The Behavioral Hierarchy
of the Mollusk Pleurobranchaea

I. The Dominant Position of the Feeding Behavior *

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Summary. Feeding behavior and the effect of its occurrence on other, unrelated behaviors were studied in the carnivorous marine gastropod Pleurobranchaea californica. The threshold of the feeding response is low and stable: it does not change in a circadian fashion (Fig. 1); it does not change during different behavioral states such as mating (Table 4) and quiescence (“sleep”; Table 5); the threshold does not change following aversive electric shock to the oral veil (Table 1); and it does not change with repeated application of food stimuli (Fig. 2). In the present paper only two physiological variables were found to elevate the feeding response threshold; excessive mechanical stimulation (Figs. 3, 4) and satiation with food (Fig. 5).

The interaction between feeding behavior and other, unrelated behaviors was examined using a choice paradigm, i.e., simultaneous presentation of the releasing stimuli for two different behaviors. When the stimulus for feeding behavior (squid homogenate) is presented at the same time as the stimulus for righting (inversion), feeding occurs and righting is suppressed (Tables 2, 3). Similarly, feeding dominates withdrawal of the head, mating and quiescence. Neither mating nor quiescence exerts a reciprocal suppressive effect on feeding (Tables 4, 5), and hence in these cases, at least, the dominance of feeding behavior is unilateral. We conclude that behavioral acts in Pleurobranchaea are organized hierarchically, and that the feeding behavior occupies a relatively dominant position in the behavioral hierarchy.

Introduction

Animals in their natural habitats are exposed to mixed and often contradictory sensory inputs, sometimes combined with multiple internal drives. Of the numerous behavioral responses that are in principle possible, some are more crucial to the survival of the species than others, and must therefore receive higher priority. Moreover, although numerous behavioral responses can in principle occur, many are in practice mutually incompatible, either because they involve different and

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conflicting movements (e.g., exploration and withdrawal), or because they to some degree utilize the same motoneurons (e.g., mastication and speech). Therefore, animals must often “choose” to perform certain behavioral responses to the partial or complete exclusion of others. Accordingly, higher animals have evolved the central nervous machinery required for making such “decisions”.

In this paper and the one that follows (Davis, Mpitsos and Pinneo, 1974), we show that such machinery is manifest in the form of a behavioral hierarchy in the carnivorous mollusk *Pleurobranchaea*. That is, the individual behavioral acts that comprise the animal’s repertory are organized into an explicit priority sequence, in which some behavioral acts are dominant over others. Previously it was shown that feeding is a relatively dominant behavior in *Pleurobranchaea*, in that it takes precedence over righting when the stimuli for both behaviors are presented together (Davis and Mpitsos, 1971). In the present paper we extend this observation and demonstrate further that the threshold of the feeding behavior is extraordinarily stable in the face of several physiological variables that might be expected to alter it. These data provide the necessary background for the second paper; there we show that during egg-laying, the feeding behavior is selectively and profoundly suppressed by a hormone(s) released into the blood by the central nervous system (Davis, Mpitsos and Pinneo, 1974). That is, egg-laying occupies a higher position in the behavioral hierarchy than feeding, and maintains its dominant position hormonally. The study provides the basis for a new formulation of the concept of a behavioral hierarchy (Discussion of the second paper) and for exploring the physiological substrates of this and related ethological and psychological phenomena, e.g., choice, attention and motivation.

**Materials and Methods**

Experiments were performed during the Spring on about 100 specimens of the carnivorous marine gastropod *Pleurobranchaea californica*, collected locally or supplied by Dr. Rim Fay (Pacific Bio-Marine, Venice, Calif.). Animals were stored in running sea water at ambient temperature (11–13°C) and fed raw squid twice weekly.

*Measurement of Feeding Response Thresholds*

The feeding behavior of *Pleurobranchaea* consists of several discrete components, including, in order of increasing threshold: 1) orientation to the food stimulus of both the oral veil and the lateral tentacles that are fused with it; 2) tonic extension of the proboscis; and 3) the rapid bite/strike of the proboscis (Davis and Mpitsos, 1971). The extension and bite/strike responses are easy to identify (Mpitsos and Davis, 1973, Fig. 1); hence they were used as indexes of the feeding behavior in the present work. To measure the behavioral thresholds of these responses, solutions of squid homogenate were applied to the oral veil in order of increasing concentration. The threshold was defined as the lowest concentration that elicited an obvious response.