

CENTRAL MECHANISMS OF TEMPORAL ANALYSIS IN THE KNOLLENORGAN PATHWAY OF MORMYRID ELECTRIC FISH

MATTHEW A. XU-FRIEDMAN^{1,*} AND CARL D. HOPKINS²

¹*Department of Neurobiology, Harvard Medical School, 220 Longwood Avenue, Boston, MA 02115, USA* and

²*Section of Neurobiology and Behavior, Cornell University, Seeley Mudd Hall, Ithaca, NY 14853, USA*

*e-mail: mfriedman@hms.harvard.edu

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Summary

Mormyrid electric fish communicate using pulse-type electric organ discharges (EODs). The fine temporal structure of the waveforms of EODs varies widely throughout the 200 or more species of mormyrids. These signals carry information about the species, the sex and even the individual identity of the signaller. Behavioral experiments have shown that some species of fish are capable of using this information. Of the four known types of electroreceptors in mormyrid fish, the knollenorgan electroreceptor is the one most likely to be involved in the detection of conspecific EOD signals. Here, we review some recent advances in understanding how the central knollenorgan pathway might be analyzing the temporal structure of the EOD waveform. Fine temporal analysis

appears to take place in the nucleus extero-lateralis pars anterior (ELA), where tightly phase-locked inputs from the hindbrain drive a direct, excitatory input through a long axonal delay line and also drive an indirect, inhibitory input with negligible delay through the ELA large cell. These two inputs converge on ELA small cells, where they are hypothesized to interact in a 'delay-line/blanking' model. This initial temporal analysis is further refined in the nucleus extero-lateralis pars posterior, where units tuned to ranges of pulse durations have been identified physiologically.

Key words: time-coding, knollenorgan, mormyrid, electric organ discharge, waveform.

Introduction

Electric communication signals retain their fine temporal structure as they are transmitted from signaller to receiver in the aquatic environment, unlike auditory signals, which are corrupted by echoes and reverberation (Hopkins, 1986b). This enables weakly electric fish to communicate useful information even with their brief electric organ discharges (EODs). EODs from different species of African mormyrid electric fish vary widely in waveform (1–4 phases), duration (60 μ s to 20 ms) and polarity. The EODs of many species show sexual differences in waveform (Kramer, 1997; Hopkins, 1999). It is possible in some cases to recognize individuals on the basis of their EODs (Crawford, 1992; Friedman and Hopkins, 1996).

Mormyrids use EOD waveforms to discriminate the species and sex of the signaller (Hopkins, 1981; Hopkins and Bass, 1981; Graff and Kramer, 1992). One behavioral study addressed the mechanism by which they perform this task. Males of the species referred to as *Brienomyrus brachyistius* (*tp*) (Hopkins and Bass, 1981) or *Brienomyrus* sp. 2 (Alves-Gomes and Hopkins, 1997) exhibit a sex difference in the EOD waveform. Males responded with courtship displays ('rasps' or bursts of EODs delivered at a high rate) when presented with square pulses of a duration that matched female EODs, but they failed to respond to shorter or longer square pulses or to pulses derived from a phase-shifted female EOD (Hopkins and Bass,

1981). These experiments suggested that the salient feature of the EOD is its temporal waveform structure.

Mormyrid fish have four different kinds of electroreceptors used for active and passive electrolocation and communication. Among these, knollenorgan receptors appear the most likely to detect and to respond to communication signals from other fish. First, they have a high sensitivity and they are broadly tuned to the spectrum of the species' own EOD (Bass and Hopkins, 1980, 1984). Furthermore, if parts of the knollenorgan pathway in the central nervous system (CNS) are lesioned, some communication behaviors are abolished (Moller and Szabo, 1981). The motor areas that generate the fish's own EOD send a strong inhibitory input to the primary sensory areas in the hindbrain (Zipser and Bennett, 1976; Bell and Grant, 1989). Thus, the primary afferents from knollenorgan receptors respond to the fish's own discharge, but this response never gets past the hindbrain electrosensory lateral line lobe (ELL), making the fish 'deaf' to its own discharges. Together, these characteristics imply that the knollenorgan pathway is specialized for detecting and processing EOD signals generated by neighboring, conspecific fish.

Knollenorgan electroreceptors are scattered over the body surface. For a stimulus consisting of a brief pulse of electrical

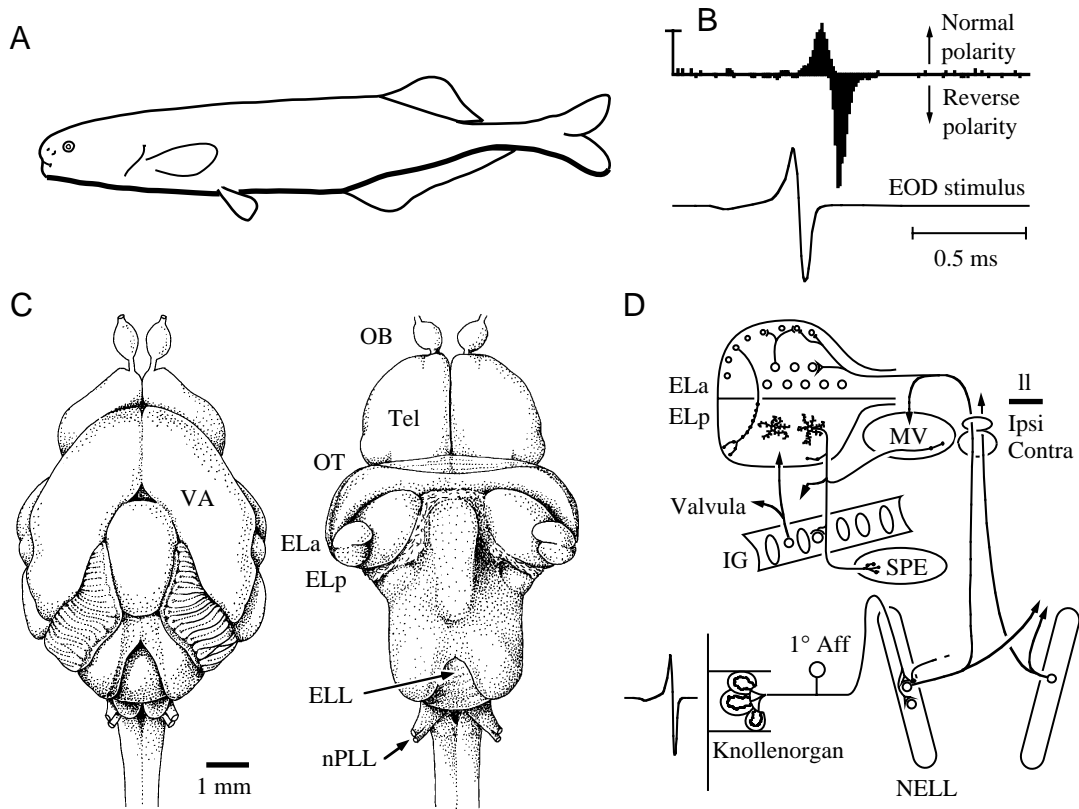


Fig. 1. Summary of the knollenorgan pathway. (A) Drawing of a mormyrid fish, *Brieniomyrus brachyistius*. (B) Response of a knollenorgan (upper trace) to an electric organ discharge (EOD) stimulus (lower trace). The response is displayed as a post-stimulus time histogram. For the upward histogram, the EOD stimulus shown was presented to the knollenorgan multiple times. For the downward histogram, the inverted EOD stimulus was presented. The downward histogram is equivalent to the responses of knollenorgans on the opposite side of the body. Thus, knollenorgans on one side of the body respond to the upward edge of the stimulus (with some delay) while knollenorgans on the opposite side respond to the downward edge. Bar, 25 spikes per bin. (C) Overview of the brain of *Brieniomyrus brachyistius*. On the right, the valvula cerebelli has been removed. ELA, nucleus extero-lateralis pars anterior; ELL, electrosensory lateral line lobe; ELP, nucleus extero-lateralis pars posterior; nPLL, posterior lateral line nerve; OB, olfactory bulb; OT, optic tectum; Tel, telencephalon; VA, valvula cerebelli. (D) Overview of the known connections of the knollenorgan pathway. Contra, contralateral; IG, isthmic granule nucleus; Ipsi, ipsilateral; ll, lateral lemniscus; MV, nucleus medialis ventralis; NELL, nucleus of the ELL; SPE, subpraeminient nucleus; 1° Aff, primary afferent. Modified from Amagai et al. (1998) and Friedman and Hopkins (1998).

current, either a square pulse or an EOD, knollenorgans on one side of the body respond to the onset of current with a phase-locked spike, and those on the opposite side of the body respond to the offset (Fig. 1B; Hopkins and Bass, 1981; Hopkins, 1986a). Therefore, fish could analyze the temporal structure of the stimulus by comparing the temporal pattern of spikes arriving from knollenorgan electroreceptors all over the body. In the simplest case, they could measure the duration of the pulse by measuring the time difference between the two sides of the body (Hopkins and Bass, 1981). This comparison must occur in the CNS, and here we describe some anatomical and physiological characteristics of the knollenorgan pathway that could provide the neural basis for this task.

Specializations for temporal analysis

Knollenorgan electroreceptors project roughly somatopically to the ipsilateral nucleus of the electrosensory lateral

line lobe (NELL) (Fig. 1D; Bell and Russell, 1978; Szabo et al., 1983; Hopkins et al., 1993). The terminals onto the NELL cells are large and electrotonic (Mugnaini and Maler, 1987b). The NELL somata are large and adendritic (Szabo and Ravaille, 1976) and are strongly immunoreactive for calretinin (Friedman and Kawasaki, 1997). These anatomical and neurochemical characteristics are commonly associated with neural pathways specialized for the preservation of fine temporal information, such as the auditory azimuthal localization pathways in birds and mammals (Konishi, 1991) and the electrosensory phase-coding systems in the electric fish *Eigenmannia* and *Gymnarchus* (Carr, 1986; Kawasaki, 1997).

The NELL sends a thick axon bilaterally up the lateral lemniscus to end in two nuclei in the torus semicircularis: the nucleus medialis ventralis (MV) and the nucleus extero-lateralis pars anterior (ELA) (Fig. 1D; Szabo et al., 1983). The axon branch to the MV is thin, and the terminals there are small *en passant* boutons (Amagai et al., 1998; Friedman and Hopkins,

1998). In contrast, the axon branch to the ELA is thick and heavily myelinated, and the terminals it makes are large and electrotonic. Thus, the ELA shows anatomical specializations typically associated with the preservation of fine temporal information, but the MV does not. In addition, the midbrain is the first stage in the knollenorgan pathway where information from all parts of the body can be compared. Therefore, the ELA is more likely to be the site where temporal analysis takes place (Szabo et al., 1983), while the MV may perform some other function, such as spatial analysis.

There are only two cell types in the ELA, large cells and small cells (also called interstitial and granule cells by Mugnaini and Maler, 1987a). They are easily differentiated by size (approximately 10 μm versus approximately 6 μm in soma diameter). The NELL axon terminates onto ELA large cells and small cells, with mixed chemical and electrical synapses, suggesting that synaptic delays are extremely short (Mugnaini and Maler, 1987a). ELA large cells and small cells both appear to be adendritic, according to intracellular dye-fills of ELA large cells with biocytin and Lucifer Yellow and retrograde labelling of small cells with biotinylated dextrans (Amagai et al., 1998; Friedman and Hopkins, 1998), although Mugnaini and Maler (1987a) found dendritic arborizations on ELA large cells using Golgi staining. In any case, the terminals from NELL axons all appear to be directly onto the large cell and small cell somata, making it possible to identify completely each postsynaptic cell contacted by an intracellularly labelled NELL axon. Reconstructions show that NELL axons terminate on 1–2 large cells, then wind extensively and terminate on small cells throughout the ELA (Fig. 2A) (Friedman and Hopkins, 1998).

ELA large cells project entirely within the ELA (Fig. 2B), terminating with large calyceal terminals that envelop their postsynaptic small cells. The large cells are probably inhibitory because they are immunopositive for glutamic acid decarboxylase, the enzyme that makes the neurotransmitter γ -aminobutyric acid (GABA) (Mugnaini and Maler, 1987a). The large cell axons project fairly directly across the nucleus, ending on more restricted bands or patches of small cells (Friedman and Hopkins, 1998).

Linear reconstructions (Fig. 2C) show that, when a NELL axon enters the ELA, it first contacts a large cell and then travels for approximately 1 mm, where it may contact a second large cell; it then travels for 3–4 mm with few terminals, before branching widely over a large number of small cells (Friedman and Hopkins, 1998). The distance between the first large cell terminal and the last small cell terminal may be as great as 7 mm, even though the ELA is only 1 mm in diameter. This difference in axonal delay translates into a NELL cell activating its first large cell 230–460 μs earlier than its last small cell, using a first estimate of conduction velocity of 15 m s^{-1} for the NELL axons (Enger et al., 1976). In contrast, the large cell axon runs only approximately 1 mm from soma to terminals (equivalent to 60 μs), so it relays signals quickly to its postsynaptic small cells. Thus, the small cell appears to receive an indirect, inhibitory input from a large cell, and a

direct, but delayed, excitatory input from a NELL cell. Also, the delays to different small cells may vary because NELL cells show a range of axonal lengths.

Like knollenorgan electroreceptors, both NELL axons and ELA large cells respond to electrosensory stimuli with a tightly phase-locked spike (Amagai et al., 1998; Friedman and Hopkins, 1998). NELL axons and ELA large cells are not segregated according to their receptive field locations because a single recording electrode advanced through the ELA runs across cells at different depths that respond to either one edge of the stimulus or the other (Amagai et al., 1998).

Mugnaini and Maler (1987a) first suggested that inhibition could be used in a temporal blanking model. Refining this model to include subsequent discoveries about physiological responses and axonal arborizations, we show how the anatomical specializations within the ELA could be responsible for fine temporal analysis (Friedman and Hopkins, 1998). In this model, a small cell receives one input from a large cell with its receptive field on one side of the body (Fig. 3A). It also receives a second input from a NELL cell with a receptive field on the opposite side of the body, but with some delay between the large cell and NELL inputs. For a sufficiently long negative-going pulse, the excitatory NELL input will arrive first, and the small cell will respond. However, if the pulse is shorter than the axonal delay, then the inhibitory large cell input will arrive first, and the NELL input will be suppressed. In other words, a small cell responds if the pulse is longer than some threshold duration, set by the length of the NELL axonal delay. Fig. 3B illustrates the predicted response probability as a function of square pulse duration and polarity. For a positive-going pulse, the inhibitory large cell input would always arrive first, suppressing responses to the excitatory input for the duration of the inhibitory postsynaptic potential (IPSP), which is presumably long enough to block all behaviorally relevant stimuli. Thus, the ELA small cell should respond only to one polarity of the stimulus. If different NELL axons have different axonal delays, then different small cells would be tuned to discriminate between stimuli of different duration. By combining the inputs of many small cells, each specialized for a different delay and for different patches of the body surface and polarities of stimulation, there should be sufficient information to make waveform duration discriminations.

This 'delay line-blanking' model is supported by some preliminary data. Recordings from the ELA, putatively from small cells, have as predicted two different kinds of synaptic activity, which can be tied to different edges of the stimulus and with different latencies (Friedman and Hopkins, 1998). These synaptic potentials are consistent with direct inhibitory input from large cells and delayed excitation from NELL axons. However, data are available from only a few small cells because their small size and adendritic somata limit successful penetrations.

Further processing of temporal information

ELA small cells project exclusively to the neighboring

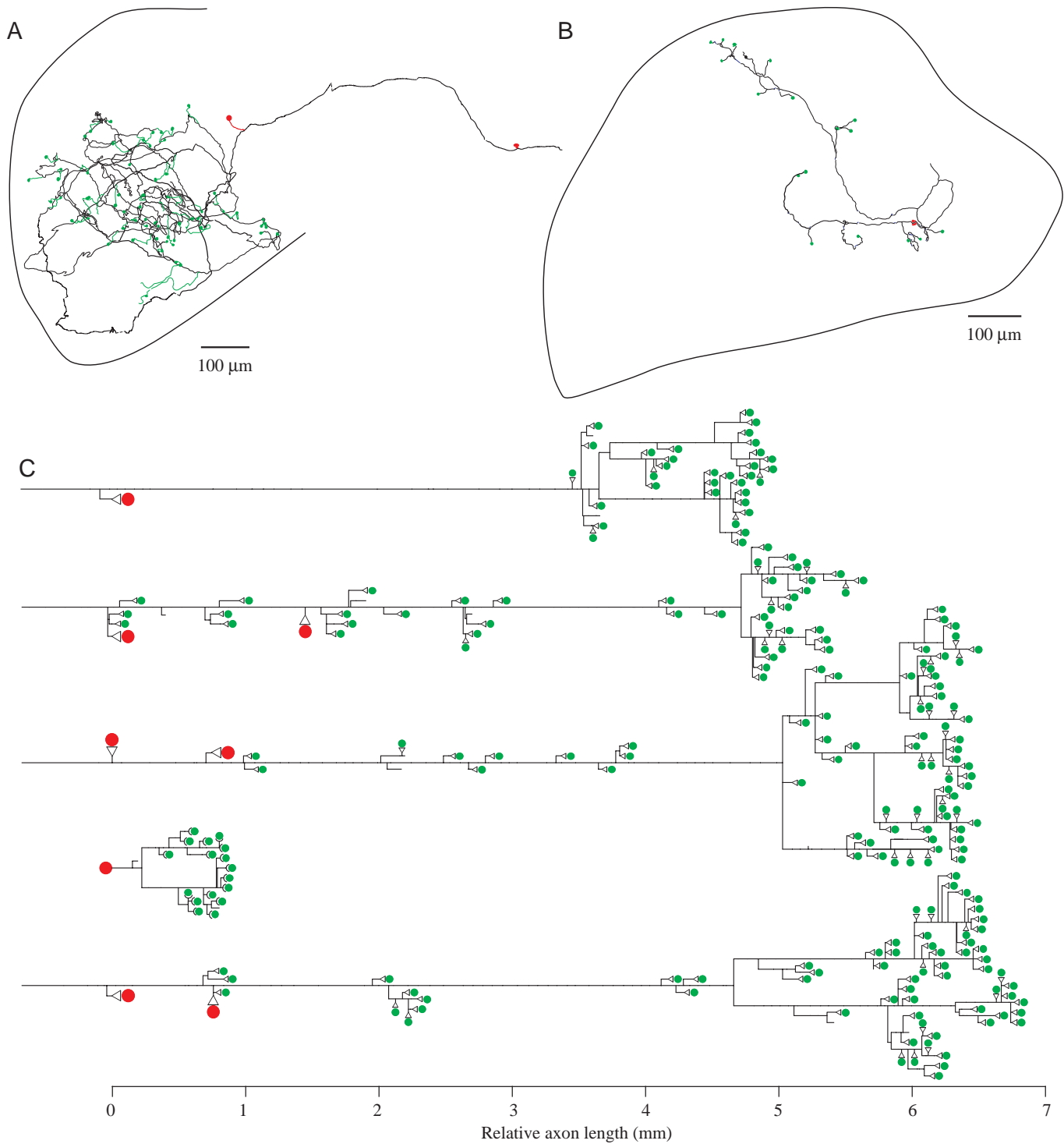


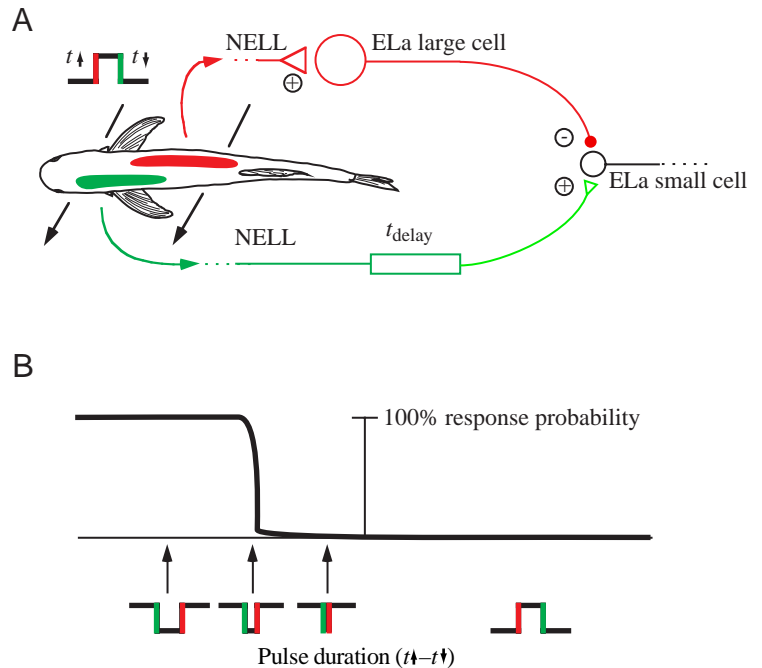
Fig. 2. Anatomy of cell types in the nucleus extero-lateralis pars anterior (ELA). (A) Reconstruction of a nucleus of the electrosensory lateral line lobe (NELL) cell axonal arborization within the ELA. Lateral is left, anterior is up. The cell was filled with biocytin, and the reconstruction is made from 15 sections of 50 μm thickness. Terminals onto small cells are green, and terminals onto large cells are red. The thickness of the axon denotes its dorsal-to-ventral extent. The outline of the nucleus is taken from the largest section encompassing the entire reconstruction. (B) Reconstruction of an ELA large cell, from seven sections of 50 μm thickness. The soma is red, and the terminals onto small cells are green. (C) Linear reconstructions of four NELL axonal arborizations and one ELA large cell. Modified from Friedman and Hopkins (1998).

midbrain nucleus extero-lateralis pars posterior (ELp) (Haugedé-Carré, 1979). The small cell axons within the ELp are thin, making small *en passant* boutons along their length.

They project straight across the nucleus, preserving their topographical organization (Friedman and Hopkins, 1998).

The ELp has two cell types, identified from extracellular

Fig. 3. Small cell model. (A) Small cell inputs. Knollenorgans in one patch of the body surface (red) respond to the upward edge of a square pulse, and contribute signals to a nucleus of the electrosensory lateral line lobe (NELL) axon that terminates on a nucleus exterolateralis pars anterior (ELA) large cell, which in turn makes an inhibitory contact onto a small cell. On the opposite side of the body (green patch), the knollenorgans respond to the downward edge of the stimulus and contribute signals to a NELL axon (green) that terminates directly on the small cell, but with a relative delay t_{delay} . This is only one example of possible receptive field organization. (B) Proposed small cell responses. The abscissa represents the duration and polarity of a square pulse stimulus, and the ordinate is the response probability. For stimuli of one polarity, small cells respond to stimuli longer than some threshold duration. The threshold depends on the delay line, which is different for different cells. Modified from Friedman and Hopkins (1998).



recordings (Amagai, 1998). Type I cells respond at a shorter latency (7–9 ms), with lower jitter and with higher response probability, whereas type II cells respond at longer latency (12–20 ms), with higher jitter and with lower response probability (Amagai, 1998). Most interestingly, type I cells respond to square pulses, provided that the pulse is longer than some threshold duration ('long pass'; Fig. 4A). The thresholds of type I cells range from 0.02 to 0.2 ms. This response profile is similar to that predicted for the ELA small cells, supporting the delay line-blanking model described above. Type II cells respond to square pulses, provided that the pulse duration is within a restricted range of durations ('band-pass'; Fig. 4B). The best response varied between 0.1 and 10 ms for different cells. The responses of type II cells could therefore be used by the fish to make decisions about the duration of a signaller's EOD. Important physiological issues left to resolve are the complex effects of stimulus amplitude and geometry on these responses (Amagai, 1998) and the mechanism that could underlie discrimination of pulse durations as long as 10 ms, since one based on axonal delay lines seems unlikely.

Of these two physiological types, only the anatomy of type I cells has been reconstructed, as shown in Fig. 4C (M. A. Friedman and C. D. Hopkins, unpublished results). They have large (150 μm), spiny dendritic arborizations that stretch perpendicular to the thin, incoming small cell axons. This morphology contrasts strongly with the anatomical specializations described in the previous section for NELL and ELA cells. This change in cellular structure is correlated with the increase in response jitter in the ELp, suggesting that the anatomical specializations evident in the NELL and the ELA allow fine temporal discrimination to be made in the ELA, after which spike times need not be so precise. The dendritic arborizations in the ELp are more likely to function to integrate

the outputs from the ELA in a manner less dependent on precise spike times, although more detailed physiological studies are necessary.

Individual type I cells project widely throughout the midbrain, with terminals in several areas: in two clusters in the ELp, one near the soma and one several hundred micrometers distant, in the medial ventral nucleus (MV), in the ipsilateral and contralateral isthmic granule nucleus (IG) and in the subpræeminential nucleus (SPE) (Fig. 4C). The terminals within the ELp imply the presence of complex local circuitry and, indeed, intracellular recordings show several phases of excitation and inhibition (M. A. Friedman and C. D. Hopkins, unpublished results). The areas outside the ELp are unexplored physiologically, so the role of the wide terminal field of individual ELp cells is not known, but it implies that the information that the type I cell carries is significant. Anatomical studies have shown that the IG projects to the valvula cerebelli (Finger et al., 1981) and that the MV projects to the optic tectum (OT; Wulliman and Northcutt, 1990). The OT (the homolog of the superior colliculus) plays a role in spatial analysis of signals from many sensory modalities in vertebrates (Bastian, 1982; Knudsen, 1982; Bartels et al., 1990; Stein and Meredith, 1993), suggesting that the MV may be involved in spatial analysis of knollenorgan information.

Comparative considerations

When we compare the known connections of the knollenorgan pathway with other octavolateral pathways, such as the ampullary/mormyromast system and the auditory system, several parallels become evident (Fig. 5). In all three systems, there is a direct pathway from the receptor, through the hindbrain, to a distinct toral nucleus and finally to the optic

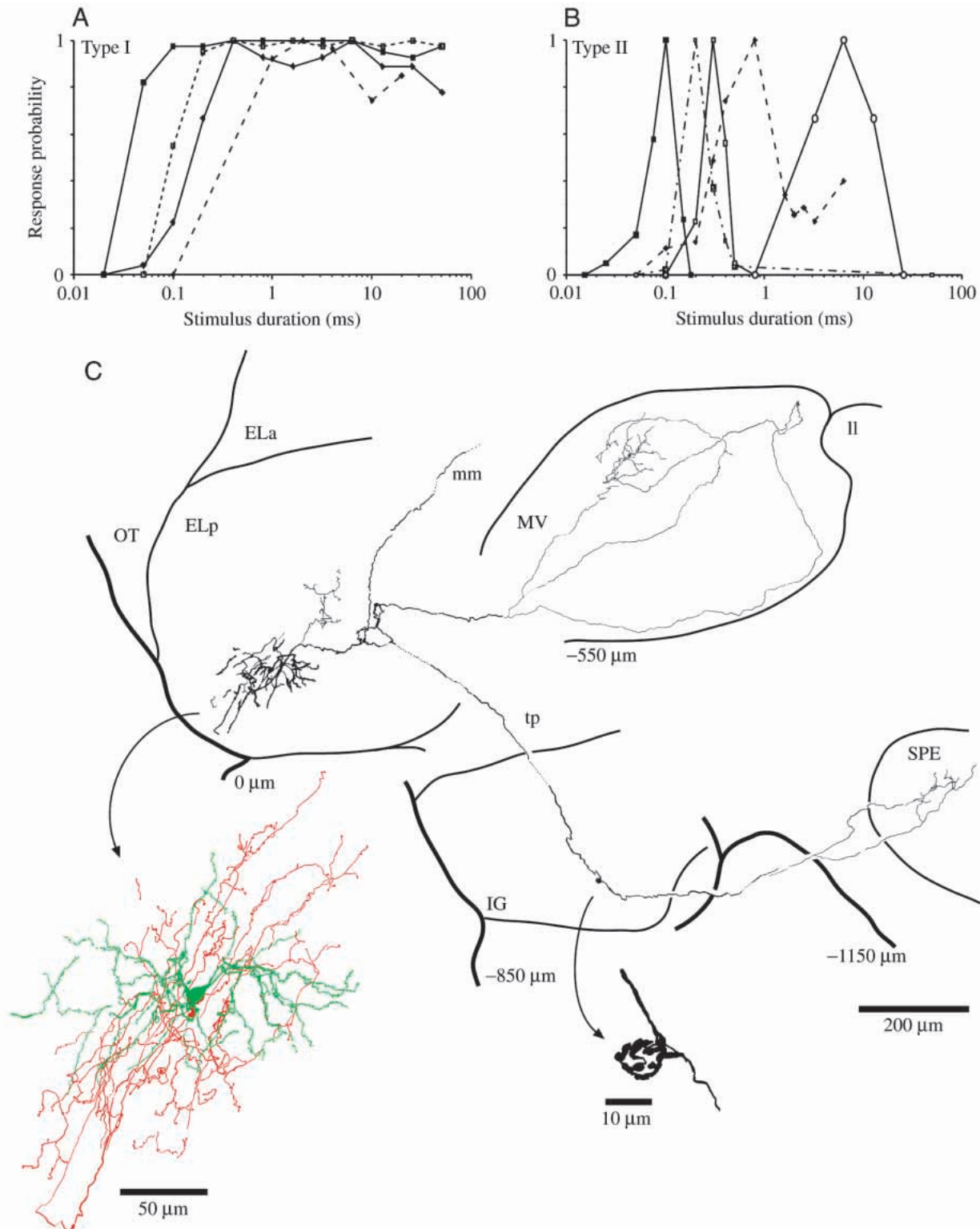


Fig. 4. Physiology and anatomy of the nucleus extero-lateralis pars posterior (ELp). (A) Normalized responses of type I cells, showing 'long-pass' tuning. (B) Normalized responses of type II cells, showing 'band-pass' tuning. (C) Anatomical reconstruction of a type I cell and terminals in other midbrain nuclei (outlined in bold). The cell was processed for biocytin staining and reconstructed from 26 sections of 50 μm thickness. Numbers next to bold outlines of other brain nuclei indicate their depths relative to the ELp soma. Terminals are found in the subpræeminential nucleus (SPE), the ipsi- and contralateral isthmic granule nucleus (IG) (enlarged in the lower right inset), the nucleus medialis ventralis (MV) and the ELp, both close to the soma (enlarged in the lower left inset, in red) and in a distinct cluster 400 μm ventral to the soma. The cells have widely branching dendritic arborizations (lower left inset, in green). ELa, nucleus extero-lateralis pars anterior; ll, lateral lemniscus; mm, mesomesencephalic tract; OT, optic tectum; tp, toropræeminential tract. A and B are modified from Amagai (1998).

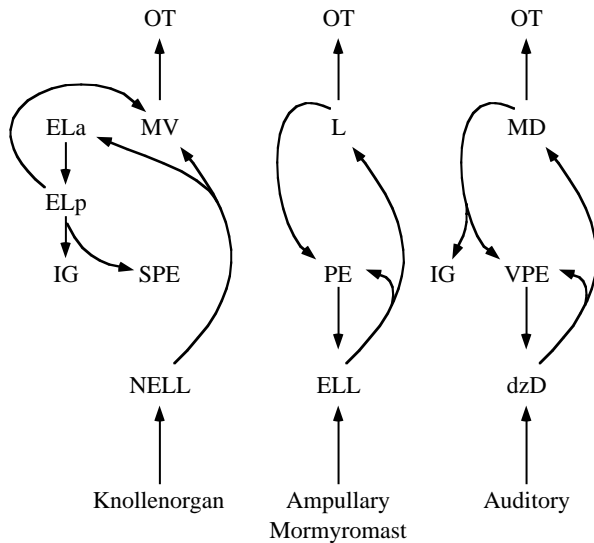


Fig. 5. Parallels in octavolateral pathways in mormyrid electric fish. Outlined are the major connections of the knollenorgan (this review), ampullary/mormyromast (simplified from Bell and Szabo, 1986) and auditory (simplified from Bell, 1981a,b; Kozloski and Crawford, 1998) pathways. dzD, dorsomedial zone of the descending nucleus; ELa, nucleus extero-lateralis pars anterior; ELL, electrosensory lateral line lobe; ELp, nucleus extero-lateralis pars posterior; IG, isthmus granule nucleus; L, nucleus lateralis; MD, nucleus medialis dorsalis; MV, nucleus medialis ventralis; NELL, nucleus of the ELL; OT, optic tectum; PE, prae-miniential nucleus; SPE, subprae-miniential nucleus; VPE, ventral prae-miniential nucleus.

tectum. The toral nucleus may also feed back to a part of the prae-miniential nucleus, which may itself feed back to the hindbrain. These parallels reinforce the hypothesis that electrosensory pathways evolved by duplication of auditory/mechanosensory pathways. The MV in the knollenorgan pathway occupies a position analogous to that of the toral nucleus lateralis (L) in the ampullary/mormyromast system and medialis dorsalis (MD) in the auditory/mechanosensory system, but the knollenorgan system uniquely adds a further two toral nuclei, the ELa and the ELp. Interestingly, the sister species to the mormyrids, *Gymnarchus niloticus*, lacks both knollenorgans and a recognizable nucleus extero-lateralis (Bass and Hopkins, 1982). The ELa and ELp are presumably necessitated by the special temporal analysis proposed to be carried out in the knollenorgan pathway.

It is also instructive to compare the knollenorgan pathway with pathways in other species that analyze fine temporal information. In the avian auditory brainstem, time differences between the two ears are compared to determine the azimuthal location of a sound. Time comparison is performed by a delay-line-coincidence detector, where signals from the left and right nucleus magnocellularis project in opposite directions across the nucleus laminaris (Young and Rubel, 1983; Carr and Konishi, 1990). The magnocellular projections are highly ordered compared with the axonal arborizations of the NELL cells. This difference presumably reflects the more complicated

computational task that the ELa is performing. In the avian brainstem, it is two ears being compared, whereas in the ELa, all parts of the body surface are being compared. In this sense, the phase-coding pathways of South American electric fish are more similar to those of the mormyrid. In *Eigenmannia*, the spherical cell afferent from the ELL ends on a giant cell and nearby small cells in layer VI of the torus semicircularis (Carr et al., 1986; Heiligenberg, 1991). In this case, the giant cell distributes the signal widely throughout layer VI, analogously to the NELL axon in mormyrids. The major departure of the mormyrid system is that it appears to use an inhibitory mechanism in measuring time differences, whereas the barn owl and *Eigenmannia* use only excitatory synapses.

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