

THE FUTURE OF RESEARCH ON ELECTRORECEPTION AND ELECTROCOMMUNICATION

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Summary

Beyond continuation of currently active areas, some less studied ones are selected for predictions of marked advance. (1) Most discoveries will be in cellular components and molecular mechanisms for different classes of receptor or central pathways. (2) More major taxa, possibly birds, reptiles or invertebrates, will be found to have electroreceptive species representing independent evolutionary 'inventions'. (3) Electric organs with weak and episodic electric discharges will be found in new taxa; first, among siluriforms. (4) New examples are to be expected, such as lampreys, where synchronized muscle action potentials sum to voltages in the range of weakly electric fish. Some of these will look like intermediates in

the evolution of electric organs. (5) Ethological significance will be found for a variety of known physiological features; e.g. uranoscopids, skates and weakly electric catfish with episodic electric discharges; electroreceptive ability of animals such as lampreys, chimaeras, lungfish, sturgeons, paddlefish and salamanders with Lorenzinian-type ampullae; gymnotiform and mormyrid detection of the capacitative component of impedance. (6) The organization of some higher functions in the cerebellum and forebrain will gradually come to light.

Key words: electroreception, electrocommunication, brain organisation, complexity, cognition.

For centuries, interest in electric fish has been concentrated on the electric organs and the production of their strong discharges in either high-voltage or high-current species. In recent decades, interest has turned to sensory reception, the functions of weak discharges and the central processing of electric information. At present, more than a score of laboratories in a dozen countries are actively investigating the anatomy, physiology, pharmacology, molecular neurobiology, behavior and field biology of strong and weak electric fish and of fish, amphibians and mammals that are electroreceptive but lack electric organs. The other papers in this volume manifest the range and level of sophistication of the current state of knowledge. It is my aim both to predict and to influence the future directions of research by pointing to opportunities with potential significance for general neurobiology in electroreception and also in the 'sensorimotor' control and production of electric discharges.

Most future research will focus upon the cellular components and molecular and pharmacological mechanisms in each of the classes of sense organ and in the central pathways. These will be germane to general problems of neurobiology, because these animals are especially favorable material. I will say no more about this active front. Instead, I will hazard predictions and highlight opportunities in several other broad domains.

Starting with the *evolution of electroreception*, I will touch only upon its distribution. I predict the discovery of more taxa

with electric organs and with electroreception, a sensory modality that has been independently invented during evolution more than three times. At least twice, it evolved with three classes of sensory receptor in the same animal, together with corresponding central pathways, not necessarily homologous in the different taxa.

Among the candidates for future discovery of electroreception, wading birds that probe in the mud are obvious possibilities, so are aquatic reptiles. Among mammals, only the monotremes have provided convincing evidence of possessing this sensory modality. One of the largely aquatic insectivores, the star-nosed mole, has been a candidate, but the negative results are more convincing than the positive claims. Other species ought to be examined using quasi-natural electrical stimuli. Ideally, this is done behaviorally but for vertebrates, evoked potentials from the midbrain are simple and reliable. If electroreception is present, it will almost certainly be evident in the first animal tested.

Very telling is the dramatic story of the discovery of electroreception in one subfamily of notopterid teleosts, though absent in its sister subfamily and in other families of the order Osteoglossiformes (Bullock and Northcutt, 1982). This was convincing because brain responses to physiological stimuli, simulating normal signals, were recorded in this one subfamily and not in others. This finding opened up the possibility that electroreception might turn up anywhere among the hundreds of fish families, especially among teleosts. It is not necessarily

an ordinal character, as it appears to be in Mormyriiformes, Gymnotiformes and Siluriformes, and it will not necessarily be homologous to previously known examples.

What about invertebrates? I know of no concerted effort to look for electroreception among these phyla. Once upon a time we dismissed all the smaller invertebrates as unlikely to be electroreceptive because the theory of how fish must do it depended on their size and their high skin resistance. It is known that this sensory modality can be useful, as in mormyrids, even when it is 20 000 times less sensitive than in ordinary rays. It would not be surprising, therefore, if an arthropod or a mollusc or even an annelid uses naturally available electric stimuli in its normal behavior. B. U. Budelmann and I performed a few experiments on the cuttlefish *Sepia*, recording from four or five places in the brain of intact, unanesthetized animals while imposing large, quasi-uniform fields across the body. We did not observe any averaged evoked potentials, but a negative finding is quite inconclusive and I would not count the cephalopods out as yet.

Electroreception and *electric organs* do not always go together. I predict that new species will continue to be found that generate and use feeble electric organ discharges – first among the thirty or so families of siluriforms, all of which are believed to be electroreceptive but only a few electrogenerative. Baron et al. (1996a,b) and Baron and Morshnev (1998) have recently reported several Ethiopian species and at least one family to add to the previously known catfishes (*Clarias*, *Synodontis*; Hagedorn et al., 1990; Baron, 1994b; Baron et al., 1994) that discharge weak electric pulses in short bursts after many hours of silence, with suggestive evidence of a social communicative function.

It has amazed me that there are not, so far, *intermediate cases* between weak electric organs and ordinary muscle bundles with a tendency for nerve endings to prefer the same side of the muscle fibers, for a single motor unit to be very large or for several motor units to spike in synchrony. We would notice such cases by the larger than usual muscle action potentials in extracellular recordings. Single, large muscle potentials synchronous with respiration have been reported for lampreys. Kleerekoper and Sibakin (1956, 1957) even suggested that these ‘spike potentials’ function with electroreception – before that term had been invented or any case of it was known. They inferred this from observations that they believed to show a role in prey detection. This unique claim, besides calling for confirmation and extension with behavioral experiments, points to the opportunity to look for other taxa that generate useful electric signals without electric organs. Ordinary gill movements as well as fin movements and body bends are associated with action potentials that sound like a ‘swish’ in the audio-monitor – coming from many asynchronous motor units. There may be a species here and there that synchronizes these potentials, as lampreys seem to do. We may find candidate stages in the evolution of electric organs in ordinary muscle.

We are on the verge of learning the *function of the weak* and occasional electric organ discharges in the rays and catfish.

Early hints in the work of Mikhailenko (1971) and Baron (1994a; Baron et al., 1994) suggest that they are used in communication for reproductive or other social roles. More puzzling and ripe for new behavioral work is the functional role of the moderately weak electric organ discharge burst of the ‘star-gazers’, marine teleosts of the family Uranoscopidae. Pickens and McFarland (1964) demonstrated that they discharge apparently simultaneously with the act of prey capture, seemingly too late to help in timing the mouth-gaping capture. Some workers question whether the very modest current, short-circuited by sea water, could effectively disorient a small prey fish. Even for the well-studied mormyrids and weakly electric gymnotiforms, only recently has good evidence begun to appear that the system is used in locating food – small, living prey.

It is not yet known definitely what normal objects are discriminated with the use of the demonstrated ability to estimate the capacitive component of impedance. We reported (Scheich et al., 1973) that 0.001 μF of capacity in parallel with the water around the fish markedly altered the response of T unit receptors. Presumably the brain, with a whole population of receptor units, could detect much less than this – which puts it in the range of capacitive impedance of smallish pieces of tissue. Walter Heiligenberg’s first exposure to the tropics was a short expedition he and I made to the Rio Negro in Brazil in 1977 to investigate this, but the main result was that he fell in love with the tropics.

All these mysteries I predict will be solved in the near future, and many new *details of the brainstem circuitry and dynamics* for analyzing electrosensory input and formulating electromotor output will be revealed. This will amplify our understanding of a system better characterized with respect to certain normal behaviors, from receptors to effectors, through second-order, third-order and more than a dozen successive orders of neuron, than perhaps any other in neuroethology.

Much more difficult to anticipate, however, is the progress that will be made in some other areas. An example is the *functional organization of the forebrain* – including its pallium, striatum and limbic divisions. This relatively neglected area might not only round out our picture of the neural basis of some electric behaviors, well studied up to the ‘tweenbrain’. With that background and the use of stimuli in several other sensory modalities, the electric fish cerebrum should be a good place to elucidate general questions about the physiology of higher centers in advanced teleosts. Ancestral fish invented the forebrain; how their modern descendants organize and use it should provide needed perspective on the vastly more studied mammalian forebrain.

Are the various sensory modalities (visual, auditory, lateral line, tactile, proprioceptive, olfactory, electric, etc.) and the highest motor centers represented in segregated areas of the brain, as in mammals, or is there a primitive, multimodal, convergent, perhaps sensorimotor, pallium? If they are even partly segregated, are there multiple areas for a given modality, as in mammals, and are they distinct not only in location but also in dynamic properties or best stimuli?

We have the beginnings of some information in a study by Precht et al. (1998) on the cerebral pallium of *Gnathonemus*. This is based on evoked potentials and multiunit spike responses recorded at many loci and depths using multiple semimicroelectrodes in response to multiple modalities of physiological stimulation. They found an astonishing degree of segregation of vision, audition, electroreception and lateral line mechanoreception. The best represented is sound reception, and it is in fact subdivided into two physiologically distinct areas – not surprising, since some mormyrids are considered to be acoustically relatively advanced fishes. We do not yet, however, know whether any of these areas – the visual, the auditory, the electroreceptive or the lateral line mechanoreceptive areas – map some aspect of the sensory world, such as visual space, acoustic frequency, body surface, object distance or relative movement. We have little idea whether there are feature-sensitive neurons with complex or ethologically significant best stimuli.

As yet we cannot say whether there is some form of modular organization in fish such as the minicolumns and the full columns of the mammalian cortex. We do not know whether there is anything like the plasticity of the mammalian cortical maps, based on the animal's recent experience. Bell and his coworkers have shown us how recent experience can change the responses of some brainstem corollary discharge neurons, within minutes, and we have to wonder whether this is reflected in the forebrain.

Even in mammals, where effort has been concentrated, we do not know the transforms of information processing in neuronal assemblages of the thalamus, striatum or cerebellum. Is it possible that the brain of fish might be more readily decoded so that we can discern the transforms? So far, apart from some examples in the brainstem of electric fish, where we think we know roughly what is happening, this field is still quite virgin.

There are other *opportunities for research* on electric or electroreceptive fish and higher central organization with broad evolutionary significance. What is the degree of modulating influence upon some standard response when the locus coeruleus and its noradrenergic system that sends axons all over the forebrain and cerebellum is activated or silenced? What are the influences of the raphe nuclei and its serotonergic system, the basal forebrain and its cholinergic system, the homolog of the substantia nigra–ventral tegmental dopaminergic system? Have these systems evolved a great deal – as the hippocampus has and the cerebellum supposedly has not? Higher functions include intermodulation of responses to a standard stimulus when delivered on a background of different brain states, such as arousal, sleep-like quiescence, directed attention or expectation.

We do not yet know what differences the fish might show in so-called cognitive responses of the forebrain compared with the well-known mammalian slow wave responses, for example to expected stimuli and to 'oddball' stimuli. Are there only quantitative or also qualitative differences in functional properties correlated with the great differences in

architecture? One thinks of the relative paucity of intrinsic, pallio-pallial connections compared with the mammalian cortico-cortical connections that Van Essen counted a few years ago – some 780 in number (counting a connection from area A to area B as one and from area B to area A as another), out of a possible 3500 or so (Mountcastle, 1995)? Is the relative paucity that I presume will be documented in the number of reciprocal connections with lower centers great enough to regard as qualitative? The same question may be posed for the relative absence of laminar-specific connections and laminar-specific current sources and sinks? These are only examples of a probably large class of differences yet to be examined. Another class is defined by functional states, including those due to our stimulation and those arising with tasks that the animal innately performs or is trained to perform. How much do we know about differences among major taxa in modulator-specific influences or in the distribution of activity-dependent changes, as in functional magnetic resonance imaging and measures of vascular circulation changes with brain state?

I parade these traits of functional differentiation of higher brain centers to suggest a realm of comparative research and to encourage new effort in a direction that surely promises a rich harvest. I have confined myself to physiology and anatomy and to presently familiar techniques and almost certainly achievable experiments. I have not touched on a long list of others, such as brain slices of higher centers, intracellular recording, pharmacological, chemical and molecular approaches.

I believe, as surely as anything I have faith in, that new principles will be found, new emergent organizational insights gained by mining these veins of precious ore. These revelations are sure to change the big picture drastically – not only the picture of how electric fish work and what teleosts with advanced brains can do, but the understanding of mammalian achievement and of the evolutionary biology of complexity. The evolution of complexity has hitherto been discussed with almost no appreciation of the uniqueness of the brain with respect to specific traits that measure complexity.

I am also sure that a real appreciation of the complexity of the 'neuro' part of neuroethology will not come before we have made a great deal more progress on the ethology part. Here also, the state of understanding of the evolutionary differences between major taxa and grades of complexity is meager, and most studies aim only at examining adaptive differences between species of approximately the same grade. Relatively neglected are comparisons between grades, for example to estimate the complexity of behavior in semiquantitative ways such as the length of the ethogram, the number of distinct social situations the animal can distinguish, the number of levels and states expressed which in ourselves would be called emotions and the number of learned items, bits or facts that we call knowledge. Certainly, these are hard-won and technically challenging goals. But there are plenty of rewards along the way and plenty of good questions that, with proper formulation, should make fundable research projects.

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