. Light-change was more reinforcing for normals while no-light-change was more reinforcing for drugged animals. Moreover, this difference was dependent on the novelty of the light-change; when familiar it was equally reinforcing for both groups [14].

The consistent changes in neotic preference produced by amphetamine and methamphetamine are also mirrored in another CNS stimulant, methylphenidate (Ritalin). This drug also induces ambulation and rearing but, simultaneously, reduces or reverses the usual preference for novelty [61, 102, 104].

The neotic behavior induced by caffeine is not as consistent as that of the other CNS stimulants but there are too few reports to properly evaluate its action. Hughes and Grieg [102] found that it reduced neotic approach but Cox [46] observed increased rates of spontaneous alternation in caffeine-injected rats (i.e., heightened neotic approach).

The sympathetic activation induced by epinephrine does not produce neotic behavior similar to that of the central stimulants. Haywood and Hunt [91] report that the novelty preference of humans is unaltered by the drug. Leventhal and Killackey [115] report that it does not alter neotic approach in rats. However, they also found that if
epinephrine-injected rats were subjected to a stimulus consisting of an intermittent light and buzzer shortly before the preference test, they exhibited longer start latencies and an almost complete avoidance of the novel compartment. This interaction between autonomic arousal and environmental stimulation is strongly reminiscent of the potentiation of emotional responses by epinephrine observed in humans [166].

The second major grouping of drugs are those which generally are seen to have a depressant or tranquilizing effect on behavior and/or CNS functioning. The drugs that have been studied are: alcohol, the barbiturates, chlorpromazine, and the benzodiazepines. Since most of these agents have anti-anxiety effects in humans it is expected that they should generally reduce neophobic tendencies in rats. At the very least, we should anticipate opposite effects to those of the stimulant drugs.

For the most part the neototic action of alcohol is consistent with expectations, although the effect only occurs with low doses. A low dose (0.4 g/kg) will enhance exploration on a hole-board for both rats and mice [68,71], although this effect occurs in rats only when the situation is relatively simple [68]. A higher dose (0.8 g/kg) tends to reduce exploration back to control levels for rats [68] and exploration in mice remains stable [71]. An even higher dose (2.0 g/kg) reduces alternation levels in a Y-maze in rats [46], thereby suggesting a reduced neototic preference.

There is also some information available on the neototic action of barbiturates. It has been reported that ambobarbital increases rearing frequency [97] and ambulation, but the same dose does not alter trough investigation in a Y-maze [110]. Sodium pentobarbital has been used by Berlyne [14], who tested the effect of a range of doses (5 to 20 mg/kg) on sensory reinforcement. All doses eliminated the usual reinforcement value of sensory change. Moreover, since the animals were tested during extinction while non-drugged, the reduction in bar-pressing cannot be attributed to a performance deficit. Apparently, then, the barbiturates do not increase neototic approach and may sometimes reduce it.

Chlorpromazine has been tested in a number of experiments and appears to have dose-dependent and task-dependent effects. Kumar [111] found that 1.5 mg/kg did not affect trough investigation and similar dose levels do not modify alternation levels [62]. But further data provided by File [67] indicate that this absence of drug action is probably due to the low dose levels employed. She found that 4.0 mg/kg but not 2.0 mg/kg increased the latency to enter a chamber containing novel objects and reduced the time spent exploring these objects. Doses at this level will also increase the avoidance of strange conspecifics [172]. In contrast to these reports, a study by Mitchell, Fairbanks and Laycock [129] revealed that chlorpromazine (5 mg/kg) almost completely eliminates container and food neophobia in wild rats. This effect was observed under both laboratory and feral testing conditions. Moreover, the choice test employed by Mitchell et al. [129] precluded the presence of enhanced consummatory behavior as a possible confound and a control experiment demonstrated that the drug did not alter taste preferences. This experiment is consistent with an anti-anxiety interpretation of the drug's action and it should be similarly tested in a number of other neophobia-inducing situations. The fact that wild rats were employed may be particularly relevant.

The neototic action of benzodiazepines has been tested in a number of tasks. Several experiments have found that chlordiazepoxide tends to reduce investigatory approach behavior [101, 104, 111] although this may not occur in female rats [104] or at doses below 5 mg/kg [101]. With male rats at a 5 mg/kg dose the reversal of neototic preferences is quite strong: saline-injected rats remain in a novel chamber 57% of the time whereas drugged rats stay there only 30% of the time. In contrast to these findings Eison and Tye [64] have reported that 4 mg/kg of chlordiazepoxide decreased emergence latencies in socially isolated rats but that 7.5 mg/kg had no effect. Similarly, File [68] has reported that 5 mg/kg of chlordiazepoxide increases exploration on a hole-board apparatus, but if the situation is made more complex the drug has no effect. A higher dose (7.5 mg/kg) had no effect or tended to reduce exploration below control levels. File's [68] finding that the complexity of the situation can be important should be investigated further.

Many of the preceding data indicate that benzodiazepines do not effect, and sometimes increase, neophobia. But in view of the purported anti-anxiety action of the minor tranquilizers in animals (cf. [124]) it should be expected to find that the drugs reduce neophobia. Just such a result has been purportedly found by Poschel [144] who reported that sated tranquilizer-treated rats drank substantially more (=300%) novel milk than their saline-injected counterparts. Poschel suggested that the tranquilizing agents counteracted the rats' usual flavor neophobia but he did not determine whether the enhanced consumption was limited to novel foods. Wise and Dawson [214] have investigated this question and found that diazepam also dramatically enhances the consumption of familiar lab chow. The socially isolated rats but that 7.5 mg/kg had no effect. Similarly, File [68] has reported that 5 mg/kg of chlordiazepoxide increases exploration on a hole-board apparatus, but if the situation is made more complex the drug has no effect. A higher dose (7.5 mg/kg) had no effect or tended to reduce exploration below control levels. File's [68] finding that the complexity of the situation can be important should be investigated further.

The final drug action to be reviewed here concerns the effect of toxic agents on flavor and container neophobia. Several investigators have found that rats subjected to a toxic agent or the absence of a necessary nutrient (e.g., thiamine) in conjunction with a food, will not only avoid that food but new ones as well [155,162]. More recently, it has been reported that rats poisoned following water ingestion subsequently exhibit an enhanced reluctance to consume a novel saccharin solution [32,42]. There are at least 2 possible explanations for these findings: (1) The 2 flavors may be similar in some aspects and the aversion conditioned to the first flavor is generalized to some degree to the second. (2) The illness experience sensitizes the animal to novel events such that its usual neophobic response is enhanced. Domjan [53, 55, 56] has conducted extensive research on this topic and his data indicate that both mechanisms are at work. In one case, the acquisition and retention of a taste aversion is necessary for an enhanced avoidance and Domjan [53] concluded that a likely explanation of these results is a general-
ized taste aversion. The generalization does not occur between all flavors, for example, a saccharin aversion will generalize to casein but not to vinegar. Moreover if the test flavor is even slightly familiar there will be no enhanced avoidance [16,53]. For this reason Best and Batson [16] have suggested that the generalization does not occur along a taste dimension but, rather, along a novelty dimension. That is, the animal learns that the class of novel foods is unsafe. This is an interesting hypothesis but it is not consistent with Domjan's [53] finding that the enhancement does not occur between all novel flavors (e.g., saccharin and vinegar). Moreover, if the rat is poisoned following consumption of a highly familiar substance, such as tap water, it will later avoid a novel fluid [32,42]. It is difficult to see how this constitutes generalization along a novelty dimension. Evidently this aspect of illness-enhanced neophobia is quite complex and requires further investigation.

The illness-induced sensitization of neophobia appears to be a simpler phenomenon. Toxicosis in the absence of edibles does not result in enhanced neophobia if tested a day or more later but does so if tested within several hours [42,56]. The amount of sensitization is closely related to the intensity of the toxic experience since it is dose-dependent and time-dependent [56]. These characteristics indicate that the sensitization only occurs while the animal is still affected by the drug. However, the attenuation of consumption is not simply due to a general debilitating effect of the drug since water consumption remains unaltered. Even if a high drug dose nonspecifically reduces intake, novel solutions are affected to a greater extent than familiar ones [42]. These data indicate that the toxicosis does not produce a general debilitation but specifically reduces consumption of novel substances and are consistent with the suggestion that the toxic experience sensitizes the usual neophobic response. While most studies of toxicosis-enhanced neophobia have examined flavors, there are also some indications that illness can sensitize container [130] and object neophobia [171].

The data on drug effects has provided some fairly consistent findings on the effects of toxic agents and CNS stimulants. Both types of drugs reduce neotic preference over a wide range of conditions and the effects tend to be dose-dependent. Further investigations are needed to determine the mechanism(s) through which these drugs affect neotic behavior. The effects of the anti-anxiety drugs are the most inconsistent. While alcohol in low doses appears to have the expected action, the other drugs either do not affect neotic behavior or, most surprisingly, reduce or reverse neotic preference. The latter finding is especially damaging for a number of theories of neotic behavior based on arousal level (e.g., [13,14]). Moreover, if one views all three classes of drugs, it is apparent that the most prevalent drug action is a reduction in neotic preference. This is an interesting finding and suggests that any drug-induced state change might be aversive for the rat. Since aversive agents such as shock reduce neotic preference, the drug state may be acting as an aversive event.

SOME METHODOLOGICAL ISSUES

In general, limiting the present review to only choice-type measures of exploration has provided a more consistent and reliable picture than that provided by open-field measures. Although the open-field is a valuable "data-snooping" tool, its usefulness as a measure of neotic approach and avoidance is severely limited by the number of confounding variables that affect activity. Accordingly, the continued use of choice measures to examine the determinants of neotic preference is recommended. A number of new measures of neotic preference have been developed, such as the hole-board apparatus, and it is hoped that validation and standardization of these tests will continue.

The intensive investigation of flavor neophobia is a comparatively recent phenomenon and it offers a great deal of promise in uncovering the mechanisms of neotic behavior. However, because it is a new phenomenon, the necessary conditions for its demonstration have not been well laid down. By definition, flavor neophobia is a temporary behavior change (as are all other neotic behaviors) and in order to conclude that flavor neophobia has been altered it is necessary to demonstrate that the altered consummatory behavior occurs only when the flavor is novel. That is, the altered consumption should change as the flavor becomes familiar and dissipate entirely with sufficient familiarity. The failure to observe this basic requirement has resulted in some questionable conclusions. Some researchers have only provided their subjects with one exposure to a novel flavor and have concluded that altered consumption is due to altered neophobia. However, they have not ruled out a more general change in consummatory behavior or in flavor reactivity. To do this, repeated or prolonged exposure must be provided.

An even more serious problem occurs when investigators do provide repeated exposures and find that the consummatory differences persist for the duration of the testing. In this case the most reasonable conclusion is that the experimental manipulations have produced a relatively permanent change in consummatory behavior or flavor reactivity. However, in two such cases reviewed by the author [31,198] the researchers claim to have modified flavor neophobia. This is a serious interpretive problem which must be guarded against in future research.

THEORETICAL CONSIDERATIONS

A detailed discussion of theoretical mechanisms has been intentionally avoided. This reflects, for the most part, the present state of the literature since most recent reports have not been directed towards the elucidation of mechanisms. However, a few comments can be offered. First, the range of factors that alter neotic behavior and the various directions in which they alter it argue against the position that any one mechanism can account for all the data. Theories that relate neotic preference to optimal arousal levels or adaptation level are especially vulnerable to this criticism. Although there are some findings that are consistent with the predictions of these theories, other findings lie completely outside their scope, and some are clearly contradictory (see [65]). While this latter evidence does not necessarily refute these theories, it does indicate that mechanisms independent of adaptation or arousal level can alter neotic preference. In fact, the diversity of effective variables suggests that many physiological mechanisms modify neotic behavior. Although there are many, as yet, unexplored possibilities, future research might be most profitably directed towards the involvement of neurochemical systems. For example, the consistent effect of amphetamine and methylphenidate in reducing neotic approach suggests the possible involvement of catecholamines. There is also an indication that serotonin levels can modify neotic preference [179]. In addition, the pituitary-adrenal system responds consistently to novel, non-gustatory stimuli (see [178] for refs.), although novel
flavors do not induce a pituitary response [178]. Unfortunately, though, since the causal relationship between the pituitary-adrenal axis and behavior has not yet been established, the meaning of these changes is not clear.

Finally, after reviewing the various determinants of neotic preference, it is apparent that reactivity to novelty is not distinctly different from reactivity to other sources of stimulation. Rather, neotic behavior is one component of a constellation of behavioral changes that is usually referred to as "emotional reactivity". This is especially obvious when the changes produced by septal lesions, amygdaloid lesions, or domestication are examined. This conclusion confirms the assumption that has been made by several researchers that responsiveness to novelty is one measure of emotionality. However this conclusion also has other implications in terms of the mechanisms that determine neotic behavior and it should be kept in mind when theoretical mechanisms for neotic behavior are proposed.

REFERENCES

EXPLORATION AND NEOPHOBIA


