Relationship of the upright agonistic posture in the foot shock situation to dominance-submission in male C57BL/6 mice¹

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The agonistic behavior of male C57BL/6 mice was observed in shock and nonshock round-robins. It was found that there was a positive relationship between dominance rank of the participants and frequency of upright reactions in the foot-shock situation. These results suggested that the upright reaction observed in the foot-shock situation be identified not as an attack behavior as is typically done, but rather as an ambivalent, threat, or defense behavior.

The purpose of this study was to determine the relationship between dominance-submission and the frequency of the upright agonistic posture produced in a foot-shock situation similar to that employed by Ulrich & Azrin (1962). This study was part of an extensive series of experiments on the usefulness of the foot-shock technique for the study of agonistic behavior in various strains of mice. Among numerous agonistic behavior patterns, the upright posture is of particular interest not only because of its ease of induction in a foot-shock situation, reliability of measurement, and known relationship to various parameters such as shock intensity, rate, floor area, etc. in rats (Ulrich, 1966), but also because of some amount of controversy over its classification (King, 1966; Scott, 1966). As further evidence, if not of controversy, at least of lack of clarity or precision as to its proper classification, the upright posture in mice has been defined as an index of submission or submissiveness (Beeman, 1947; Clark & Schein, 1966; Ginsburg & Allee, 1942; Scott & Fredericson, 1951; VanAbeelen, 1966; Warne, 1947), as fighting (Tedeschi, Tedeschi, Mucha, Cook, Mattis, & Fellows, 1959), and as defensiveness (Bauer, 1956; Kahn, 1951, 1954; Scott, 1946, 1947, 1966; Scott & Fredericson, 1951; Scott & Marston, 1953).

When observed in rats in the foot-shock situation it has most often been defined as an attack or fighting response (Ulrich, 1966; Ulrich & Azrin, 1962). While important species differences do exist, the similarity of agonistic behavior in mice and rats has been frequently stressed (Scott, 1966). There is a certain danger in assuming that even

topographically similar patterns are functionally equivalent in different species (Kimbrell, 1968). In an extensive series of observations, Grant & McKintosh (1963) have shown that the upright posture in mice and in rats seems to be equivalent not only in topography but in function and in controlling relationships. They classified the upright posture as ambivalent, meaning that it was under the control of simultaneously produced but incompatible flight and attack "tendencies" or "drives." It might be pointed out that postures and behaviors of this variety are usually referred to as threat behaviors by ethologists.

The present study was intended to determine the relationship of the upright posture observed in foot shock situations to dominance-submission and from this hopefully to formulate a clearer notion of the "meaning" or identity of the upright posture as an element of agonistic behavior when produced by foot shock.

METHOD

The Ss were five male C57BL/6 Cum mice housed in isolation from age 44 days throughout the experiment. Age at beginning of the shock round-robin was 94 days, and at the nonshock round-robin, 149 days.

All observations were made while the mice were paired in a grid box (stainless steel rods 4 mm diam, spaced 1 cm center-to-center) and covered by an inverted 1,000-ml glass beaker (10.5 cm diam x 13.5 cm high). Shock (.8 mA) was supplied by an Applegate 228 constant-current dc stimulator delivered to the grid through a Grason-Stadler E1064GSP polarity scrambler. A recycling timer network (two Hunter 111-C) controlled shock duration (.2 sec) and rate (30/min). Behavioral events were recorded on a Gerbrands event recorder.

Mice were handled by the tail with padded forceps, and the grid box was wiped clean between bouts. Each mouse participated in only one bout per day.

In the shock round-robin, each mouse was paired once with each of his four opponents. A bout consisted of placing a pair of mice under the beaker. After an observation period of 5 min, 3 min of shocks were delivered. This was followed by a 2-min observation period. Total bout length was thus 10 min.

In the nonshock round-robin, the mice

were paired as above except that no shocks were given and bout length was extended to 20 min. Following the method of Clark & Schein (1966), dominance in a given bout was estimated by degree of control exercised by one animal over the other.

RESULTS

A variety of agonistic acts were observed in the shock period of the foot-shock round-robin. Pre- and postshock periods were characterized by nonagonistic grooming and scanning, and occasional sniffing or nosing of possible agonistic nature. In the shock period one serious methodological difficulty involved the identification of an animal performing a particular postural reaction or act. In most cases, this was virtually impossible to do. This being the case, only the total frequency of simultaneous upright posturing by both animals upon shock delivery is analyzed in this study. Bout totals of these simultaneous upright reactions ranged from 0-49.

In the nonshock round-robin, attention was focused upon the identity of an animal performing a given act so that a judgment as to the dominant animal in that bout could be made. As mentioned earlier, these judgments were made on the basis of degree of control exercised by one animal over the other. For example, if one animal frequently aggressively groomed the other, or if nosing, sniffing, or touching resulted in withdrawal by the other animal, the animal doing the grooming, nosing, etc., would be judged dominant and the opponent submissive. It might be pointed out that no full-blown fights or attacks were observed. An animal was assigned a rank in the dominance hierarchy (5 being most dominant) on the basis of the total number of bouts in which he was judged dominant.

Figure 1 presents the sum of upright reactions for each animal's four shock round-robin bouts as a function of dominance rank as determined in the nonshock round-robin.

Bout totals of upright reactions in the shock round-robin varied considerably (0-49). The dominance rank obtained in the nonshock round-robin can be used to analyze the upright reaction data in a bout-by-bout fashion. Figure 2 presents each animal's four bout totals plotted as a function of his rank (R_i) minus his opponent's rank (R_j).

From this it can be seen that the observed frequency of upright reactions appears to be a function of the position in the dominance hierarchy and difference in position as conveniently expressed by $R_i - R_j$.

DISCUSSION

The results seem clearly to indicate a positive relationship between dominance rank and frequency of upright reactions observed in the foot-shock situation. The

Fig. 1. Total upright reactions (summed over four bouts) plotted as a function of dominance rank.

Fig. 2. Bout-by-bout analysis of upright reactions as a function of dominance rank (R) as expressed by difference in rank ($R_i - R_j$).

role of experience in the development of this dominance hierarchy cannot, of course, be determined from this brief study. The results are valuable, however, in suggesting the true nature or meaning (i.e., proper classification) of the upright posturing observed in foot-shock situations.

As mentioned earlier, Grant & McKintosh (1963) classified the upright posture as an ambivalent posture, thereby stressing the control of this posture by simultaneously aroused but incompatible flight and attack "tendencies" or "drives." If we accept this for the moment (without getting sidetracked about what we mean by "tendencies" or "drives"), some degree of sense about the upright posture in the foot-shock situation begins to emerge. The shocks control the probability of flight, but complete flight (escape) from the shocks is

precluded by the apparatus itself. The presence of another animal may control flight, attack, investigatory behavior, etc. When shocks are paired with the presence of another animal, we might assume that flight and attack tendencies might predominate rather than investigatory, etc. Thus, when flight-attack are simultaneously aroused in reasonable balance (assuming flight tendencies due to shock are roughly equivalent in both animals), we would expect to observe more upright posturings when both animals have approximately the same degree of attack tendency as they would be expected to have if high and close in the dominance hierarchy. Possibly the upright posture has a releasing effect on the agonistic behavior of the opponent. Likewise, when difference in rank is large, we might expect that a dominant animal is stimulated in the flight-attack fashion, but that a submissive animal is stimulated more in a flight fashion (summation of shock and flight stimulation produced by the behavior of other animal).

This is consistent with traditional interpretations of similar ambivalent behaviors (threat behaviors) as being those which produce flight, or other agonistic behavior in the opponent (Verplanck, 1957). Perhaps actual full-blown fighting is rarely observed in the foot-shock situation due to continual shock-produced flight tendencies resulting in an attack inhibition even in dominant animals.

By choosing appropriate values of dominance, shock level, shock rate, escape opportunity, etc., it would seem theoretically possible to maintain the attack-flight balance (or to alter it as desired) for a specified length of time. Indeed, the data (Ulrich & Azrin, 1962) indicate just this.

To conclude, it appears that the upright reaction is best identified or classified as a defensive threat behavior, or, if the Grant & McKintosh (1963) vocabulary is preferred, as an ambivalent behavior. The above analysis is admittedly speculative. What is needed is data (and technique) to independently vary and assess flight and attack "tendencies" and to combine them in various degrees. This work is now in progress in the author's laboratory.

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NOTES

1. This report is adapted from a portion of a dissertation presented to the graduate council of the University of Tennessee in partial fulfillment of the requirements for the PhD degree in Psychology. The author is grateful to E. Furchtgott, W. S. Verplanck, W. H. Calhoun, and J. C. Howell, not only for assistance and guidance during the course of the research, but also for several pleasant and profitable years of association. Special thanks are due NSF Visiting Scientist U. Weidmann from The University, Leicester, England, for serving as an unofficial adviser during the course of the research.

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