NEURAL REPRESENTATION OF A BEHAVIOURAL PATTERN: FISH RESPIRATION

by

C. M. BALLINTIJN

(Department of Animal Physiology, Postbox 14, 9750 AA Haren, The Netherlands)

SUMMARY

A description is given of the neural organization of the respiration control system in fishes. Some interactions of respiration with other systems are evaluated.

INTRODUCTION

Both ethological and physiological research is aimed at explaining how animal behaviour and functioning is controlled. The subject is, however, approached from opposite directions in these two disciplines. It is like building a tunnel through a mountain where drilling starts from both sides and eventually leads to unison near the centre. The ethologist approaches from the outside of the animal, studying complex behavioural patterns under conditions which more or less closely resemble the natural situation. He develops models explaining the causation of behaviour and the coordination of behavioural systems. The physiologist starts from the inside, at the level of the elements of the control systems (receptors, neurons, muscles, endocrine organs) and aims at unravelling the elementary circuits and their interactions which ultimately form the basis of all behaviour. The best insight into the operation of such a complex mechanism as an animal is obtained if the results of both approaches are integrated (Baerends, 1971; 1976; 1979). In the present paper attention is focussed on the nervous system. The role of the endocrine system in the control of behaviour will not be considered.

Behaviour is a combination of simpler actions which in turn are composed of more or less stereotyped series of movements. Endeavouring to bridge the gap between "muscles and motivation" Gallistel (1980a; 1980b), inspired by Sherrington's work, introduced the concept of "units of behaviour". These are neural circuits which in themselves contain all the elements for action. Thus they comprise of at minimum: a receptor, a nervous conductor and an effector. The simplest unit, an elementary unit of behaviour, can not be further broken down into complete units of behaviour. Sets of elementary units can be combined in a complex unit of behaviour. This pro-
duces a functionally integrated behavioral pattern which none of the constituents can produce alone. The central nervous part of such a complex unit of behaviour is also called a pattern generator by many investigators and is largely coincident with Doty's (1976) concept of a centre as "a functionally linked set of neurons which are activated only by appropriately encoded stimuli and which are interrelated in such a manner that their combined activity yields a predetermined and reproducible pattern of behaviour".

There are only a very limited number of different elementary units of behaviour. Gallistel (1980a; 1980b) distinguishes three kinds:

a). the reflex, where the output depends solely on the input and the unit’s neural transfer function.
b). the servo mechanism, where negative feedback from output to input plays a crucial role.
c). The oscillator, which generates rhythmic activity with pacemaker neurons or neural pacemaker circuits.

He demonstrates, on neurophysiological data from the literature, that the complex units of behaviour regulating locomotion are composed of these three elements.

Gallistel's use of the term "reflex" is confusing because he adopts a definition which is much narrower than is generally accepted. The well known knee jerk reflex, for instance, is functionally a feedback servo system and therefore not a reflex as defined by Gallistel. To avoid this problem the term "feed forward control" instead of "reflex" (a), would be probably less confusing and compare well with "feedback servo system" (b).

In the present paper the neural control mechanism of fish respiration and its interaction with other systems will be evaluated. It can, like locomotion, be divided into Gallistel’s three units of behaviour.

EXPERIMENTAL RESULTS

For a rhythmic process such as respiration one of the first questions to be asked is: where and how is the basic rhythm generated. Then, there are problems like: how are the muscles that cause the movements controlled; in which way are external disturbances eliminated; which factors modulate the performance of the overall system.

This paper reviews data which partly answer these questions.

Localization of the Respiratory ‘‘Centre’’ and the Generation of Respiratory Rhythmicity

Respiration persists in fishes after transection of the brain at the rostral and caudal border of the medulla oblongata (fig. 4, TR) and