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Neuroethological Perspectives on Aversively Motivated Behavior

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From an ethological perspective, the behavioral effects of independent variables and the selection of dependent variables are viewed with regard to the natural habitat and to the specific responses or response patterns used in that habitat by the species under study. Neuroscience is the study of the nervous system and behavioral neuroscience is concerned with the function of the central nervous system in the control of behavior. Therefore, a neuroethological perspective would involve the study of central nervous system function within the context of ethological considerations. In the previous topic sections, the usefulness of the neuroethological perspective has already been emphasized. For example, the importance of gustatory cues in the learning of food aversions by rats and the relative unimportance of auditory or visual cues (see Garcia, this volume) can be understood from a consideration of the natural habitat of the rodent. Thus, whereas visual and auditory cues in the environment may be associated with a particular food source, they may be less likely to be associated consistently with a particular food type; taste cues, on the other hand, would be highly predictive of a particular type of food and could, therefore, be the better predictor of toxic substances.

Furthermore, odor cues associated with taste cues followed by nausea might be expected to lead to

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powerful aversions for the same reason. Odor cues on their own might be expected to be poor cues for aversion learning because they, like visual and auditory cues, may be encountered in the absence of ingestion of the toxic substance. This is exactly what has been found in laboratory studies (Garcia, this volume). Further analyses of the taste, odor and exteroceptive cues in aversion learning indicated that Garcia's double dissociation was even more complicated than was originally thought and place a greater descriptive burden upon the configurations of the compound stimuli presented in the typical taste-aversion experiment (Archer, Sjöden & Nilsson, 1985; Archer, Sjöden, Nilsson & Carter, 1980). Notwithstanding these complications, the excellent work of Bermudez-Rattoni and Prado-Alcala (this volume), has of late demonstrated different neuroanatomical substrates for gustatory-illness versus olfactory-illness conditioning and provides a good example of a neuroethological perspective on aversively motivated behavior.

Apart from its neuroethological perspectives, the long-delay learning effect of taste-aversion conditioning, by which taste aversions are learned even over long taste-poison intervals has important consequences for the general processes of the laws of learning (e.g. Garcia, McGowan & Green, 1972, but see also Overmier & Archer, this volume). On both counts Revusky's interference theory (1971) bears some consideration. This account suggests that long-delay conditioning depends on two general factors: retention of the conditioned stimulus (CS) at the time the unconditioned stimulus (US) is presented and mutual "relevance" in the relationships of the CS, US and the contextual events. In accordance with the principle of *stimulus relevance*, introduced by Capretta (1961), associations are learned more readily between two events of the same class than if one belongs to a different class. Thus, the associative strength of a cue with some consequence depends, in part, on the nature of the consequence (Dietz & Capretta, 1967). Associations between taste and illness are more powerful than any other "interfering" associations, since the stimulus events which predominate at the time of conditioning and in any CS-US interval (i.e., exteroceptive stimuli) belong to a different class. The principle of *situational relevance* implies that associations are more likely to occur between two events (e.g., taste and illness) that occur in the same environment than between events occurring in different environments. These two principles have been incorporated by Revusky (1977) in a rule of concurrent interference by which "... the strength of an association between any cue and an aftereffect changes as an inverse function of the number and strengths of the competing associations of other cues with the same aftereffects". (p. 42).

The neuroethological section was represented by two presentations (one by Stephen Suomi, the other by Giorgio Bignami) that differed widely with respect to the species being studied (rhesus monkeys versus rats and mice), the types of aversive independent variables being manipulated (separation from the social group versus electrical footshock) and the behavioral dependent variables recorded (social behavior upon reintroduction to the group versus escape and avoidance running responses). (Stephen Suomi's chapter never materialized. He made an

excellent presentation at the conference and we shall try to outline a few salient aspects.) Suomi discussed the effects of genetic pedigree as an independent variable and measured catecholamines and metabolites as additional dependent variables that may provide indications regarding the possible contribution of these neurotransmitter systems to the observed behaviors. Bignami compared rats to mice, using ethological information regarding their behavior in a naturalistic environment to better understand the differential responses of these two species to a variety of independent variables in avoidance learning including prehandling, time of shock offset/onset, size of door (hurdle) between compartments, length of intertrial interval, modality of conditioned stimulus, shock intensity and a variety of pharmacological compounds. In spite of the differences in the approaches taken by Suomi and Bignami to their study of aversively motivated behavior, the work of both of these scientists can be related from the neuroethological perspective. Thus, both were concerned with the ways that a consideration of the behaviors of the species under study in its natural environment can contribute to a better understanding of the behaviors observed in their experiments and the possible neural and/or neuropharmacology mechanisms involved.

Suomi's presentation described a long series of longitudinal studies of the social behavior of rhesus monkeys, both in captive colonies and in natural environments. He found large inter-monkey variability in responses to isolation from the social group and sought to identify the contribution of genetic and neurochemical variables to this phenomenon. His results revealed that individual responses to aversive events such as separation from the social group were highly heritable. Moreover, physiological changes including levels of catecholamine metabolites or adrenocorticotrophic hormone varied among individuals and seemed to be correlated with the perception of or ability to cope with the aversive stimulus. In recent exciting work Suomi has found that the behaviors of free-ranging monkeys of a different species showed similar inter-individual variability in response to aversive events and is seeking to identify genetic and biochemical components in the response. These studies, by virtue of a unique width (species), duration (time span) and depth (numbers of individuals), provide an excellent neuroethological perspective on the aversively motivated behavior of monkeys.

The studies of Bignami, reported in this section, with their focus upon a very standard behavior (i.e. two-way active avoidance) and the species most commonly used for animal experiments, rats and mice, complement those of Suomi. Bignami demonstrates that the acquisition of active avoidance responses of rats and mice is affected by a wide range of methodological and neuropharmacological variables. Furthermore, he has found that the effects of some of these variables on rats and mice differ. For example, when required to approach a lighted area to escape and learn to avoid electrical footshock, rats were found to be more impaired than mice. From an ethological perspective this might be understood with reference to the behavior of the two species within a naturalistic setting. Thus, the rat is usually almost totally inactive during the day but the mouse, with a higher metabolic rate, is seen to be active both during the

night and day. Perhaps rats are less inclined than mice to approach a lighted area to avoid shock because of this stronger natural tendency to remain inactive in the light. Of course this hypothesis should be tested in other paradigms to establish its generality, but it provides a useful neuroethological perspective that aids in unravelling the meaning of striking species differences in the effects of relatively minor procedural variations in avoidance methodologies.

There are many other aversively motivated behaviors that could also have been included in this section covering neuroethological perspectives. Indeed, it should eventually be possible to relate all aversively motivated behaviors to the behavior of the species under study in its natural habitat and to identify the neural basis of these behaviors (à la Bolles, 1985). Some of the other behaviors include taste aversion learning, defensive burying, swimming to safety and predator escape and avoidance. Defensive burying is a phenomenon that involves returning to the source of an aversive stimulus and burying the source (Pinel & Treit, 1978). The act of approaching environmental stimuli that signal an aversive event seemed contrary to the widely held belief that animals avoid such stimuli.

However, burying will only be seen if appropriate burying material is available and if the source of the unconditioned aversive stimulus can be identified; neither condition is normally met in a shock avoidance paradigm. Here again, a consideration of the behavior of rats and other species in their natural habitat provides some clues to understanding this behaviour. Thus, a number of species, including rats, are seen to bury potentially harmful stimuli. Rats' species-specific predisposition to bury objects potentially associable with or associated with aversive stimuli is now well documented (Terlecki, Pinel & Treit, 1979; Wilkie, MacLennan & Pinel, 1979) and is certainly important from a neuroethological viewpoint in conforming to the species-specific defence-repertoire (SSDR) formulation by Bolles (e.g., 1970, 1975). The possible involvement of neurotransmitter systems in this phenomenon has also been studied (Beninger, MacLennan & Pinel, 1981; Treit, 1985a). From a neuropharmacological perspective it is of interest to note the mitigating effects of anxiolytic agents, e.g., the benzodiazepines, upon defensive burying (e.g., Treit, Pinel & Fibiger, 1981, 1982). This action has been shown also to be independent of any possible analgesic effects of these compounds (Treit, 1985b).

A related phenomenon to conditioned defensive burying in rats is marble burying generally shown by single mice placed alone in a cage in which a large number (generally 20 to 25) of brightly coloured glass marbles are placed upon the sawdust bedding material. Glass marbles appear to (collectively) provide an effective unconditioned aversive stimulus which "provokes" burying behavior in both rats and mice (Broekkamp, Rijk, Jol-Gelouin & Lloyd, 1986; Poling, Cleary & Monaghan, 1981). One important condition seems to be the removal of socially housed mice to a test cage where they are isolated and confronted by the novel marbles. It is possible that this isolation experience is the aversive stimulus "triggering" defensive burying in a similar manner to that of shock presentation in conditioned defensive burying (Treit, Pinel & Terlecki,

1980). Recently, Archer, Fredriksson, Lewander and Söderberg (1987) developed a technique for measuring marble burying concomitantly with spontaneous motor activity in mice by utilising automated activity cages; an interesting interaction between burying behavior and locomotor activity was revealed. The mice were assigned to either a "marbles" or a "no marbles" group and measures were taken during 60 min sessions over sessions on each of three consecutive days. The "marbles" groups performed significantly less locomotor behavior than the "no marbles" group on the first day of testing but showed significantly more locomotion by the third and final day of testing (see Fig. VI.1). However, the "marbles" group mice buried all their marbles on all three occasions.

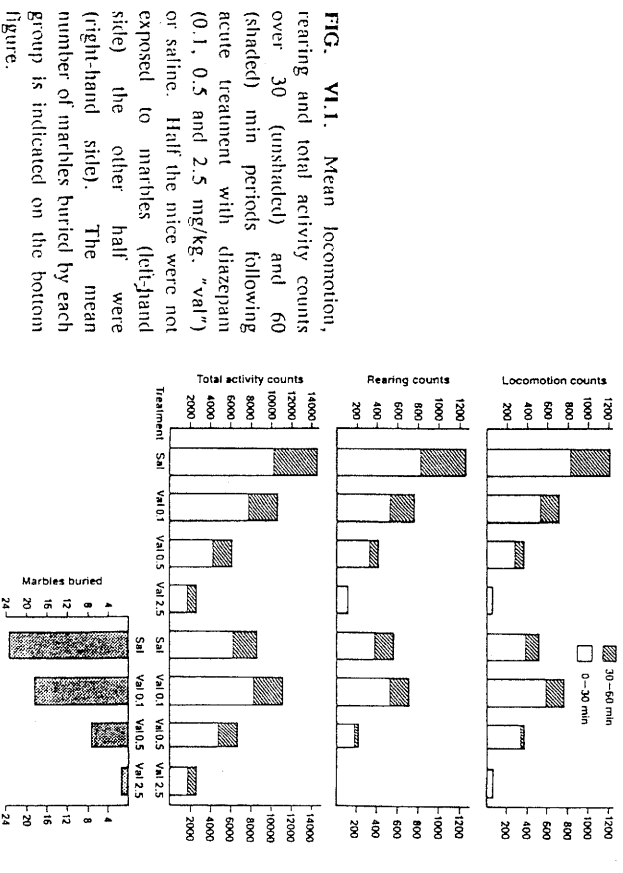


FIG. VI.1. Mean locomotion, rearing and total activity counts over 30 (unshaded) and 60 (shaded) min periods following acute treatment with diazepam (0.1, 0.5 and 2.5 mg/kg, "val") or saline. Half the mice were not exposed to marbles (left-hand side) the other half were (right-hand side). The mean number of marbles buried by each group is indicated on the bottom figure.

Two points can be made from the neuroethological perspective: (1) Burying initially interfered with locomotor activity, and (2) the mice learned to bury their marbles more quickly by Day 3 and then indulged in their locomotor activity, implying a need for locomotor activity suppressed initially by the presence of the aversive marbles. The concurrent behavior analysis has been applied to assess the efficacy of anxiolytic compounds but swim-induced grooming activity has been used as the "activity" variable (Broekkamp et al., 1986). There are both procedural and conceptual (i.e., physiological changes following submergence in a water bath) grounds for suggesting that the concomitant burying-locomotor activity technique is preferable to the concurrent burying-grooming technique but it is clear that reliability and robustness of the burying phenomenon in general offers much scope for further investigation of animal models of drug action in a neuroethological perspective.

For the purpose of a neuroethological awareness certain points may be considered: (1) macromolecular as opposed to specific characteristics of behavior must be weighed in the neuroethological analysis of any given situation. (2) In the application of neuroethological principles the selection of species for the study of animal models of behavioral disturbances may prove to be essential, e.g., primates for affective disorders and rats for stereotypy models of schizophrenia. (3) The utilization and exploitation of individual differences in the behavior of a given population may lead to inferences necessary to the neuroethological analysis. Thus, Suomi has found that individual monkeys sitting on a stretch of road may vary considerably in their response to the approach of an automobile or truck. A few individual disappear immediately, the majority move off to a position of observation out of immediate danger but a few individuals remain unconcerned and expectant. Given a vehicle of evil intent (hunters and/or dangerous drivers) the disappearing individuals ought to be selected for survival whereas in conditions of chronic food shortage the approach of a possible food source provides advantages for the unconcerned individual. In a controlled laboratory analysis (Archer, unpublished data) it was found that the degree of taste-aversion conditioning to saccharin was positively correlated with the degree of taste neophobia shown at the initial presentation of the novel taste saccharin (see Fig. VI.2). Given the aversive circumstances of taste-aversion

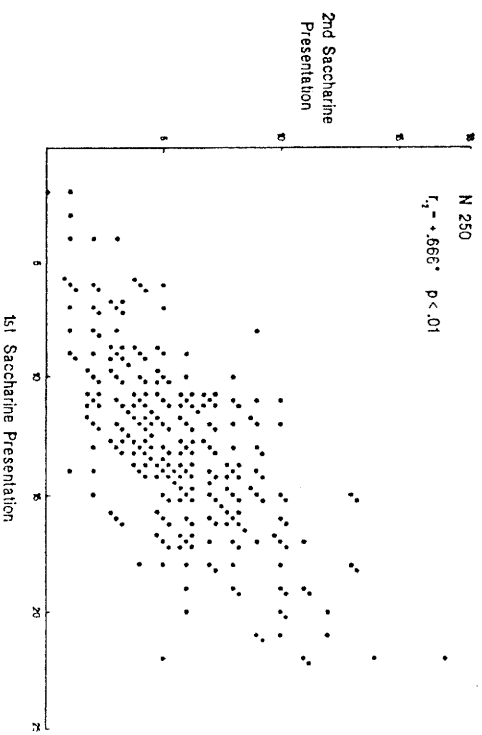


FIG. VI.2. Saccharin intake of 250 rats on two successive presentations. Rats in different conditions (see Table 2) received both saccharin presentations in identical contexts on both presentations. An i.p. LiCl injection followed the 1st presentation. The correlation between saccharin intake values on the 1st and 2nd presentation was positive and significant ($r_{12} = +.666$, $p < .01$).

learning the survival benefits of a high degree of taste neophobia (assuming that the novel taste contained poison) are determined by a low

intake of toxin and developed by a stronger avoidance of the taste. However, in conditions of limited access to nutrients the individuals consuming the large amounts of saccharin might be at an advantage. This positive correlation confirmed that of earlier studies (Archer & Sjöden, 1979a, b). Thus, it is to be hoped that analyses of aversively motivated behavior in terms of a neuroethological perspective may prove to be of long term benefit.

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