Technical Comments

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 suggest, 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 understanding 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.

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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.

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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 this attitude is unrealistic for three reasons.

First, the existence of such adaptive hypotheses does not in itself rule out alternative evolutionary explanations. As we stated in our article, it is never possible to exclude completely the possibility of any feature's having some functional significance. What we have argued is that, in the examples given, the available evidence fits the nonadaptive evolutionary hypotheses better than it fits the adaptive ones. While, for obvious reasons, we concentrated on the systems we know best, we did not restrict ourselves to these. In particular the existence of "motoneurons" with axons that do not connect with a muscle is unlikely to be adaptive (*2*). Indeed, the segmental giant neuron in the escape circuitry of the crayfish has an apparently functionless, blind ending in the first root [see (*3*) for a discussion of the evolutionary significance of this feature]. Jones and Leise have not addressed the question of the relative value of alternative hypotheses, but merely suggested some new ones.

Second, even when a feature may be shown to have a function, this does not mean that it was adapted for that purpose. For example we argued that the flight interneurons in the locust, which clearly have a function, were originally adapted for ventilation and only secondarily co-opted for use in the control of flight. We fail to see any circularity in the argument. The observations of (i) the undisputed morphological arrangement and abdominal origin of the interneurons and (ii) the lack of any obvious advantage for flight that this particular arrangement and origin might confer are best explained by the hypothesis that the organizational feature is preadaptive for flight as a result of wings originating according to the pleural appendage theory. The second observation is clearly open to dispute, but familiarity with the system allows one to rule out the possibility, along with many others, that the arrangement serves to introduce phase delays. The significance of such an argument is that, if current organization owes a substantial part of its makeup to prior history, then systems with different histories are likely to be substantially different; and general principles relating organization and function become more difficult to find.

Third, the generation of multiple alternative hypotheses is, in itself, a weak form of argument, since it implies that no single hypothesis has a high probability of being correct. Rather it demonstrates the inventiveness of the authors. It is because of this that we feel new hypotheses assigning adaptive value to the features we have described should be measured against consideration of how these circuits may have evolved.

In addition, Jones and Leise put forward adaptive hypotheses to counter our arguments for nonadaptive evolutionary processes, an approach that contradicts two statements they make elsewhere in the comment. They state that teleology has no place in the consideration of biological design, and yet their arguments for adaptive value of these neuronal circuits are implicitly teleological. Elsewhere they state "One must be cautious when speculating about the adaptive value of individual neurons or particular neuronal features." This is exactly the point we were trying to make in our article, but it seems to us inconsistent with their earlier speculations of adaptive value.

Another example of inconsistency is the contention by Jones and Leise that in pointing out that organizational principles have been slow to emerge we are unjust to the biologists, presumably including ourselves, who work on these systems. (This was not our intention—the point of our article was to try to understand the difficulties, not belittle the many achievements in this field.) Yet one of the references they give clearly supports our position (*4*). This states: "On the motor side there are virtually none of these types of organizational principles. Faced with an apparent lack of success in providing principles of this type, there has been growing pessimism within the ranks of many neurobiologists." Furthermore, in their concluding paragraph Jones and Leise state "we will not obtain our knowledge of the underlying organizational processes easily." They seem to be in agreement with us.

Finally, Jones and Leise do not take into account the diverse processes controlling evolution. They call for more comparative studies (the value of which we discussed) in order to "comprehend how neural circuits are shaped by natural selection." Yet natural selection is only one of the many processes involved in evolution. Indeed, as we illustrated in figure 3, neural circuitry is not directly accessible to natural selection; only the behaviors produced are. Jones and Leise allude briefly to the role of developmental processes in guiding evolution and to the potential value of seemingly functionless neurons as a source of variability for future change. But they do not mention that both these points are examples of the nonadaptive processes in evolution, whose importance we believe should be recognized, and that they are discussed in our article. The evolutionary arguments we used are well established in the literature (*5*). In our article we tried to demonstrate their significance to the understanding of neuronal circuits. Jones and Leise appear to be saying that the use of such arguments should be restricted because they are, in their opinion, premature. This seems to us an unnecessary limitation of the framework for understanding the nervous systems of today, which are, after all, the products of evolution.

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