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The Octavolateralis System and Mauthner Cell: Interactions and Questions

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Abstract

This paper is an overview of some of the major points to arise in the accompanying contributions of this special symposium issue. The symposium arose out of discussions among investigators interested in the inner ear-Mauthner cell, with the focus on hydrodynamic components that activate the Mauthner cell through the octavolateralis system. The intention of the symposium was to investigate the possibility of using our knowledge of the Mauthner system to help understand acoustic processing by the ear, and of using knowledge of fish hearing to better understand Mauthner cell function. This is the first attempt to take a broad look at both systems to see how they might function together. As such, these proceedings can serve as a mini-tutorial for investigators interested in one system or the other. In this summary paper we identify some of the major uncertainties in our understanding of the ear-Mauthner connection. These include questions about: (1) the identity of the acoustic stimuli that are neuroethologically relevant to the Mauthner system; (2) the relative importance of the various octavolateralis inputs (acoustic, vestibular, lateral line); (3) the contribution of the different various acoustic endorgans to the Mauthner system; (4) whether the Mauthner system can distinguish sound source location, and (5) whether Mauthner neurobiology is compatible with the prevailing model (the phase model) for determining sound source location in fishes. We believe these issues provide potentially useful avenues of future investigation that should give important insights into both acoustic processing by fish and the function of the Mauthner system.

Introduction

This special issue of *Brain, Behavior and Evolution* is the outcome of a symposium in which fish hearing and Mauthner system investigators met at the Third International Congress on Neuroethology in Montreal (August, 1992). The fish auditory and the Mauthner cell systems are

each well studied preparations that have been separately in focus for many previous comparative and neuroethological investigations. Although diverse evidence supports the notion that Mauthner initiated escape responses (or C-starts) are activated by acoustic input via the ear [e.g. Furukawa, 1964; Furukawa, 1966; Moulton and Dixon, 1967; Eaton et al., 1977; Zottoli, 1977; Faber and Korn, 1978; Blaxter

al., 1981; Canfield and Eaton, 1990], we know very little about the effects of natural acoustic stimuli on the Mauthner cell. Conversely, although the auditory system in fishes has been extensively investigated, very little is known about how acoustic information is processed in the brainstem of fishes. Moreover, it is not clear why many types of fishes hear as well as they do, or how these abilities evolved [Fay and Popper, 1980; Schellart and Popper, 1992; Popper and Fay, 1993].

It is reasonable to think, however, that insights into these issues could be gained by studying how auditory information is processed by the Mauthner system. The Mauthner cell is readily accessible for neurophysiological studies, and its associated behavior, the C-start, is extensively characterized in a variety of neuroethological contexts [Eaton and Hackett, 1984; Eaton, 1991; Canfield and Rose, 1993a, 1993b]. Moreover, the controlling networks and output circuits of the Mauthner cell are well known [Faber et al., 1991; Fetcho, 1991]. Especially important for studies in hearing is the fact that when a Mauthner cell fires, we know that a fish has perceived the stimulus as coming from a particular direction. Thus, the Mauthner initiated behavior is a potentially useful, unconditioned assay for studying aspects of brainstem processing of acoustic signals in fishes.

These ideas began to emerge at a symposium on the Neuroethology of the Mauthner Cell, at the Second International Congress of Neuroethology in Berlin in 1989 (see papers in Eaton [1991]). There we decided that a symposium that included individuals with expertise on fish ears and Mauthner systems would be the best way to summarize our understanding of the relation between the systems and to define the major unsolved issues. Thus arose this special issue in which the four main papers were produced by laboratory groups with long-term interests in either the inner ear or the Mauthner system.

In this introductory paper we first highlight some of the major findings and questions that emerged both from the symposium and the associated papers in this issue. The papers consolidate much of what is known about the acoustic inputs involved in activating Mauthner initiated escape responses (or C-starts) of teleost fishes, but the papers also emphasize that there are critical gaps in our knowledge of the relationship between the ear and the Mauthner system. We believe that these uncertainties can provide the basis for potentially fruitful avenues of future investigation.

We next discuss some of the major issues regarding the relationship between the ear and the Mauthner cell. Our presentation is guided by an outside-to-inside perspective in which we start with the predator and the types of acoustic stimuli that might activate the escape response, and we

then proceed through the various octavolateralis inputs to the Mauthner system and how it might process these stimuli. We end with a consideration of the production of the associated motor response and what it can, and cannot, tell us about acoustic processing.

What are the Stimuli that Various Predators Make during Attacks on Fishes?

It is often implicitly assumed that hearing in fishes evolved to detect communication signals: that is, signals intended to be heard. The Mauthner system may have evolved to do the opposite: to detect predatory signals that are intended to be concealed. The Mauthner system is found in all the aquatic anamniote vertebrate classes and probably evolved in response to predatory attacks that take place under water. In a strike, some types of predators are known to begin with a rapid acceleration of the head towards the prey [Lauder, 1983, 1985]. This type of strike should cause a significant, low frequency, compressive pressure with displacement toward the prey. The massive connection of the Mauthner lateral dendrite to afferent from the ear corresponds to the supposed importance of this potential stimulus and suggests that sounds associated with predatory attacks were very possibly important in the evolution of the Mauthner system. Because of its broad appearance in anamniotes, it is likely that the Mauthner system preceded the development of complex hearing innovation in fishes, such as the swimbladder-Weberian ossicle system used for sound pressure detection by hearing specialists. Could it be that predator detection played a major role in the evolution of acoustic mechanisms in fishes?

If the Mauthner system evolved in response to detecting the hydrodynamic components of a predatory attack, it becomes an important issue to characterize these components. Although these have not yet been measured quantitatively, strike kinematics are well studied [Lauder and Prendergast, 1992; Lauder and Shaffer, 1993]. Interestingly, there are common kinematic patterns among diverse predators which suggest that they might employ a kind of 'stealth kinematics' to avoid acoustic detection. As predators accelerate toward the prey, various species open their oral cavities with a velocity equivalent to a 10–20 Hz signal. This initial mouth opening does not suck the prey toward the mouth rather it may reduce acoustic or hydrodynamic components associated with the predator's acceleration. Interestingly, it is only after the prey has crossed the plane of the predator's jaws that suction is employed to help pull the prey into the oral cavity [Lauder and Prendergast, 1992]. Thus, mouth opening, and other adaptations, may reduce the acoustic detection of the predator's acceleration. Clearly, since fish

do escape from predators [Webb and Skadsen, 1980; review Webb, 1986; Fuiman, 1989; Blaxter and Fuiman, 1990], we would like to know what the Mauthner cell could be listening to in the predatory signal. If the Mauthner cell responds to very low frequency signals, the mechanism for detection of such signals needs to be addressed.

Acoustic, Vestibular or Lateral Line?

As described in greater detail in a number of recent reviews [e.g. Schellart and Popper, 1992; Popper and Fay, 1993], the ear is stimulated when a fish's body moves, along with the water mass relative to the otolith that overlies the inner ear sensory epithelium. Since, in water, the motions associated with acoustic stimulation are basically a continuum with vestibular stimulation, it becomes difficult to differentiate between what might be 'vestibular' and what might be 'auditory'. For purposes of this paper, we will generally refer to stimulation of the Mauthner cell as being auditory. Yet, in the long run, it is critically important to keep in mind that stimulation might also be very low frequency motions [Karlsen, 1992a, b] that, in air, might be considered vestibular stimulation.

Because predatory strikes are from a very close distance, it also seems likely that the lateral line may play a role in activating the Mauthner system. Blaxter and Fuiman [1990] showed that there is a significant rise in C-start responsiveness in herring larvae (*Clupea harengus*) that coincides with the development of the canal neuromast system (the free neuromasts do not appear to be important in activating the C-start to predatory attacks in the herring). In addition, C-start responsiveness dropped significantly, in comparison to that in control animals, in larvae that were treated with streptomycin to damage the sensory hair cells of the lateral line. From these and other data, Blaxter and Fuiman [1990] concluded that both the ear and lateral line canal system may function in initiating escape.

As pointed out in the paper by Zottoli et al. [1995], we really know very little about the projections of the lateral line to the Mauthner cell, and how stimulation of the lateral line (or parts thereof) can activate the C-start response. We do know that there are lateral line projections, probably via interneurons, to the medial region of the lateral dendrite of the Mauthner cell [Korn and Faber, 1975; Zottoli and van Horne, 1983]. These studies primarily dealt with input from the posterior lateral line nerve (pLL) which subserves the body of the fish. To our knowledge, no one has looked at whether the anterior lateral line nerve (aLL) from the head region sends direct projections to the Mauthner cell, or whether it, like the posterior lateral line, sends projections via interneurons. A related question would be whether there

are any interactions on the Mauthner cell between the pLL and aLL or between lateral line nerves and those from the inner ear (see below). Taking these questions one step further, is it possible that there may be a topographic representation of lateral line input from different body regions to the Mauthner cell? Such information would provide, along with information about hydrodynamic stimulation from discrete regions of the body.

As with the projections from the ear, we also need to raise the possibility that input from the lateral line (if present) to the Mauthner cell may vary in different species. The extensive interspecific variation in the gross structure of this organ [e.g. Coombs et al., 1992] lead us to at least raise the question of inter-specific diversity of relationship between the lateral line and the Mauthner cell.

Depending upon how input to the Mauthner cell from the ear and from the lateral line is resolved, an additional question may need to be broached – whether the Mauthner cell may actually combine the inputs from the two systems to elicit the C-start response. Such combined inputs provide a fish with a good deal of information about the nature of the stimulus as well as its location in space relative to the fish. Of course, a restriction on the use of input from the two systems would be that the stimulus falls within the frequency response characteristics of both systems. That is quite feasible, however, since the frequency ranges of the two systems tend to include signals from below 100 Hz in some species [Karlsen, 1992a, b] to possibly as high as 200 Hz [e.g. Münz, 1989]. While it is possible that the lateral line is involved with the Mauthner system, recent evidence on two species of hearing non-species suggests that these species can detect infrasound below 1 Hz using the saccule [Karlsen, 1992a, b]. Thus for very low frequencies we cannot specify whether it is the ear or the lateral line that is involved in triggering Mauthner-initiated behaviors.

What are the Auditory Endorgan Inputs to the Mauthner System?

A number of investigators have suggested that the primary input to the Mauthner cell arises from one of the otolithic endorgans of the ear, the saccule [e.g. Bart, 1915; Lin et al., 1983; see Popper and Edds-Walton, 1990, for review]. However, it cannot be ruled out that input to the ear may be from any one of several endorgans innervated by the posterior branch of the eighth nerve, including the saccule, lagena, and posterior semicircular canals (as well as the macula neglecta in species having a macula endorgan). Moreover, while very limited, there is some evidence that the utricle may project to the Mauthner cell.

several species [Zottoli and Faber, 1979; Meredith and Butler, 1983]. In fact, Zottoli et al. [1995] have presented new preliminary data also supporting this contention. Finally, as pointed out by Popper and Edds-Walton [1995], there is the very distinct possibility that projections to the Mauthner cell may differ in various teleost species. More specifically, Popper and Edds-Walton suggest that there may be different projections to the Mauthner cell in hearing specialists and non-specialists. This notion is potentially supported by the observation of Zottoli et al. [1995], described below, that the latency for a Mauthner cell response differs in hearing specialists and non-specialists.

There are several reasons for the less than clear-cut data on projections to the Mauthner cell. First, many of the studies were done without using modern experimental neuroanatomical techniques: therefore they lacked the capacity to do the detailed analyses of origins of innervation in the ear. Second, in a number of instances, the neuroanatomical tracer (e.g. horseradish peroxidase) was placed in a position whereby it could have been picked up by fibers from any one of several endorgans.

Can the Mauthner System Distinguish Sound Source Location?

Is Mauthner Neurobiology Compatible with the Phase Model?

Fay [1995] has pointed out that an effective C-start probably depends on an optimal decision regarding which direction to take. Do fishes use acoustic cues alone in making this decision? As reviewed by Eaton et al. [1995], the behavioral experiments of Blaxter et al. [1981] and Mueller [1981] support this contention. Although unproven, directional hearing using the Mauthner system makes sense. Predators often strike from close distance, thus allowing the prey little time for neural processing of possible escape directions. If the prey animal can determine the direction of sounds associated with predatory strikes, then the auditory system may provide the requisite speed for predator avoidance. Indeed, the auditory-Mauthner system connection may short-circuit longer and potentially more complex sensory pathways, such as vision, or localization decisions on stimuli from greater distances, which would probably be computed using other neural circuitry.

For fish, the underlying neurobiology of directional hearing is not fully understood, but several theoretical analyses have suggested that fishes can determine the direction of underwater sound by utilizing a comparison of the phase of acoustic particle motion and pressure. On the basis of particle motion of a sound, a fish can theoretically tell that a sound is on an axis that runs from right to left, but it can

not discriminate whether the source is to the right or left without additional pressure information. Schuijf [1981] and others [e.g. Buwalda, 1981; Popper et al., 1988; Rogers et al., 1988] have proposed that fish need both particle displacement (directly mediated by the ear) and pressure information (as re-radiated via the swimbladder) to resolve the 180° ambiguity. This is known as the phase model, which is described in qualitative terms by Eaton et al. [1995]. Consistent with this model are several experimental studies involving conditioned behavioral responses [i.e. Buwalda et al., 1983]. These considerations suggest that an acoustically directed Mauthner-initiated response needs both pressure and particle displacement information.

Fay [1995] suggests that in the presence of a large acoustic signal to both Mauthner cells, directionality might be determined by 'small [particle motion] deviations from perfect [binaural] correlation'. In other words, directional hearing is not only a result of central [rather than peripheral] processing but also requires input from both ears. A response results when both Mauthner cells receive a large identical, acoustic pressure stimulus which has the capacity to cause both to fire.

Eaton et al. [1995] take a different approach and propose a logical model for how the Mauthner system may discriminate sound sources on either the left or right of a fish. They do this by showing how the properties of the Mauthner system neurons could mediate a neurophysiological implementation of the phase model for directional hearing. Eaton et al. emphasize the differences in phase of the particle motion of the stimulus as it is detected by oppositely oriented hair cells [Fay, 1984] and conveyed to the PHP (for passive hyperpolarizing potential) cells. These inhibitory interneurons are already known to be sensitive to sound and to regulate Mauthner threshold [Faber et al., 1991]. In this model the pressure component would potentially excite both Mauthner cells, but the Mauthner cell on the side opposite the stimulus (e.g. the 'wrong' Mauthner cell) would be prevented from firing by the PHP cells. The trick is in understanding how inhibitory neurons, like the PHP cells, could use the displacement information to block the 'wrong' Mauthner cell. In fact, Eaton et al. suggest that the PHPs cannot do it on the basis of particle motion alone. From a computational implementation of the system [Guzik and Eaton, 1993, 1994], Eaton et al. [1995] propose that the PHP cells do this by virtue of their parallel distributed processing of both displacement and pressure sensitive afferents. Just as acoustic fibers have combinations of sensitivities to different phases of displacement and pressure, Eaton et al. [1995] suggest that the PHP cells are not homogeneous and also have different sensitivities to these components

Thus, this analysis poses a very specific answer to the question asked by Fay: 'Why does the combination of sound pressure and particle motion activate Mauthner cells while particle motion is, by itself, insufficient?'

In principle, if given both displacement and pressure inputs, the Mauthner system should be able to make its decision about sound direction on the basis of the first half cycle of sound onset. This makes sense because such short response times are probably an essential feature for successful escape, since predators typically have closing times of 100–150 msec [Webb and Skadsen, 1980; Lauder, 1983]. As discussed by Eaton et al. [1995], previous studies on goldfish show that the Mauthner cell responds within a few milliseconds to low frequency sounds. The goldfish is classified as a 'hearing specialist', compared to species that have no adaptations to enhance hearing, the hearing 'non-specialists' [e.g. Schellart and Popper, 1992]. Interestingly, Zottoli et al. [1995] report that in a species considered to be a hearing non-specialist, the Mauthner cell takes significantly longer to fire when tested under the same conditions as used to test goldfish. Thus, hearing specialists and non-specialists may differ in their ability to quickly determine the direction of aversive acoustic stimuli.

Whereas the Mauthner system can be useful for studies in directional acoustic processing, we do not wish to oversell the case. This is especially true when one considers the complexity of the entire escape response. The neuroethology of the Mauthner initiated escape response was recently reviewed in this journal [Eaton, 1991] and is not specifically addressed by this symposium issue. However, the behavioral context is very important in understanding how the Mauthner system could, and could not, be used to gain insights into general mechanisms of directional acoustic processing in fish. We next discuss this briefly.

Assuming that the Mauthner system can respond directionally to sound source location, it is most likely that this network would respond only to initial information on general sound source direction and could determine only whether the sound was originating on the left or right of the fish. Our reasons for thinking this have to do with the relatively simple motor output of the Mauthner cell itself compared to the complexity of the escape behavior in which the Mauthner cell participates. In response to a given stimulus, one of the two Mauthner cells fires only one action potential [Zottoli, 1977; review, Eaton et al., 1991]. This produces a turn of about 40° to 45° from the initial orientation of the fish [Nissanov et al., 1990]. (This turn is toward the side of the fish opposite the Mauthner cell soma that fired, because the Mauthner axon activates motoneurons on the side of the body opposite its soma.)

However, the corresponding escape response can be much more complex than suggested by this simple 'defensive' movement when just the Mauthner cell is activated, recently shown by Foreman and Eaton [1993], regardless of which of the Mauthner cells fires, a fish can achieve, at the end of the response, any orientation in the 360° plane around itself. The variability in the trajectories is a function of the perceived direction of the stimulus and the location of surrounding objects that might block the escape route [Eaton and Emberley, 1991]. It is only the initial orientation that involves firing of the Mauthner cell and its motoneuron pool. Thus, the complex regulation of the escape response suggests that, besides the Mauthner cell, additional cells of the brainstem escape network are involved in determining the escape trajectory to a given stimulus angle [Eaton and Emberley, 1991; Foreman and Eaton, 1993]. For example, additional cells that process sound source location would be clearly necessary for stimuli originating in quadrants in front of, or behind a fish. For rostral stimuli, a fish can produce a very large escape turn of 180°, or more, from initial orientation. Caudal stimuli elicit a small initial orientation to the side, followed by a large counter turn, or a direction change, that straightens the trajectory so the fish accelerates forward along the line of its initial orientation [Foreman and Eaton, 1993].

Thus, if a fish can produce an accurate escape trajectory to an aversive sound stimulus, the brainstem escape network would have to be capable of activating both ipsilateral and contralateral motoneuron pools, and it would have to be capable of variably recruiting these pools, especially for stimuli that originate either in front or behind the fish. In fact, for stimuli either in front of or behind the fish, it does not make any difference which Mauthner cell fires. The complex activation of the spinal motor circuits and the escape goes far beyond the capability of a single action potential produced by one of the Mauthner cells. Firing of the escape trajectory clearly requires participation of the brainstem escape network. It is the investigation of acoustic processing by these cells that may provide the most and more subtle insights into general mechanisms of directional hearing in fishes.

Conclusions

The role of acoustic signals in Mauthner activation is clearly a fruitful potential issue for future investigation. The detailed discussion of these issues forms the core of the following papers. Nevertheless, it is important to bear in mind that it is unlikely that the Mauthner system, or

the brainstem escape network, receives all brainstem auditory information. Thus, these networks could not give a complete picture of brainstem auditory processing. Finally, there are many other important aspects of the acoustic signal, such as distance [Popper et al., 1988; Rogers et al., 1988], which would not be coded in the outputs of escape triggering neurons. In fact, we suspect that acoustic processing by the Mauthner system should be relatively simplistic and only start the initial orientation of the escape to either the left or right. It is because of this simplicity, however, that we think that the Mauthner system may be quite useful for developing insights into more sophisticated mechanisms of brainstem auditory processing.

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