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Modulation of aerial respiratory behaviour in a pond snail☆

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Abstract

Aerial respiratory in *Lymnaea* is driven by a three-neuron CPG whose sufficiency and necessity has been directly demonstrated. While this CPG is 'hard-wired' it displays a tremendous amount of plasticity. That is, it is possible by employing specific training procedures to alter how it functions in a specific hypoxic environment. Thus, it is possible to study directly the causal mechanisms of long-term memory formation, forgetting, and modulation of the memory at a single cell level. Thus, it is possible to use a relatively simple three-neuron CPG to study not only important questions concerning regulation of important homeostatic mechanisms but to also use it to study how learning and non-declarative memory are mediated at a cellular level.
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Keywords: Respiratory CPG; Learning; Memory; *Lymnaea*

1. Introductory remarks

As physiologists in one-way or another our research is concerned with 'the where', the 'why' and 'the how' of homeostasis and quite possibly the neural control of respiration is the quintessential homeostatic system. Our laboratory has focused on the neuronal mechanisms underlying control of two molluscan (*Aplysia* and *Lymnaea*) respiratory systems. However, our primary reason for using these model systems was not to study respiratory behaviour per se; but rather to use these systems to study the neuronal mechanisms of learning, memory, and forgetting. We will concentrate this review on key aspects of aerial respiration in *Lymnaea* and show how this behaviour can be modified by experience, the environment, and ageing.

Homœstasis is defined as in the following manner: "to designate stability of the organism" and according to the OED was first used in the English language by Walter Canon in 1926. Unsurprisingly then the word may imply to some the necessity of constrained plasticity in the neural system that controls a specific homeostatic behaviour; however, we feel that the ability to maintain homeostasis can only come about because *there is plasticity* within the neural control system. Let us explain what we mean by this. The 'hard-wired' neural system that controls aerial respiration in *Lym-*

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naea is a good example of a homeostatic system that displays both ‘rigidity’ and ‘plasticity’. It is ‘hard-wired’ in the sense that the neurons, which comprise the central pattern generator (CPG), only form appropriate synapses with the cells that they should ‘talk’ to and not others even when given the opportunity to do so in cell culture. Further, in cell culture these neurons, which ‘self-connect’ recapitulate the patterned neural output seen in isolated ganglion and semi-intact preparations that drive aerial respiratory behaviour. The ‘plasticity’ inherent in this system enables us to have one of the premier model systems in which to study not only how the nervous system controls breathing per se but *also* the neuronal mechanisms of learning, long-lasting memory formation and forgetting. We thus study a ‘malleable hard-wired’ system. Aerial respiratory behaviour in *Lymnaea* is pliant because the behaviour, which is driven by the CPG, can be changed (i.e. learning occurs) and that change can be remembered (i.e. memory) and then be possibly forgotten.

2. Aerial respiration in *Lymnaea*

The snail, *Lymnaea stagnalis* (L) that we work with satisfies its respiratory needs in two different ways: via its skin and via a lung. That is, this snail is a bi-modal breather (Jones, 1961; Lukowiak et al., 1996; Taylor and Lukowiak, 2000). Gas-exchange occurs across the snail’s skin (cutaneous respiration) and across an exchange surface located within its lung (aerial respiration), when the lung is ‘in contact’ with the atmosphere via the respiratory orifice – the pneumostome. At its most basic, aerial respiratory behaviour in *Lymnaea*, can be described as the opening and closing the pneumostome (the respiratory orifice that leads to the lung) at the water surface (Fig. 1). Thus, this behaviour is easily observable and quantifiable (i.e. number of breaths and duration of breath). However, it is more complicated than that. To perform aerial respiration the snail comes to the surface of the water and once there fully opens its pneumostome; the mantle muscles then contract expelling the lung gas into the atmosphere (i.e. expiration). These muscles then relax, allowing passive re-inflation of the lung by its elastic recoil (i.e. inspiration). This contraction followed by relaxation occurs a number of times before the pneumostome is finally closed by the contraction of

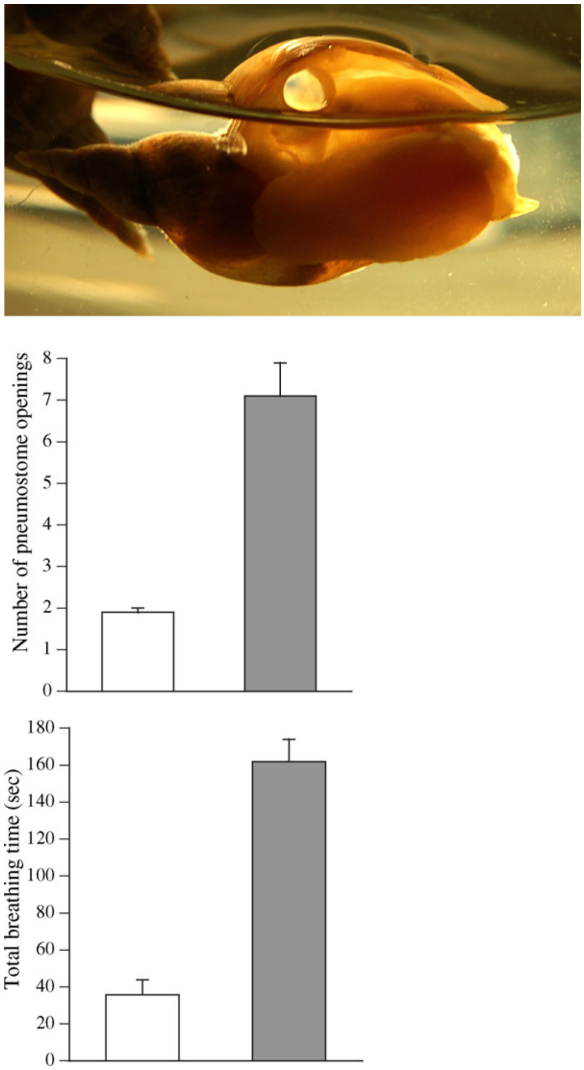

Fig. 1. Aerial respiration in *Lymnaea*. The photograph shows an adult snail (shell length 2.5 cm) at the surface of the aquarium with its pneumostome (the respiratory orifice) open. As the snail opens its pneumostome it contracts muscles in the mantle and pneumostome area to force ‘stale’ air out of the lung. As these muscles relax, ‘fresh air’ enters the lung. Aerial respiration can only occur at the surface of the water. As shown in the two graphs below the picture of the snail in eumoxic conditions (clear bars) aerial respiration as measured by either the number of pneumostome openings (top graph) or the total time the pneumostome is open (bottom graph) occurs significantly less often ($p < 0.01$) than when the snails are placed in hypoxic conditions (filled graphs).

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