ABSTRACT

Egg laying activity of the pond snail Lymnaea stagnalis changes with age. Initially there is an increase of egg laying activity. At an age of about 250 days egg laying activity starts to decrease and eventually ceases. Lymnaea thus has a clear post-reproductive period during its life cycle. In order to locate mechanisms which are responsible for the cessation of egg laying activity electrophysiological, behavioural and injection experiments were done and the morphology of the neurons controlling egg laying activity (the caudodorsal cells, CDCs) were studied. On the basis of the results of the foregoing experiments and observations it is hypothesized that due to degeneration of particular CDCs in old animals, input to the egg laying control system is terminated resulting in cessation of egg laying.

KEY WORDS: CDC, reproductive ageing, neuronal degeneration, egg laying, Lymnaea, mollusc.

INTRODUCTION

Fundamental mechanisms of ageing processes are still poorly understood. This is illustrated by the great number of theories to explain ageing which exists at present (ADELMAN & ROTH, 1982; CRISTOFALO, 1988). Most theories to date are primarily concerned with ageing as a type of pathology. These theories often concern general mechanisms of damage occurring at different levels of the organism. From a biological point of view, however, the ageing process is of special importance to the organism (KIRKWOOD & ROSE, 1991). In this view and according to ecological optimisation theories, each organism has a strategy to allocate its resources between biologically important functions like maintenance, growth and reproduction in such a way that it maximizes its fitness under a given set of constraints. As a consequence organisms keep a balance between functions like life span (defined by energy spent to maintenance), growth and reproductive activity. This implies that organisms contain (genetic) mechanisms which define life span, growth and length of the reproductive period.
In natural optimal conditions life span is adjusted to the duration of the reproductive period of an organism. Environmental conditions will then define the level of energy expenditure needed to survive this period; if conditions are severe, much energy is needed for maintenance of the organism. As a result in culture conditions many animals survive their reproductive period and have a distinct period during which reproduction has ceased. As pointed out above, mechanisms of reproductive stop can be considered as part of the ageing mechanism. By studying such mechanisms insight can thus be gained in fundamental aspects of ageing. The present paper puts together knowledge on central nervous system (CNS) control of (cessation of) female reproductive activity of the pond snail *Lymnaea stagnalis* related to ageing in order to gain insight into possibilities to study neural ageing mechanisms.

**POST-REPRODUCTIVE LIFE IN MOLLUSC**

Only of few molluscan species the fate of animals after their reproductive period is known. The opistobranch *Aplysia* (van Heuken, 1979) and the cephalopod *Octopus* die shortly after cessation of reproductive activity. In *Octopus* this is caused by inhibition of eating behaviour after the production of eggs (Wodinsky, 1977). Only in pulmonate snails a distinct post-reproductive period has been described. In these animals the post-reproductive period starts after growth has ceased (Comfort, 1957; 1979).

**REPRODUCTIVE CONTROL IN THE PULMONATE SNAIL**

*LYMNAEA STAGNALIS*

Reproductive control in *Lymnaea* has been studied now in our laboratory for several decades (see e.g. Geraerts et al., 1988). In *Lymnaea* egg laying is controlled by hormones secreted by the DBs (DB-hormone) and by peptides secreted by the CDCs (CDC-peptides). DB-hormone controls cellular differentiation, growth and synthetic activity of the accessory sex organs. The CDC-peptides control ovulation, egg laying behaviour and synthesis and packaging of the eggs (Joosse, 1988). The CDCs contain two members of a gene family which encode for the CDCH-I and II preprohormones [in addition a third gene has been found recently (A.B. Smir, pers. comm.)]. Each prohormone gives rise to about 11 different peptides among which the CDC-hormones CDCH-I and II (Geraerts et al., 1991).

Just before the start of ovulation and egg laying the CDCs become electrically active. Upon activation they secrete CDC-peptides in the haemolymph. This induces a stereotyped pattern of overt and covert