

Deciphering the Brain's Codes

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The two sensory systems discussed in this review use similar algorithms for the synthesis of the neuronal selectivity for the stimulus that releases a particular behavior, although the neural circuits, the brain sites involved, and even the species are different. This stimulus selectivity emerges gradually in a neural network organized according to parallel and hierarchical design principles. The parallel channels contain lower order stations with special circuits for the creation of neuronal selectivities for different features of the stimulus. Convergence of the parallel pathways brings these selectivities together at a higher order station for the eventual synthesis of the selectivity for the whole stimulus pattern. The neurons that are selective for the stimulus are at the top of the hierarchy, and they form the interface between the sensory and motor systems or between sensory systems of different modalities. The similarities of these two systems at the level of algorithms suggest the existence of rules of signal processing that transcend different sensory systems and species of animals.

1 Introduction ---

Both peripheral and central sensory neurons do not respond to all stimuli or stimulus variables but to a certain modality, range, configuration, or pattern of stimuli or stimulus variables. This property of sensory neurons will be called stimulus selectivity or, simply, selectivity. Some neurons are selective for primary stimulus variables, such as frequency and wavelength, and others are selective for more complex patterns of stimulus variables, such as direction, velocity, and disparities. In some systems, lower order neurons show selectivity for simpler stimuli and higher order neurons for more complex stimuli. Such a correlation between stimulus selectivities and the anatomical levels of a sensory system suggests the possibility of finding where and how selectivities for complex stimuli are derived from the integration of selectivities for simpler stimulus variables. Of particular interest are sensory systems that contain higher order neurons selective for the same stimuli that cause specific behaviors or percepts. If these systems are amenable to analysis of successive stages of processing leading to the selectivity of these neurons, we may

understand how the whole system is designed to analyze behaviorally relevant stimuli. For various reasons, many complex sensory systems are not amenable to this form of analysis. However, in the auditory system of the barn owl and the electrosensory system of the electric fish, *Eigenmannia*, such an analysis has been successfully carried out (Heiligenberg 1986; Konishi *et al.* 1988). In this review, I shall discuss what we can learn from these examples about neural codes, neural algorithms, and network organization.

2 Behavioral Analysis

The sense organs and the brain of an animal must be designed for the processing of the stimuli that are relevant for its survival and reproduction. It is, therefore, important to determine what stimulus to use in the analysis of neuronal selectivities. This section describes first the characteristics of the stimulus for sound localization by the barn owl and then the stimulus for the electric fish. On hearing a sound, the owl turns its head in the direction of the sound source (Knudsen *et al.* 1979). Experiments show that the owl uses interaural time differences for localization in azimuth and interaural amplitude differences for localization in elevation (Moiseff and Konishi 1981; Moiseff 1989). Of two possible sources of interaural time differences, namely, stimulus onset time and phase disparities, the owl extracts and uses the interaural phase differences of all audible frequencies contained in the signal. The vertical asymmetries of the barn owl's ears enable the owl to use interaural amplitude differences for localization in elevation. A higher sound level in the right ear and left ear causes the owl to turn its head upward and downward, respectively. The owl obtains both binaural disparities simultaneously from a single sound signal. Each location in the owl's two-dimensional auditory space is thus uniquely defined by a combination of interaural time and amplitude differences.

The second example is the electric fish, *Eigenmannia*. This species creates electrical field potentials around its body to detect objects having conductivities different from the conductivity of the water. The electrical potential varies almost sinusoidally over time, and the fish can change its frequency. When the electrical fields of two fish have only slightly dissimilar frequencies, the fish try to increase the differences in signal frequency. This behavior is called the jamming avoidance response (Heiligenberg 1986). The main problem that a fish must solve in encountering another fish is to determine whether its own frequency is higher or lower than that of the other fish. The pacemaker cells that drive the electrical organ cycle by cycle could, in theory, provide a copy of the efferent command for comparison with the frequency of the incoming signal. *Eigenmannia* does not, however, use this method. Instead, the fish determines the sign of frequency differences from the waveform created by the mixing

of its own and the neighbor's signals. The phase and amplitude of the waveform at one locus on the body surface are different from those at another locus, because the sources of the two electrical fields are located within the bodies of the two fish that are separated in space. The fish uses these phase and amplitude differences between many loci on its body surface to determine the sign of frequency differences (see Fig. 1 for further explanation).

3 Successive Stages of Signal Processing

Complex sensory pathways have input, intermediate, and output stages. In the "bottom-up" approach, one starts with the sense organ and proceeds to higher order stations in the ascending sequence. The study of neuronal selectivities need not start with the input stage. In the "top-down" approach, one starts with output or other higher order neurons and goes downward through intermediate stages to the sense organ. Neither approach is easy when the neural network is complex. The bottom-up approach is difficult because of nonlinear properties of most neural systems. The top-down approach is difficult because the output neurons of the network may not be easily found. The output neurons of a hierarchically organized neural network occupy the anatomically highest stage of the hierarchy and project to other functionally identifiable networks such as the motor system and other sensory systems. Under favorable circumstances, the point of transition from one network to the next can be recognized by combinations of anatomical and physiological methods. Starting with higher order neurons has distinct advantages because the investigator has the defined goal of explaining the stimulus selectivity of the higher order neurons. In the owl, we were lucky to start with what has turned out to be the output neurons. The following description of the owl's auditory system similarly starts with the output neurons and explains how their stimulus selectivity is established.

3.1 The Top-Down Approach in the Owl. We looked for higher order auditory neurons that responded only when sound came from a restricted area in space. A cluster of such cells, which are called space-specific neurons, occurs in the external nucleus of the inferior colliculus (Knudsen and Konishi 1978; Moiseff and Konishi 1983). This nucleus is the highest station in that part of the owl's auditory system that processes the stimulus for sound localization (cf. Fig. 3). Experiments with earphones show that these neurons are selective for a combination of interaural time and amplitude differences (Moiseff and Konishi 1981; Olsen *et al.* 1989). The neurons are selective for a particular spatial location, because they are tuned to the combination of interaural time and amplitude differences that results when the sound source is located at that site. We also know that a neuron's selectivity for interaural time and amplitude

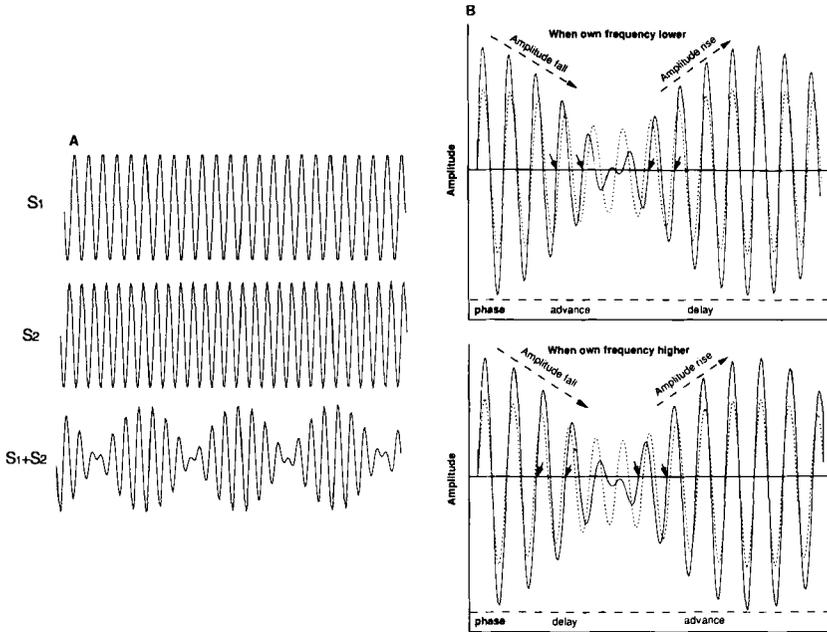


Figure 1: Determination of the sign of frequency differences by the electric fish, *Eigenmannia*. (A) Electrical signals. *Eigenmannia* generates nearly sinusoidal electrical signals for navigation and orientation. When an individual (S_1) encounters another individual (S_2), they avoid jamming each other by changing the frequency of their signals. The fish uses the beat waveform (S_1+S_2) to determine whether its own frequency is higher or lower. (B) The fish uses differences in the phase and amplitude of the beat waveform between different body loci to determine the sign of frequency differences. In this figure, the solid-line and dotted-line waveforms show different degrees of contamination of S_1 by S_2 ; the solid-line waveform registered at one body locus is more contaminated and the dotted-line waveform registered at another locus is less contaminated. The small arrowheads indicate the phase relationships between the two waveforms. The left-slanted arrowheads indicate that the phase of the solid-line waveform is advanced relative to that of the dotted-line waveform. When these phase relationships and the rise and fall of amplitude are considered jointly, the sign of frequency differences can be determined unambiguously. Thus, the sequence, a fall in amplitude with a phase advance followed by a rise in amplitude with a phase delay, indicates that the fish's own frequency is lower than that of the other fish.

differences determines, respectively, the azimuthal and elevational centers and widths of its receptive field.

It is reasonable to assume that a neuron's selectivity for a complex stimulus is due both to its intrinsic morphological and biophysical properties and to the integration of information conveyed by the input channels converging on it. Thus, the next step in the top-down approach is to determine what circuits and processes underlie the stimulus selectivity of space-specific neurons. A survey of all binaural stations below the level of the external nucleus of the inferior colliculus showed that they could be classified into two groups, one containing neurons sensitive to interaural amplitude differences and the other containing neurons sensitive to interaural phase differences (Moiseff and Konishi 1983; Sullivan and Konishi 1984; Takahashi *et al.* 1984). Subsequent anatomical studies established separate pathways from the cochlear nuclei, the first auditory stations of the brain, to the inferior colliculus in the midbrain (Takahashi and Konishi 1988a,b). These findings led to the hypothesis that the owl's auditory system uses parallel pathways for separate processing of interaural phase and amplitude differences. A more direct test of this assumption came from an experiment in which the response of space-specific neurons to interaural time and amplitude differences was observed while one of the two pathways was partially inactivated by injection of a local anesthetic.

The beginning stage of the "time pathway" is one of the cochlear nuclei, nucleus magnocellularis, and that of the "amplitude pathway" is the other cochlear nucleus, nucleus angularis. Partial inactivation of the nucleus magnocellularis drastically changed the response of space-specific neurons to interaural time differences without affecting their response to interaural amplitude differences. The converse was observed when the nucleus angularis was partially anesthetized. These cochlear nuclei are both anatomically and physiologically different from each other. Neurons of the nucleus magnocellularis are sensitive to stimulus phase but insensitive to variation in stimulus amplitude. By contrast, neurons of the nucleus angularis are sensitive to variation in stimulus amplitude but insensitive to stimulus phase. The phase sensitivity means that the neuron fires at or near a particular phase angle during the tonal period. This phenomenon, phase-locking, occurs at frequencies as high as 8.3 kHz in the owl. Neurons do not fire during every tonal period of such a high frequency, but whenever they fire, they phase-lock to the stimulus. When the stimulus is noise, neurons phase-lock to the phase of the spectral components to which they are tuned.

The next step in this research was to determine where and how the neuronal selectivities for interaural phase and amplitude differences are established in the two pathways. The third-order nucleus in the time pathway, nucleus laminaris, is the first station that contains neurons selective for interaural phase differences. The owl uses phase-locked spikes from the left and right ears to measure interaural phase differences from

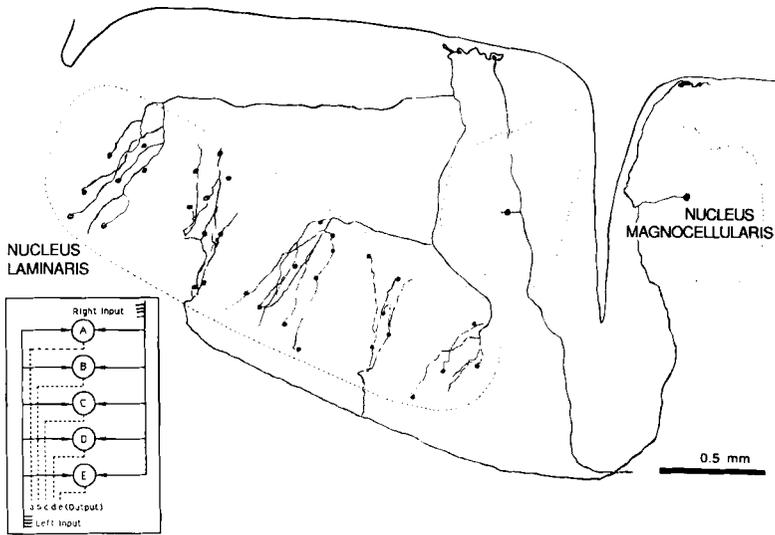


Figure 2: Neural circuits for the detection of interaural time differences. The inset shows a model of neural circuits for the detection of interaural time differences. It uses the principles of coincidence detection and delay lines. Binaural neurons, A, B, C, D, and E, fire maximally when impulses from the two sides arrive simultaneously. Except for C, the paths for impulse transmission to each neuron are different between the two sides. These asymmetries cause interaural differences in the arrival time of impulses. A neuron fires maximally when an imposed interaural time difference compensates for the asymmetry in impulse transmission time. This array of neurons thus encodes different azimuthal locations of sound systematically. The main figure shows the neural circuits. Nucleus magnocellularis is one of the first brain stations in the owl's auditory system. Nucleus laminaris receives inputs from both the ipsilateral and contralateral magnocellular nuclei. The figure shows axon collaterals from single ipsilateral and contralateral neurons projecting into nucleus laminaris, which contain binaural neurons. For the sake of clarity, the ipsilateral and contralateral axons are shown separately, although they interdigitate in reality. These interdigitating axons serve as delay lines, and the laminaris neurons as coincidence detectors. Interaural phase differences are computed separately for each frequency band.

which it eventually derives interaural time differences. The circuits that compute interaural phase differences use the principles of delay lines and coincidence detection (Fig. 2), corresponding to a model first proposed by Jeffress (1948). Laminaris neurons are innervated by axons from both

ipsilateral and contralateral magnocellular neurons. The parts of these axons that lie within the boundaries of the nucleus laminaris act as delay lines, and laminaris neurons themselves as coincidence detectors (Carr and Konishi 1988, 1990). A binaural disparity in the arrival time (Δt_a) of impulses at a laminaris neuron includes the difference in the acoustic transmission time to the two ears (ITD) and the difference in the impulse conduction time (Δt_c) from the two ears to the neuron, hence $\Delta t_a = \text{ITD} + \Delta t_c$. Both ITD and Δt_c vary, but the delay lines are organized such that for each neuron Δt_c equals a particular ITD in magnitude but opposite in sign (i.e., $\text{ITD} = -\Delta t_c$); impulses from the two sides arrive simultaneously and the laminaris neuron fires maximally. Laminaris neurons are, however, not perfect coincidence detectors, because they pass monaural signals. Interestingly, an unfavorable phase difference elicits a smaller number of impulses than that triggered by either of the monaural signals. Nonlinear processes such as inhibition may thus contribute to the computation of interaural phase differences.

All of these processes occur in each audible frequency band. Laminaris neurons thus convey their selectivity for interaural phase differences to higher order nuclei in separate frequency channels. A single laminaris neuron responds to multiple ITDs that are separated by integer multiples of the stimulus period. This phenomenon occurs because phase is a circular variable. Thus, if an interaural time difference ITD corresponds to an interaural phase difference, IPD, then all $\text{ITD} + nT$ also correspond to IPD, where n and T are integer and the period of the stimulus tone, respectively. Laminaris neurons respond to all $\text{ITD} + nT$ as long as they are within their physiological range.

Laminaris neurons send their axons, in separate frequency channels, to two higher order nuclei, the central nucleus of the inferior colliculus and one of the lemniscal nuclei. The inputs from the nucleus laminaris endow the neurons of these nuclei with selectivity for interaural phase differences. Consequently, these neurons also respond to multiple ITDs. The neurons of the central nucleus of the inferior colliculus are, however, more sharply tuned to interaural phase differences. These neurons project to the lateral shell of the central nucleus of the inferior colliculus, and the neurons of this nucleus project, in turn, to the external nucleus of the inferior colliculus where space-specific neurons reside.

Unlike the lower order neurons, space-specific neurons are broadly tuned to frequency and respond only to one ITD when a broad-band signal is used. This fact indicates that space-specific neurons receive inputs from the frequency channels that are selective for the same ITD and its phase equivalents ($\text{ITD} + nT$) (Wagner *et al.* 1988). Space-specific neurons or their immediate precursors in the lateral shell get rid of the frequency dependent variable $\text{ITD} + nT$. This ability of space-specific neurons to respond exclusively to one interaural time difference is due to excitatory and inhibitory interactions between the different frequency channels that they receive (Takahashi and Konishi 1986; Fujita 1989).

The last issue in the synthesis of the stimulus selectivity of space-specific neurons concerns their ability to respond selectively to combinations of interaural time and amplitude differences. This capacity derives from the convergence of the two pathways in the lateral shell of the central nucleus of the inferior colliculus. Interaural amplitude differences are first encoded, however, in one of the lemniscal nuclei (Manley *et al.* 1988). Stimulation of the contralateral ear excites and that of the ipsilateral ear inhibits the neurons of this nucleus. The response of these neurons is, therefore, determined by interaural amplitude differences. These neurons are, however, not exclusively selective for interaural amplitude differences, because the contralateral ear alone can drive them. The outputs of these neurons are eventually used to produce the ability of space-specific neurons to tune to interaural amplitude differences. The convergence of the two pathways is not a simple addition but involves another nonlinear operation, which endows space-specific neurons with the ability to respond only to a combination of interaural time and amplitude differences.

3.2 The Bottom-Up Approach in the Electric Fish. In the electric fish, Heiligenberg and his associates have used the bottom-up approach to discover the neural mechanisms for the determination of the sign of frequency differences in the jamming avoidance response. It should be noted, however, that they used the results of behavioral analysis to guide their search for relevant neuronal stimulus selectivities. I shall briefly review the steps by which they discovered the output neurons.

The selectivities for primary stimulus variables, phase and amplitude, are established in the sense organs themselves. The electric fish has two kinds of electroreceptive sensory cells in the skin (Scheich *et al.* 1973). One of them fires a single impulse at each positive zero-crossing of the nearly sinusoidal electrical signal. The fish uses these impulses to convey to the brain information about the phase angles of the signal over the entire body surface. The other type of sensory cell is sensitive to variation in the amplitude of the electrical signal.

The phase and the amplitude-sensitive cells are mixed over the body surface, but they project to different layers of the first brain station. These layers constitute the starting points of separate pathways for phase and amplitude (Carr *et al.* 1982; Heiligenberg and Dye 1982). Each layer contains three separate maps of the electrical field variables over the body surface, and the phase and amplitude maps are in register (Shumway 1989a,b). This nucleus, the electrosensory lateral line lobe, contains neurons and their circuits that are sensitive to the rise and fall of signal amplitude (Saunders and Bastian 1984; Shumway and Maler 1989).

The electrosensory lateral line lobe projects to the multilayered torus semicircularis, presumably the homolog of the inferior colliculus. Like the owl, the electric fish uses special neural circuits for the computation of phase differences between different body loci. These circuits are found

in lamina 6 of the torus (Carr *et al.* 1986). Of the two classes of output neurons of these circuits, one responds to phase advance and the other to phase delay. Neurons selective for the rise or fall of amplitude occur in other laminae of the torus.

As in the owl, the phase and amplitude pathways converge on each other in specific layers of the torus. This convergence gives rise to four classes of neurons that are selective for four different combinations of amplitude and phase, that is, amplitude fall–phase advance, amplitude rise–phase delay, amplitude fall–phase delay, and amplitude rise–phase advance (Heiligenberg and Rose 1986; Rose and Heiligenberg 1986). The first two amplitude–phase combinations indicate that the fish's own frequency is lower, and the second two that the fish's own frequency is higher. These four neuron types are, however, not exclusively selective for particular amplitude–phase combinations, because they show some responses to other combinations. Also, the response of these neurons depends on the relative orientation of the fish's own electrical field and that of its neighbor, because their receptive fields are restricted to small body surface areas (Heiligenberg 1986).

The next stage of processing takes place in the nucleus electrosensorius where sensory channels from different body surface loci converge on single neurons (Keller and Heiligenberg 1989). The response of these neurons to amplitude–phase combinations becomes largely independent of the relative orientation of overlapping electrical fields. The final stage of processing is the prepacemaker nucleus in the diencephalon (Rose *et al.* 1988). Its neurons unambiguously discriminate between the signs of frequency differences.

4 The Output Neurons

The owl's space-specific neurons are the output neurons of the network involved in sound localization, because they occupy the top of the hierarchy of the brainstem and pontine auditory nuclei and project to the optic tectum. These neurons are selective for the same stimulus that induces the sound localizing response in the owl. This stimulus selectivity is a result of all parallel and serial computations that are carried out by lower order neurons in the pathways leading to the output neurons. Space-specific neurons form a map of auditory space in the external nucleus of the inferior colliculus (Knudsen and Konishi 1978). This map projects to the optic tectum where an auditory-visual map of space is found (Knudsen and Knudsen 1983). This bimodal map appears to be linked to the motor map of head orientation. Electrical stimulation of the optic tectum elicits saccadic head movements, which are similar to those released by natural sound stimuli. The spatial locus to which the owl orients corresponds to the receptive fields of auditory-visual neurons located at the site of electrical stimulation (Du Lac and Knudsen 1990;

Masino and Knudsen 1990). The exact mechanisms of translation from sensory codes to motor codes are, however, not yet known.

In the electric fish, neurons of the prepacemaker nucleus in the diencephalon are the output neurons of the system for the determination of the sign of frequency differences, because they occupy the top of the hierarchy of nuclei involved in this behavior and project directly to the premotor nucleus that controls the electrical organ (Rose *et al.* 1988). The stimulus selectivity of prepacemaker neurons is a result of all parallel and serial computations that take place in lower order nuclei in the pathways leading to them. These neurons fire more when the fish's own frequency is higher and less when the fish's own frequency is lower. This response pattern is exactly what the fish shows in response to the sign of frequency differences; when its own frequency is higher, the fish raises it, and when its own frequency is lower, the fish lowers it so that the frequency difference between the two fish becomes larger. Moreover, just as the fish's response is rather independent of the relative orientation of the other fish, so is the response of prepacemaker neurons. A rise and fall of the discharge rate in these neurons, respectively, raises and lowers the frequency of firing in pacemaker neurons that trigger each discharge cycle of the electrical organ.

5 Stimulus Selectivities and Neural Codes _____

Neural codes are pieces of information that neurons convey to other neurons. This section discusses first neural codes in the above sense and then the relationships between these codes and behavior. In the owl and the electric fish, we see how the timing and rate of impulses in the input stage are directly correlated with the phase and amplitude of the stimulus, respectively. Furthermore, we know how the selectivities for phase and amplitude disparities are derived from these inputs. Thus, phase-locked and rate-variable impulses are the neural codes for phase and amplitude, respectively. However, neither impulse timing nor rate is uniquely correlated with amplitude and phase disparities. Nevertheless, convergence of neurons selective for phase and amplitude disparities gives rise to neurons selective for combinations of the two disparities, indicating that the disparity-sensitive neurons convey relevant information to other neurons. The only code for this information is the neuron's place or address. "Place-coding" is the most universal signaling method in all neural systems. It is, therefore, justifiable to equate stimulus selectivities with neural codes, and the study of stimulus selectivities in successive stages of a sensory network can show how complex stimuli are encoded.

The two examples show that the neurons at the top of a hierarchically organized system represent the final result of all computations that are carried out by lower order neurons. Representation of a large network by a small number of output neurons is an interesting problem

from the point of view of network organization and coding. When a study of intermediate stages of a sensory system uncovers only neurons selective for simple stimulus features, this observation does not necessarily allow the investigator to conclude that the output of the system is encoded by a large ensemble of simple neurons. For example, Heiligenberg and associates interpreted the results of their early studies in terms of activities of a large ensemble of neurons. They found that the fish would fail to determine reliably the sign of frequency differences, if sensory inputs from a large part of its body surface were eliminated. Their models also indicated that comparisons of phase and amplitude between many pairs of body loci are necessary for the determination of the sign of frequency differences. In addition, their early studies of lower order nuclei uncovered only those neurons selective for separate lower order features of the stimulus for jamming avoidance. These observations prompted them to write papers with titles such as "The jamming avoidance response revisited: The structure of a neuronal democracy" (Heiligenberg *et al.* 1978) and "The neural basis of a sensory filter in the jamming avoidance system: No grandmother cells in sight" (Partridge *et al.* 1980). However, when they studied the diencephalon, which contains the nucleus electrosensorius and the prepacemaker nucleus, they found extensive convergence of inputs from the body surface onto single neurons. These neurons, particularly prepacemaker neurons, unambiguously discriminated the sign of frequency differences. This finding resulted in a paper entitled "'Recognition units' at the top of a neuronal hierarchy? Prepacemaker neurons code the sign of frequency differences unambiguously" (Rose *et al.* 1988). Thus, one cannot predict either from behavioral analyses alone or from the study of intermediate stages of a network how its output stage encodes relevant stimuli.

In both the electric fish and the owl, we see extensive convergence of lower order neurons onto the output neurons that are selective for the behaviorally relevant stimulus. The ratio of the output neurons to lower order neurons has not been determined in either system, but the volume of tissue containing the output neurons appears to be much smaller than that of lower order nuclei in both systems. The prepacemaker nucleus, being about 100 μm in diameter, is the smallest nucleus in the electrosensory system (Keller *et al.* 1990). Moreover, this nucleus consists of two parts, one for the control of the jamming avoidance response and the other for "chirps," which occur in courtship and aggression. The number of neurons in the "chirp" area is estimated to be about 200 on each side of the brain and the jamming avoidance area contains perhaps twice as many neurons (Heiligenberg, personal communication). These numbers are small in a system in which most lower order nuclei contain thousands of neurons.

Intracellular stimulation of a single "chirp" neuron can induce weak "chirps" and stimulation of many neurons with glutamate induces strong "chirps" (Kawasaki and Heiligenberg 1988; Kawasaki *et al.* 1988). These

neurons are somewhat similar to the command fibers of invertebrates. Recent reports show that a group of command fibers contributes to the control of several different motor output patterns, but the amount and nature of the contributions by different fibers vary in different patterns (Larimer 1988). Some of the oscillator circuits of invertebrates also show elements of combinatorial control of multiple output patterns by a small group of neurons (Getting 1989). Thus, in some systems, a small number of neurons represents the outputs of a network and controls relatively complex behaviors.

6 Similarities in Algorithms

In the present context, an algorithm refers to steps and procedures in signal processing. Figure 3 compares the algorithms for the processing of the signals for sound localization by the owl and for the jamming avoidance response by the electric fish. Both systems use parallel pathways for the processing of different stimulus features. Signal processing within each of the pathways occurs in a hierarchical sequence of nuclei. First, the codes for the primary stimulus variables, phase and amplitude, are sorted out at an early stage and routed to appropriate pathways, then different stimulus features are detected and encoded in each pathway by special neural circuits. Further processing in higher order stations makes the neural representations of the stimulus features more accurate and less ambiguous. Finally, the codes for these features are brought together by convergence of the parallel pathways.

The result of convergence is not simply the addition of the codes from the input channels but the creation of a new code. In both examples, the inputs to the output neurons carry the codes for phase and amplitude disparities, but the output neurons do not respond to either feature alone but only to a combination of the two features. The output neurons of the entire network can be recognized in both the owl and the electric fish. These neurons occur at the top of the hierarchy of processing stages, and they encode the signals for sound localization and jamming avoidance unambiguously. The output neurons serve as the interface between the signal processing and motor system or between signal processing networks of different modalities such as the auditory and visual systems in the owl.

There are thus remarkable similarities between the owl and fish algorithms (Konishi 1991). Both the auditory and electrosensory systems are thought to have evolved from the lateral line system, which the fish uses to detect disturbances in the surrounding water. This explanation does not account for specific aspects of the algorithms, such as the separation of the phase and amplitude codes in two different nuclei in the owl and two different layers of a nucleus in the electric fish. The fact that both

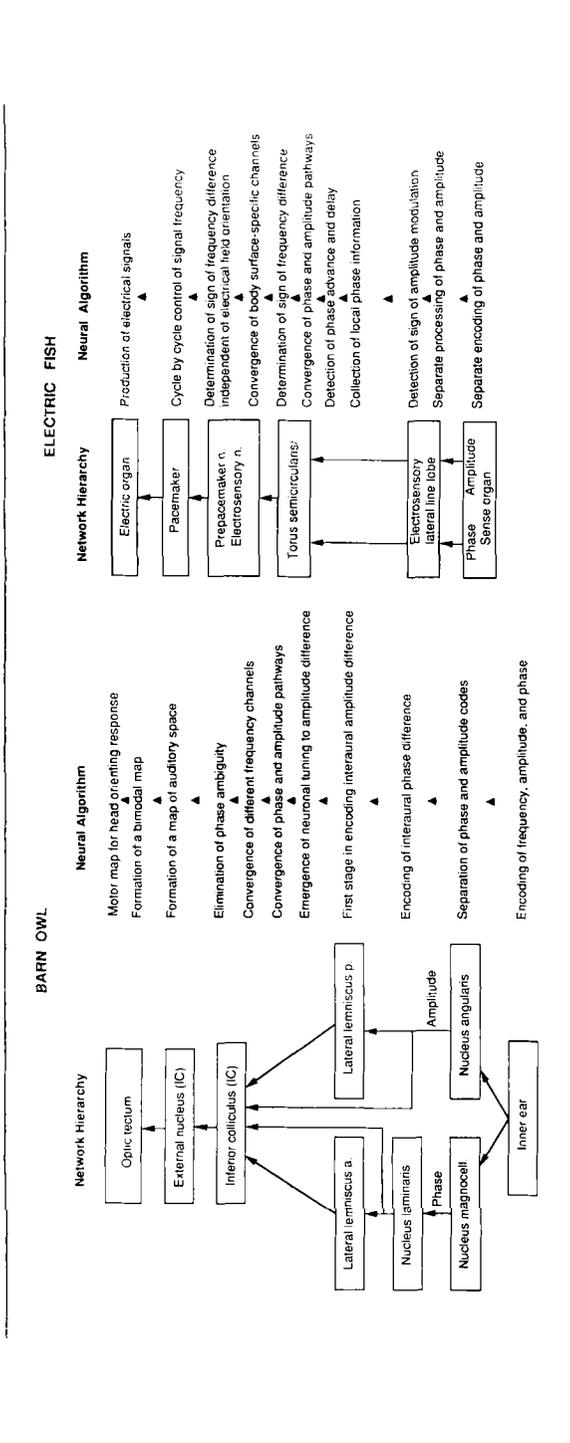


Figure 3: Similarities in neural algorithms. The owl's auditory system computes the combinations of interaural time and amplitude differences that uniquely define separate loci in auditory space. The electric fish's electrosensory system determines the sign of frequency differences between the fish's own and a neighbor's signal by detecting the differences between body loci in the phase and amplitude of the waveform resulting from the mixing of the two signals. Both systems compute phase and amplitude disparities to synthesize the codes for phase-amplitude combinations. This figure shows where in the brain and in what steps the two systems carry out the synthesis of the codes. The boxes show the brain nuclei and the arrows indicate the direction of connections. The process that takes place in each nucleus is posted on the right of the corresponding box. The multiple processes performed by one nucleus are listed as a group. The arrowheads between processes indicate the sequence in which the different processes occur.

animals deal with sinusoidal signals may be the reason for the similar algorithms, because the primary stimulus variables are the same in both sound and electrical signals. The goals of the two systems are also similar, because both systems ultimately encode combinations of phase and amplitude disparities. The neural implementations of the algorithms are, however, different between the systems. The electric fish uses different sensory cells to encode phase and amplitude, whereas the owl uses the same auditory neurons to encode both phase and amplitude. The electric fish uses electrical synapses to transmit phase-locked spikes in all relay stations below the stage where phase differences are computed. The owl uses chemical synapses for the same purpose, although they are specialized synapses. The electric fish uses the differences in the arrival time of phase-locked spikes between somata and dendrites to detect phase disparities between different body loci, whereas the owl uses axonal delay lines. Both animals use the convergence of different input channels to eliminate ambiguity in neuronal stimulus selectivity, but the convergence occurs in different parts of the brain, the midbrain in the owl and the diencephalon in the fish.

Do similar algorithms occur in other complex sensory systems? The answer to this question is difficult to obtain, because few studies of complex sensory systems have investigated successive stages of signal processing. The visual system of the macaque monkey is the only other system that has been studied well enough for the discussion of algorithms. This complex system is also organized according to parallel and hierarchical design principles (Van Essen 1985; Maunsell and Newsome 1987; Hubel and Livingstone 1987; Livingstone and Hubel 1987, 1988; De Yoe and Van Essen 1988); parvocellular and magnocellular pathways are physiologically and anatomically distinct and the way stations in each pathway within the extrastriate cortex are hierarchically organized. These network hierarchies appear to be correlated with the processing hierarchies. Lower order features such as stimulus orientation are encoded in the striate cortex, whereas relatively higher order features, such as velocity and geometric patterns like faces, are encoded in higher stations, the middle temporal area encoding velocity and the inferotemporal area encoding faces (Gross *et al.* 1972; Perret *et al.* 1982; Maunsell and Van Essen 1983). However, much remains to be explored before we can understand the mechanisms and functional significance of feature extraction in this system as well as we do in the electric fish and the owl.

7 Concluding Remarks

Neuroethology, which studies the neural bases of natural behavior, has something to offer to the students of computational and neural systems. The tenet of neuroethology states that the brain is designed to process biologically relevant stimuli and control behavior essential for the

survival and reproduction of the animal. Only behavioral observations and analyses can identify biologically significant stimuli. The two systems discussed above could not have been analyzed adequately and understood without use of and reference to such stimuli. These examples also show that the study of successive stages of signal processing is essential for the understanding of both the algorithm and its neural implementation.

These examples are relevant to computational neuroscience the aim of which is to understand the workings of the brain. This field is, however, theory-rich and data-poor. To achieve its goal, the field needs benchmark neural systems in which both the algorithm and its neural implementation have been worked out. The electric fish and the owl provide such frames of reference for those who explore or model sensory networks.

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