Neuroecology

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The nature of the neural circuits that control behaviors is determined by several overlapping constraints: functional, material, developmental, evolutionary, and ecological. The functional constraint relates to the computational task that the circuit undertakes, for example, edge detection, rhythm generation, phase-specific feedback control, and information storage. The problem of completing these tasks must, however, be solved using biological materials (proteins, lipids, membranes, solutions of ions). Putting a nervous system together during development requires mechanisms of considerable complexity and it is easy to imagine that certain theoretical solutions for correct construction would be unfavorable from developmental perspectives. It is well established that neural circuits reflect their evolutionary histories such that they can have features of arguably less than optimal design for current tasks, as a result of adaptations for prior function and roles (Dumont and Robertson, 1986). Finally, circuits evolve and function in the context of an environment and the organism's ecological niche and these change over all the biological time scales: moment to moment, daily, seasonal, and evolutionary. Whereas many neuroscientists are primarily interested in mechanistic answers to the computational problems, there is a growing awareness that such an approach is limited in its ability to explain the structure, function, and behavioral role of nervous systems (Chiel and Beer, 1997). *Neuroethology* takes a comparative approach to understanding how nervous systems control behavior by instead focusing on the mechanisms underlying the natural behaviors of diverse species in a natural context. Clearly, evolution has matched the design of the circuitry to the functional demands of an organism's ecological niche. This means that full understanding of existing neural mechanisms requires, at the very least, consideration of the ecology of the organism investigated. Appreciation of this general observation has spawned integrative disciplines such as evolutionary physiology (Feder et al., 2000), ecophysiology (Le Maho, 2002), and neuroecology.

An early, and now archaic, use of the term *neuroecology* was with reference to the interactions of individual nerve cells striving to survive during development in a competitive extracellular environment (Purves and Lichtman, 1985). Current usage pertains to investigations of the specializations of nervous systems in the context of the ecological niche that an organism occupies. At its simplest, this encompasses comparative studies of how neural mechanisms and processes may have been shaped by evolution to be optimally suited for particular ecological niches. The hope is that an interdisciplinary approach incorporating neuroscientific and ecological techniques and mindsets will inform both disciplines by clarifying the constraints that principles of each impose on the other. Legitimate concerns exist about the utility of a strict neuroecological approach for discovering causative neural mechanisms (Bolhuis and Macphail, 2001) but an emerging consensus suggests that a consideration of the functional and ecological demands on circuitry is indispensable when trying to determine how it operates (e.g. Dwyer and Clayton, 2002).

An ecological variable that affects neural circuitry and may have constrained (or enabled) its evolution into different pathways is the nature of the diet in terms of both energy content and the provision of the raw materials for neural construction. Neural tissue is energetically expensive to maintain and this is primarily in order to preserve the unequal concentrations of ions across neuronal membranes required for signaling. It is possible to estimate the metabolic energy required to run the ion pumps that restore the gradients after a disturbance, such as a signal, and also to estimate the information content in that signal. Thus it is possible to estimate the metabolic cost of neural information processing in terms of molecules of ATP per "bit" of information (Laughlin et al., 1998). This opens the way for an ecological cost/benefit analysis of different neural strategies for solving computational and behavioral problems. Properties of the potassium conductances of dipteran photoreceptors are matched to the ecology of the flies (e.g., diurnal fast flying versus crepuscular slow flying) in a way that is attributed to trading high temporal visual resolution for reduced energy consumption when high temporal resolution is not required. In other insects these properties can change on a circadian basis. It is increasingly clear that neural circuits have designs that are optimized for energy efficiency in terms of numbers of ion channels and synaptic connections, and lengths of communication pathways (Laughlin, 2001). In addition to energy content, the make-up of the diet can have a profound effect on circuit function. For example the production of the important neuromodulator, serotonin, requires an adequate and continual supply of the precursor tryptophan in the diet. Without sufficient quantities of serotonin there are marked effects on mood, appetite, and sleep. The ratio of different dietary fatty acids affects the distribution of membrane phospholipids in the central nervous system and has been shown to alter locomotor behavior and learning in rats. Similarly, the ability of fruit flies to learn and remember a visual task is sensitive to the specific content of the diet being reduced in flies fed on a low-protein:high-carbohydrate diet, although the mechanisms underlying this effect are unclear.

A more complex neuroecological issue related to phenotypic plasticity in the nervous system is that the state of neural circuitry at any one time depends on current environmental conditions and the ecological history of the organism. Changes to neural structure and function (i.e., adaptive neural plasticity) need not be mediated in a traditional fashion by the collection of information about the environment via the sensory array and the subsequent central processing of this information, but will also involve direct effects of physical parameters of the environment on the material structure of the nervous system, and the physiological feedback responses to this. Thus there exist separate pathways for changing circuitry in adaptive fashions whereby information in the environment directly affects the neural hardware without being mediated by electrical activity. For example, it is well established that physical environmental conditions such as temperature, oxygen levels, and barometric pressure directly affect neural functions such as axonal conduction and synaptic transmission. It is also now well known that cellular properties of neurons (e.g., membrane lipid order) acclimatize to changing environmental conditions and that there are circadian and seasonal variations in circuit properties. In several instances, difficulty in repeating experimental findings and much variability in the results have been shown to be due to these factors. How circuits exist and operate depends on the history of environmental experience.

One example of the profound way in which environmental conditions affect neural function is the long-term effect of a prior environmental stress such as hypoxia or a heat shock. Cells, tissues, and organisms all demonstrate acquired thermotolerance as a result of prior stress such that they are able to survive normally lethal temperatures. This is often associated with the increased expression of a suite of proteins known as the *heat shock* or *stress proteins*. Under extreme environmental conditions, however, organisms in their niches are at risk from neural circuit failure long before cells start to die. For example, impairment in the ability to recall spatial information or impairment of the operation of escape reflexes or the circuitry for vital functions such as ventilation is likely to be lethal for the organism prior to cell death. The same conditioning treatments that induce acquired thermotolerance also reduce the thermosensitivity of neural function such that action potentials can be generated and synapses can transmit information at higher temperatures than normal, and for longer, thus increasing the temperature at which circuits fail (Robertson, 2003). The neural hardware is able to sustain a higher thermal dose before function fails and to recover more quickly when normal conditions resume. The central pattern generators for both locust flight and locust ventilation can be conditioned by prior stress. The mechanisms underlying this neuroprotection are unknown, but involve the HSP70 family of heat shock proteins. Increasing the levels of HSP70 at synapses either by genetic engineering or by exogenous application mitigates the disruptive effect of increasing temperature in *Drosophila* larvae and in a mouse brainstem slice. Prior heat shock or anoxia increases the durations of locust flight motoneuron action potentials and reduces potassium conductances of neuronal somata.

The giant axons of squids from different thermal environments support action potentials of different durations due to different potassium conductances and this is interpreted as an adaptation to prevent high-temperature failure of conduction in the squids from the warmer environments. Thus current circuit function depends on the recent history, as well as the evolutionary history, of environmental conditions.

Genetically identical strains of mice maintained and tested in different laboratories vary in their ability to perform a suite of behavioral tests (Wahlsten et al., 2003). In other studies the prenatal and postnatal environments are sources of epigenetic variation for behavioral testing. Behavioral variability ascribed to epigenetic factors associated with idiosyncratic laboratory environments illustrates the potent role that environmental factors, however subtle, have in determining circuit characteristics. It further underlines the need for a neuroecological approach to understanding the neural bases of behavior.

1. See also

Evolution of vertebrate brains
Temperature regulation and fever
Visual system development, invertebrates

2. References

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