

Neuronal Circuits and Evolution

We agree with Dumont and Robertson (1) that the design of nervous systems is not necessarily optimal. That teleology has no place in the consideration of biological design is at the very heart of modern evolutionary theory. However, we take exception to several aspects of their article. (i) Their premise that the study of simple circuits and behaviors has been slow to lead to any fundamental principles of neural function does an injustice to the biologists who work on these systems (2). (ii) Their points are illustrated primarily with two examples taken from their own work in arthropods; we believe there are multiple interpretations of the functional and adaptational significance of their results. (iii) They contend that the adoption of an evolutionary perspective is necessary to "explain" many features of neuronal organization. Whereas nervous systems are clearly products of evolution, the direct study of living neural systems has been, and is, the best approach for elucidating unifying principles. As we cannot study ancient behavior or neural organization, we can only use data from extant species to deduce possible evolutionary processes. We cannot "explain" the production of behavior or principles of neural organization with evolutionary speculation.

The occurrence of serially homologous flight interneurons in abdominally derived neural segments of the locust is indeed interesting. As was previously suggested (3), this finding, combined with fossil evidence, may be consistent with the pleural-appendage theory of the evolution of insect flight. Little more can be said with certainty; to suggest that evolutionary theory can then be used to explain the modern organization of this system is close to circularity. We do not know if these interneurons, or even their precursors, were present in early flying insects. Also, it is possible that this intriguing morphological arrangement does have a physiological function, such as introducing a phase delay through conduction time differences. The speculations of Dumont and Robertson regarding the lack of adaptive significance of this arrangement appear, therefore, to be premature at best.

With regard to the seemingly anomalous connection between the lateral giant (LG) and fast flexor (FF) neurons in crayfish, we believe that possible integrative, and therefore adaptively significant, functions for these connections cannot be ruled out. It is possible, as Dumont and Robertson sug-

gest, that inhibition has hidden these connections from the forces of natural selection that may eventually have caused their elimination. However, we do not know that the remaining LG to FF connections are never used in natural behavior. For example, a small amount of excitation reaching the posterior flexor muscles in these segments might provide rigidity that is necessary to keep the abdomen from hyperextending during the tail flip. It is also possible that the excitation produced in the FFs by the LG may sum with excitation from other sources under some conditions of sensory stimulation. Alternatively, these connections could be gated by presynaptic inhibition of the sensory interneuron endings on the FFs and the flexor inhibitor. In either of the last two examples the result would be the production of variant types of escape behavior; such variability could be an extremely adaptive defense against intelligent vertebrate predators such as raccoons and herons.

Dumont and Robertson cite the example of head-scratching in birds as evidence that evolutionarily neutral neuronal features may be conserved even when they are no longer useful. They do not point out that, whereas all reptiles and mammals scratch their heads with the hindlimb passing over the forelimb, not all birds exhibit this behavior (4, 5). In fact, even within some bird species there is individual variability regarding whether the hindlimb passes over or under the wing during head-scratching (4). It would appear that some type of evolutionary modification has occurred in this system. Also, in birds that exhibit the reptilian type of head-scratching, the wing may be held extended for some purpose (for example, greater balance) while the hindlimb is elevated. The authors did not suggest a selective advantage for self-awareness of mortality or musical ability in humans. The awareness of one's own mortality seems extremely adaptive in an organism whose reproductive abilities can span several decades, and a propensity toward musical ability would seem to be adaptive in an organism that is unique in its social and communicative orientation. We do not know that these traits are adaptive, or even whether they are "hardwired" in the human brain, but we cannot rule out such possibilities.

One must be cautious when speculating about the adaptive value of individual neurons or particular neuronal features. We do not yet have the required basic understand-

ing of how neuronal connectivity is established during development. Seemingly functionless neurons may continue to exist if they are a source of variability in neural systems. During changing environmental conditions such a pool of "vestigial" neurons may provide a selective advantage if the rearrangement of connections can be accomplished more rapidly than the creation of new neurons with appropriate connectivity patterns.

To gain a better understanding of the forces that shape neural systems, we must have more comparative studies of invertebrate neural circuits aimed at identifying similarities and differences occurring at the order, family, and generic levels (6). Ideally these studies would use systems that have already been thoroughly studied in one or a few species. Also, we must continue to build our understanding of the rules governing development in invertebrate nervous systems. The nervous systems of animals and humans are extremely complex, and we will not obtain our knowledge of the underlying organizational processes easily. Nevertheless, only through the continued study of living systems can we hope to comprehend how neural circuits are shaped by natural selection.

BRADLEY R. JONES
ESTHER M. LEISE
*Department of Zoology,
University of California,
Davis, CA 95616*

REFERENCES AND NOTES

1. J. P. C. Dumont and R. M. Robertson, *Science* **233**, 849 (1986).
2. T. H. Bullock, in *Simpler Networks and Behavior*, J. C. Fentress, Ed. (Sinauer, Sunderland, MA, 1976), pp. 52-60; M. Burrows, *J. Exp. Biol.* **112**, 1 (1984); P. A. Gettings, *Symp. Soc. Exp. Biol.* **37**, 89 (1983); S. Grillner and P. Wallén, *Annu. Rev. Neurosci.* **8**, 233 (1985); E. R. Kandel, *Grass Lect. Monogr.* **1** (1977).
3. R. M. Robertson, K. G. Pearson, H. Reichert, *Science* **217**, 177 (1982).
4. J. L. Brown, *The Evolution of Behavior* (Norton, New York, 1974), pp. 8-9.
5. K. Z. Lorenz, *Sci. Am.* **199**, 67 (December 1958).
6. An example of this kind of comparative work has recently been reported [W. H. Watson and A. O. D. Willows, *Soc. Neurosci. Abstr.* **12**, 241 (1986)]. These authors have studied identified peptidergic neurons in the buccal ganglia of several marine mollusks in the order Nudibranchia.

26 September 1986; accepted 5 March 1987

Response: Jones and Leise do not challenge in any major way the substance of our article (1). Their comment is marred by both internal contradictions and an incomplete discussion of evolutionary processes. The essence of their argument appears to be that, as long as it is possible to generate more hypotheses for adaptive significance of certain features of neuronal circuits, it is "premature" to consider alternative evolutionary explanations for their existence. We believe