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REVIEW

Multiplexed temporal coding of electric communication signals in mormyrid fishes

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Summary

The coding of stimulus information into patterns of spike times occurs widely in sensory systems. Determining how temporally coded information is decoded by central neurons is essential to understanding how brains process sensory stimuli. Mormyrid weakly electric fishes are experts at time coding, making them an exemplary organism for addressing this question. Mormyrids generate brief, stereotyped electric pulses. Pulse waveform carries information about sender identity, and it is encoded into submillisecond-to-millisecond differences in spike timing between receptors. Mormyrids vary the time between pulses to communicate behavioral state, and these intervals are encoded into the sequence of interspike intervals within receptors. Thus, the responses of peripheral electroreceptors establish a temporally multiplexed code for communication signals, one consisting of spike timing differences between receptors and a second consisting of interspike intervals within receptors. These signals are processed in a dedicated sensory pathway, and recent studies have shed light on the mechanisms by which central circuits can extract behaviorally relevant information from multiplexed temporal codes. Evolutionary change in the anatomy of this pathway is related to differences in electrosensory perception, which appears to have influenced the diversification of electric signals and species. However, it remains unknown how this evolutionary change relates to differences in sensory coding schemes, neuronal circuitry and central sensory processing. The mormyrid electric communication pathway is a powerful model for integrating mechanistic studies of temporal coding with evolutionary studies of correlated differences in brain and behavior to investigate neural mechanisms for processing temporal codes.

Key words: sub-millisecond timing differences, duration tuning, interval tuning, coincidence detection, anti-coincidence detection, delay line, temporal filter, weakly electric fish, electric organ discharge.

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Introduction

Neurons transmit information with trains of action potentials, or spikes. The relationship between spikes and the information they represent is referred to as a neural code (Perkel and Bullock, 1968). Information can be encoded in the spike trains of single neurons or in the activity of a population of neurons. Scientists trying to understand a neural code are faced with two challenges: first, how is stimulus information encoded by the circuit; and second, how is this information decoded by postsynaptic neurons? The study of sensory systems in a wide range of animal models has revealed a variety of neural codes (Churchland and Sejnowski, 1992; Rieke et al., 1997), including rate codes, place codes, population codes and sparse codes. Here we focus on temporal codes, in which the precise timing of action potentials carries information (Lestienne, 2001; Theunissen and Miller, 1995). Temporal codes have been implicated in the processing of somatosensory (Jones et al., 2004), olfactory (Laurent, 1997), gustatory (Di Lorenzo et al., 2009), visual (Victor and Purpura, 1996), auditory (deCharms and Merzenich, 1996), vestibular (Sadeghi et al., 2007), mechanosensory lateral line (Goulet et al., 2012) and electrosensory stimuli (Carlson, 2008b).

A sensory system can employ multiple types of codes (Ainsworth et al., 2012). For instance, the barn owl auditory system computes two sound localization cues, using a rate code for interaural level differences and a temporal code for interaural timing differences (Konishi, 1993). In addition, central circuits often convert information from one type of code to another (Groh, 2001). For example, the temporal code of the barn owl is converted into a place code within the hindbrain (Carr and Konishi, 1990). Finally, information about multiple stimulus features can be transmitted simultaneously through a single pathway by encoding information about each feature at different time scales of neural activity. Such a coding scheme is called temporal multiplexing and is found in visual, olfactory, auditory, electrosensory and hippocampal pathways (Friedrich et al., 2004; Middleton et al., 2011; Panzeri et al., 2010). Temporal multiplexing is an efficient way for neural circuits to increase information transmission without requiring additional neurons.

The rich sensory coding literature provides numerous examples of temporal coding. However, with notable exceptions (i.e. coding for interaural timing differences in birds, reptiles and mammals), we still know relatively little about the circuitry and synaptic mechanisms by which temporal codes are decoded by central neurons. Mormyrid weakly electric fishes represent an ideal system for addressing this problem because: (1) they employ two different temporal codes in a single circuit (temporal multiplexing); (2) the circuit is accessible for *in vivo* and *in vitro* electrophysiology and imaging; (3) spike timing can be easily manipulated in behaviorally relevant ways both *in vivo* and *in vitro*; (4) the behavioral significance of the multiplexed temporal codes is clear; and (5) evolutionary change in this circuit allows for a comparative approach

that links changes in neural circuitry to differences in behavior. From the perspective of the central nervous system, there is no difference between the electrosense and other modalities – all stimuli are represented as patterns of spiking. Therefore, the mechanisms by which mormyrids process temporally coded information are relevant to understanding basic principles for how any neural circuit can solve this problem.

Electric signals in mormyrid fishes communicate sender identity and behavioral state

Two components of electrocommunication: EOD and IPI

Mormyrids produce an electric organ discharge (EOD) to communicate and actively sense their environment (Hopkins, 1986). These fish have three types of electroreceptors in their skin: mormyromasts are used for active sensing, ampullary receptors for passive sensing and knollenorgans for communication (Bell, 1989; Bennett, 1965; Szabo and Fessard, 1974; Zakon, 1986). Communication in mormyrids consists of the discrete EOD produced with variable interpulse intervals (IPIs; Fig. 1). The EOD waveform is species-specific, and in some species it provides additional identifying information such as sex, maturity and dominance status (reviewed in Carlson, 2002a). EOD waveforms can vary in polarity, number of phases, duration of each phase, inflection, rise/fall times and total duration (Hopkins, 1980; Hopkins, 1981). The number of phases varies from one to four, and the duration ranges from <200 μs in some species to >30 ms in others (Arnegard et al., 2010; Carlson et al., 2011; Sullivan et al., 2000).

Signaling fish vary IPIs to communicate their behavioral state, such as dominance, submission, aggression and courtship. IPIs can range from just under 10 ms to several seconds (Carlson, 2002a; Hopkins, 1986). Several temporal patterns of IPI sequences have been identified: irregular random patterns, regularized patterns, pauses in signaling called cessations, and bursts of short-interval pulses (reviewed in Carlson, 2002a). At least three categorically distinct burst signals, called scallops, accelerations and rasps, have been demonstrated in *Brienomyrus brachyistius*, with each signal hypothesized to play different behavioral roles (Carlson and Hopkins, 2004b). An additional signal in *B. brachyistius*, called a creak, has also been reported (Wong and Hopkins, 2007). Like rasps, creaks appear to function as a male courtship signal. Electrical duetting, in which males and female alternately generate rasps and bursts, respectively, has also been described in *B. brachyistius* (Wong and Hopkins, 2007).

Additional IPI patterns include preferred latency or echo responses, in which a fish emits its own EOD at a defined interval after the EOD of another fish, and preferred latency avoidance, in which fish avoid a specific range of latencies (Arnegard and Carlson, 2005; Bauer and Kramer, 1974; Bell et al., 1974; Heiligenberg, 1976; Kramer, 1974; Kramer, 1978; Lucker and Kramer, 1981; Russell et al., 1974). The social significance of these signals is not known, though hypotheses include jamming avoidance, active jamming, dominance/submission and sexual recognition. Other IPI patterns may serve functions such as schooling, group cohesion and adult–young interactions (Arnegard and Carlson, 2005; Hopkins, 1977; Moller, 1976; Westby and Kirschbaum, 1978).

Electric signal generation

The EOD is produced by an electric organ located at the base of the tail (reviewed in Bass, 1986a; Bennett, 1971; Caputi et al., 2005). Individual cells, called electrocytes, act as batteries in series such that when they are activated synchronously their action potentials summate to produce the EOD. The morphology and physiology of the electrocytes determine EOD waveform (reviewed in Hopkins, 1999), and steroid hormones act directly on the electrocytes to establish EOD sex differences (Bass, 1986b; Bass and Volman, 1987; Freedman et al., 1989).

EOD production is controlled by a central electromotor command network (Fig. 2) composed of the command nucleus (CN), the medullary relay nucleus (MRN) and the bulbar command-associated nucleus (BCA) (Bell et al., 1983; Grant et al., 1986). The MRN projects to the electromotor neurons (EMNs) in the spinal cord, which innervate the electrocytes of the electric organ (Bennett et al., 1967; Grant et al., 1986). The EMNs, as well as neurons in the CN and MRN, are extensively connected by gap junctions both within and between nuclei to promote synchronous activation of electrocytes (Bennett et al., 1967; Bennett et al., 1963; Elekes et al., 1985; Elekes and Szabo, 1985; Grant et al., 1986). EOD production is primarily influenced by excitatory inputs to the CN from the midbrain precommand nucleus (PCN) and the dorsal posterior thalamic nucleus (DP) (Bell et al., 1983; Carlson, 2002b; Carlson, 2003; Carlson and Hopkins, 2004a; von der Emde et al., 2000).

The electromotor command network also gives rise to a corollary discharge pathway that provides motor-related inputs to electrosensory pathways. This corollary discharge is initiated in the BCA, which projects to the paratrigeminal command-associated nucleus and the mesencephalic command-associated nucleus (MCA) (Bell et al., 1983; Carlson, 2002b). The MCA in turn projects to the sublemniscal nucleus (slem), which delivers inhibition onto neurons in the electrosensory hindbrain that blocks responses to the fish's own EOD (Bell and Grant, 1989). The DP and PCN also receive corollary discharge-mediated inhibition from the dorsal portion of the ventroposterior nucleus (VP) of the torus semicircularis, which receives input from the MCA (Carlson, 2002b; Carlson, 2003; Carlson and Hopkins, 2004a; von der Emde et al., 2000). This recurrent inhibition appears to regulate EOD output (Carlson and Hopkins, 2004a).

Playback experiments reveal the behavioral significance of EOD waveform and IPI patterns

Electric signals are easy to record, manipulate and play back, allowing investigators to present modified versions of natural signals to identify the specific signal components relevant to any given behavior. Such studies reveal that mormyrids vary in their ability to discriminate temporal variation in EOD waveform (Carlson et al., 2011). There are two subfamilies of mormyrids, the Mormyrinae and Petrocephalinae (Fig. 3) (Sullivan et al., 2000). A specific lineage of mormyrines called 'clade A' can detect small phase shifts in the EOD waveform, as small as 2 μs in *Pollimyrus adspersus* (Paintner and Kramer, 2003). By contrast, most non-clade-A species are unable to detect even maximal phase shifts in the EOD waveform, and this perceptual difference is related to key anatomical differences in their peripheral and central electrosensory systems (Carlson et al., 2011).

The functional significance of EOD waveform variation for electric communication has been addressed in several behavior studies on clade A species, which suggest a key role for the EOD in species recognition and mate choice (Arnegard et al., 2006; Feulner et al., 2009; Hopkins and Bass, 1981; Machnik and Kramer, 2008; Markowski et al., 2008). In species with sex differences in EODs, the male EOD is always longer than the female EOD (Carlson and Arnegard, 2011; Hopkins, 1986). In *Marcusenius macrolepidotus*, EOD duration correlates with male body length, and longer EODs elicit more male aggression than shorter EODs, suggesting that the EOD in this species may be an honest indicator

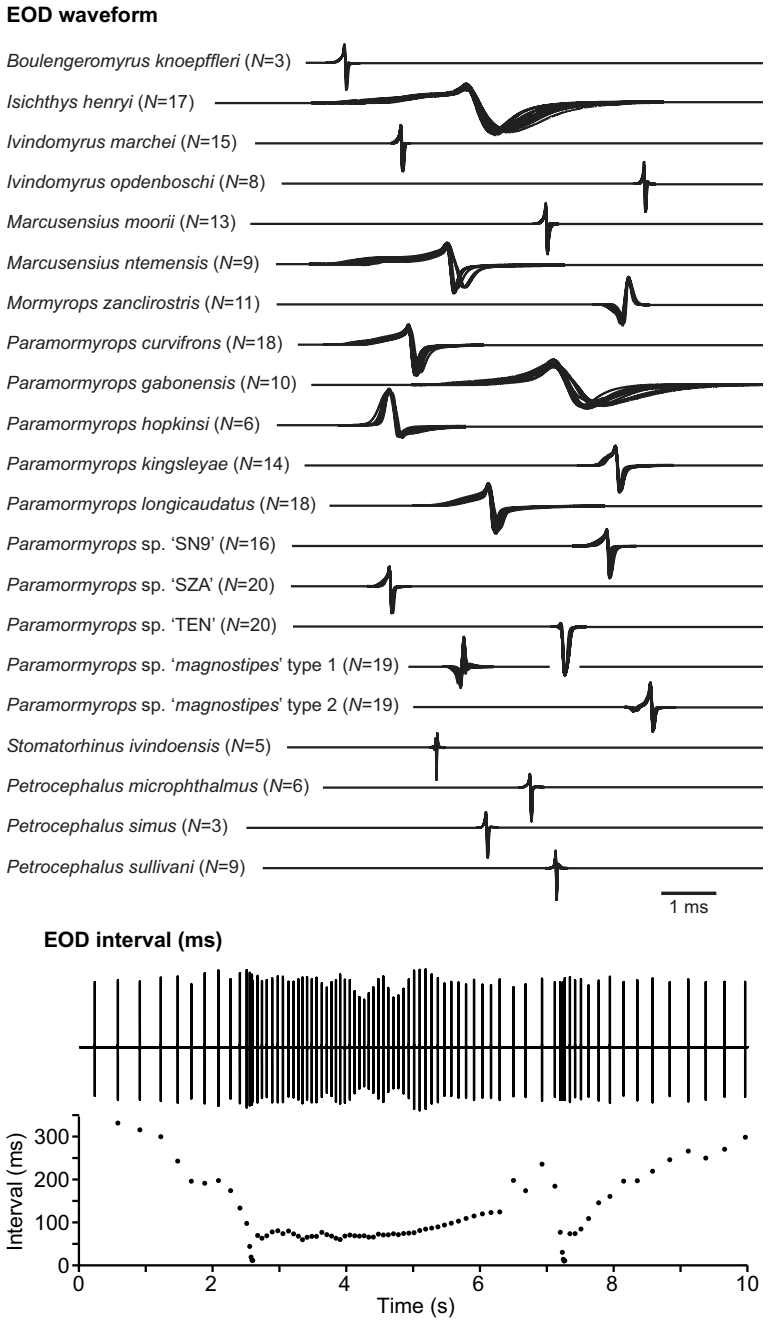

Fig. 1. Mormyrid electrocommunication consists of a fixed electric organ discharge (EOD) produced at variable interpulse intervals (IPIs). Top: EOD waveforms recorded from the 21 known species within the Ivindo River of Gabon reveal that the waveforms are species-specific and span a wide range of durations (modified from Carlson et al., 2011). In each case, EOD waveforms from different individuals of the same species are normalized to the same peak-to-peak height, superimposed and aligned to the head-positive peak (except for *Paramormyrops* sp. 'TEN', for which waveforms are aligned to the head-negative peak). Bottom: 10 s of a raw electrical recording from an isolated *Brienomyrus brachyistius*. The spike-like nature of the EODs is evident, and the amplitude changes throughout the recording as a result of the fish moving with respect to the recording electrode. Below, the raw recording has been converted into a plot that illustrates the sequence of IPIs over time.

of size (Hanika and Kramer, 2005). *Pollimyrus isidori* and *Gnathonemus petersii* can be trained to distinguish individual differences in EOD waveform (Graff and Kramer, 1992), and *M. macrolepidotus* appear to recognize familiar individuals on this basis (Hanika and Kramer, 2005).

Playback experiments have also revealed the critical role of IPIs in social behavior. *Gnathonemus petersii* display more aggression towards a playback electrode delivering IPI patterns recorded from attacking fish than from resting fish (Kramer, 1979). In addition, *G. petersii* approach a playback electrode more often when a natural sequence of IPIs is presented than when a randomized sequence of the same IPIs is presented (Teyssedre and Serrier, 1986). Therefore, the precise serial ordering of IPIs, and not just overall IPI distribution, appears to carry important information. Species differences in IPI patterns may even mediate species recognition in some cases (Kramer and Kuhn, 1994). IPIs may be particularly important for species recognition in non-clade-A species that cannot detect EOD waveform variation (Carlson and Arnegard, 2011).

Peripheral coding of communication signals: two temporal codes, one circuit

Electrocommunication signals are detected by peripheral sensory receptors called knollenorgans (KOs) (Derbin and Szabo, 1968; Franz, 1921). The locations of KOs on the body surface are remarkably diverse (Fig. 3). In clade A species, KOs are widely distributed across the head, back and underbelly of the fish (Carlson et al., 2011; Harder, 1968). In one clade A genus, *Mormyrus*, KOs are also found on the side of the body (Harder, 1968). In most petrocephaline species, however, KOs are clustered into distinct rosettes, with one rosette near the eye, one near the gill and one

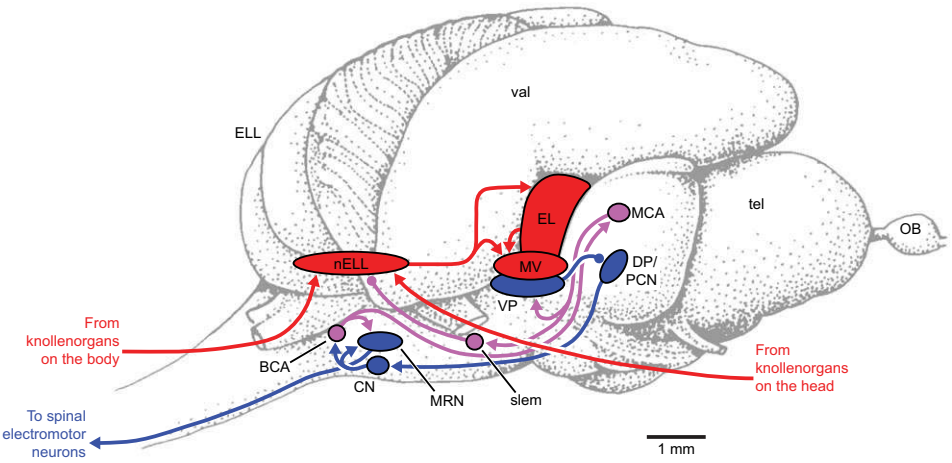

Fig. 2. Neuroanatomy of the knollenorgan electrosensory (red), electromotor (blue) and corollary discharge (purple) pathways. Excitatory connections are indicated by arrows and inhibitory connections by punctate terminals. Knollenorgan electroreceptors project somatotopically to the hindbrain nucleus of the electrosensory lateral line lobe (nELL), which projects to two nuclei of the torus semicircularis: the exterolateral nucleus (EL) and the medioventral nucleus (MV). Each EOD command originates in the command nucleus (CN). The CN projects to the medullary relay nucleus (MRN), which in turn innervates the electromotor neurons in the spinal cord that innervate the electric organ. CN output is influenced by excitation from the precommand nucleus (PCN) and the dorsal posterior thalamic nucleus (DP), both of which receive inhibition from the ventroposterior nucleus (VP). When the CN initiates an EOD, it sends a copy of this signal to the bulbar command-associated nucleus (BCA), which projects to the MRN and to the mesencephalic command-associated nucleus (MCA), which mediates inhibition of the motor pathway through the VP, and inhibition of the KO sensory pathway through the sublemniscal nucleus (slem). ELL, electrosensory lateral line lobe; OB, olfactory bulb; tel, telencephalon; val, valvula of the cerebellum.

near the base of the pectoral fin (Carlson et al., 2011; Harder, 1968; Lavoué et al., 2004; Lavoué et al., 2010). Two petrocephaline species are exceptional in having a broad distribution of KOs similar to that of clade A species (Carlson et al., 2011; Lavoué et al., 2010). Finally, the only non-clade-A mormyrine genus, *Myomyrus*, is unique in having an intermediate pattern, with a single rosette near the back of the head and a relatively sparse distribution of receptors across the head, back and underbelly (Carlson et al., 2011).

Each KO consists of a canal in the epidermis that opens into a chamber lined with flattened epithelial cells (Derbin and Szabo, 1968). The canal is filled with a plug of loose epithelial cells, which adds a series capacitance to the organ (Zakon, 1986). This capacitance, along with the parallel resistive properties of the surrounding skin, makes the organ AC-coupled, establishing tuning to the high frequencies that characterize the power spectra of EODs (Bennett, 1965; Lyons-Warren et al., 2012a). Inside the chamber

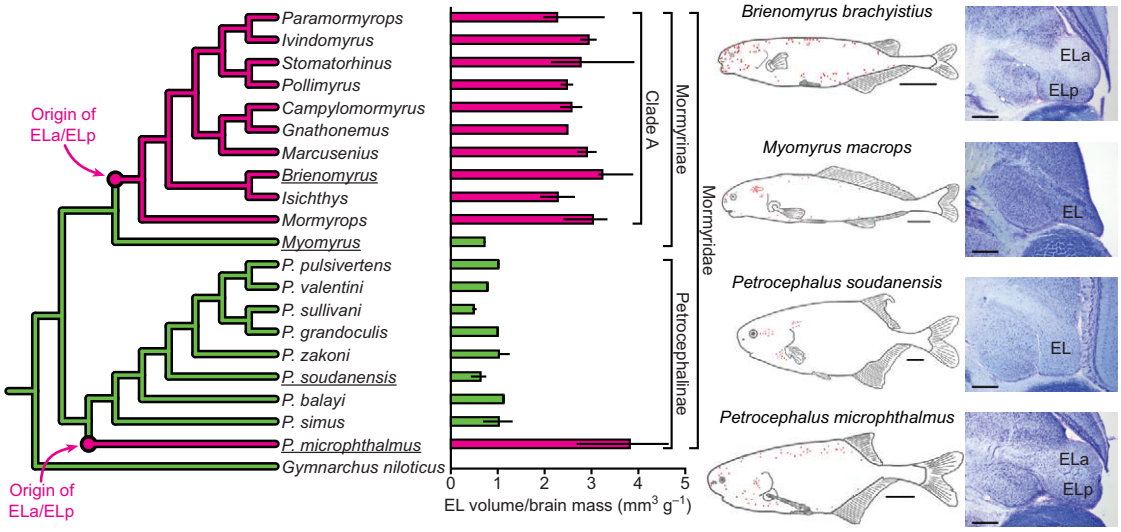

Fig. 3. Evolutionary change in the knollenorgan electrosensory system (modified from Carlson et al., 2011). The cladogram on the left illustrates the transition from a relatively small exterolateral nucleus (EL, green) to an enlarged EL with separate anterior and posterior subdivisions (ELa/ELp, magenta). Normalized EL sizes of each branch are shown to the right (median ± range). A parsimonious reconstruction suggests that ELa/ELp evolved twice, once in the lineage leading to clade A within the subfamily Mormyrinae and once in the lineage leading to *Petrocephalus microphthalmus* within the subfamily Petrocephalinae. The locations of knollenorgans on the body surface (red dots) and 50 µm horizontal sections of the midbrain highlighting the EL and ELa/ELp from four different species are shown at the far right (these species are underlined in the cladogram). Scale bars are 1 mm for the fish outlines, and 300 µm for the brain sections.

are one to 10 sensory cells (up to 40 in petrocephaline rosettes) (Derbin and Szabo, 1968; Harder, 1968; Szabo, 1965). A single myelinated afferent fiber branches to innervate all sensory cells within a KO (Derbin and Szabo, 1968; Jørgensen, 2005).

Our understanding of KO stimulus encoding is limited to studies of broadly distributed KOs in clade A species, which generate spike-like potentials in response to electrosensory stimuli (Bennett, 1965). The rosette-type KOs of petrocephalines do not appear to spike; instead, they continuously oscillate at up to 3 kHz (Harder, 1968). How rosette-type KOs encode electric signals remains unknown.

Clade A KOs are tuned to frequencies roughly matching the power spectrum of the species-specific EOD (Hopkins, 1981), and their sensitivity increases with increasing pulse duration (Lyons-Warren et al., 2012a). Variation in duration tuning among KOs may establish a population code for pulse duration at low intensities, when signaling fish are at a distance (Lyons-Warren et al., 2012a). At higher intensities, however, when signaling fish are close by and most of the receptors are responsive, a temporal code is used for encoding duration (Hopkins and Bass, 1981; Lyons-Warren et al., 2012a).

KOs spike with a latency of ~100 µs in response to positive changes in voltage across the skin, or inward current (Bennett, 1965). Because they are AC-coupled, KOs respond both to the onset of positive voltage steps and to the offset of negative voltage steps. As each KO faces ‘out’ towards the surrounding water, KOs on opposite sides of the body point in opposite directions. Thus, for any given electrical potential, KOs on one side of the body will receive an inward current whereas KOs on the other side of the body will receive an outward current, and this results in differences in spike timing between receptors on opposite sides of the body. For instance, in response to a positive voltage step applied to one side of the body, ipsilateral KOs will spike at the onset, whereas contralateral KOs will spike at the offset. These observations led Hopkins and Bass (Hopkins and Bass, 1981) to propose a start–stop temporal code for the EOD waveform, in which KOs on one side of the body respond to the start of a signal, KOs on the opposite side of the body respond to the end of the signal, and the difference in spike timing between them encodes signal duration. More complex, multiphasic signals, such as natural EODs, would result in different subsets of KOs responding to different stimulus edges, depending on stimulus intensity at the receptor pore (Fig. 4). Therefore, spike timing differences, in the submillisecond-to-millisecond range, between KOs represent the EOD waveform.

KO afferents follow stimulation rates up to 500 Hz, corresponding to interspike intervals of 2 ms (Bell and Grant, 1989). The shortest IPI observed in signaling fish is just below 10 ms (Carlson, 2002a; Hopkins, 1986), meaning KOs faithfully represent the timing of each EOD with a single, phase-locked spike. Therefore, interspike intervals, on the order of tens of milliseconds to seconds, within each KO represent the IPIs in electrocommunication signals.

The responses of peripheral receptors thus establish two distinct temporal codes for electrocommunication signals: differences in spike timing between KOs code for EOD waveform, and interspike intervals within KOs code for IPI (Fig. 4). Both of these temporal codes are similar to those used in other sensory systems. For example, sound localization, echolocation, localization of tactile stimuli, and visual motion detection rely on response timing differences between different sensory receptors, and timing sequences within a stimulus are used for the discrimination of tactile texture, and the pitch, timbre and rhythm of speech (Cariani, 2001). Whereas the importance of temporal coding in sensory systems is clear, our understanding of how these temporal codes are processed is still developing.

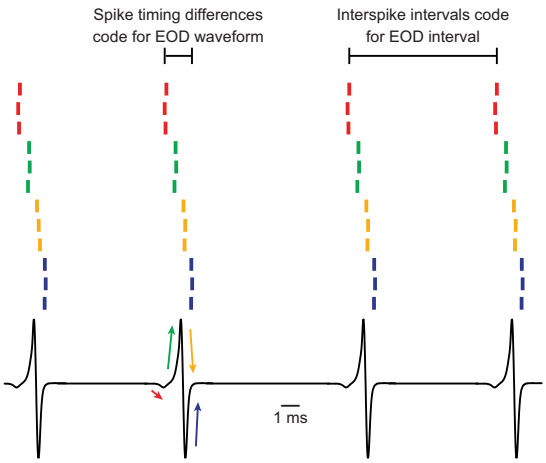

Fig. 4. Temporal multiplexing of electrocommunication signals by knollenorgans. This schematic representation shows a train of EOD stimuli at the bottom, with the responses of different knollenorgans to these stimuli above. Each row represents a different knollenorgan and each tick mark indicates the timing of an individual spike. The location of each knollenorgan on the body surface with respect to the electric field determines which edge of the EOD waveform it will respond to, and the spikes are color-coded for the edge (arrows) to which the knollenorgan is responding. Spike timing differences between different knollenorgans represent EOD waveform, whereas interspike intervals within each knollenorgan represent EOD intervals.

The use of different time scales and different temporal coding schemes to encode multiple features of communication signals by KOs is a textbook example of temporal multiplexing (Panzeri et al., 2010). Another example of multiplexing occurs in the zebrafish olfactory bulb, where mitral cells represent general odor category in the precise phase-locking of spikes to oscillatory field potentials, and specific odor identity in non-phase-locked spike rates (Friedrich et al., 2004). Analyzing mitral cell output with low temporal resolution provides information about precise odor identity, whereas analyzing with higher temporal resolution provides information about broad odor category. Temporal filtering of mitral cell output in the telencephalon therefore allows for the extraction of odor identity without distorting the code for odor category (Blumhagen et al., 2011). We will see that a similar computation is performed in the KO pathway.

A sensory pathway devoted to communication behavior

Electrocommunication signals are processed by a dedicated sensory pathway (Fig. 2). KO afferent fibers conduct at 40 m s^{-1} to the ipsilateral nucleus of the electrosensory lateral line lobe (nELL) in the hindbrain (Enger et al., 1976a), where corollary discharge inhibition blocks responses to the fish’s own EOD (Bell and Grant, 1989; Zipser and Bennett, 1976). That is, each time an EOD motor command is generated, nELL neurons receive inhibition that prevents them from responding to sensory input. In this manner, the KO pathway is dedicated to processing communication signals: responses to the fish’s own EOD never get past the hindbrain (Carlson, 2008a).

The axons of nELL neurons project bilaterally through the lateral lemniscus to the midbrain torus semicircularis (Fig. 2), homolog of the mammalian inferior colliculus (Nieuwenhuys et al., 1998). These axons conduct at 15 m s^{-1} (Amagai et al., 1998; Enger et al., 1976a; Enger et al., 1976b). The main projection from nELL is to the

exterolateral nucleus (EL), although en route the ascending axons give off small branches that terminate in the medioventral nucleus (MV) (Amagai et al., 1998; Enger et al., 1976a; Enger et al., 1976b; Friedman and Hopkins, 1998).

The structure of the mormyrid EL can take one of two forms (Fig. 3). In clade A, EL is subdivided into anterior (ELa) and posterior (ELp) regions (Xu-Friedman and Hopkins, 1999). In most petrocephalines and in the non-clade-A mormyrine genus *Myomyrus*, however, the EL is a relatively small, homogeneous structure lacking any apparent subdivisions (Carlson et al., 2011). A subdivided ELa/ELp has been found in one non-clade-A species, *Petrocephalus microphthalmus* (Carlson et al., 2011). Interestingly, this species also has broadly distributed KOs typical of clade A, and it is the only known petrocephaline with the ability to discriminate variation in EOD waveform.

Virtually nothing is currently known about the circuitry and physiology of EL, whereas we are starting to understand quite a bit about ELa/ELp (Fig. 5). The axons of nELL neurons terminate in ELa, which contains two cell types: large GABAergic inhibitory interneurons and small excitatory projection neurons (Friedman and Hopkins, 1998; George et al., 2011; Mugnaini and Maler, 1987a; Szabo et al., 1975). Local circuitry within the ELa performs the first stages of EOD waveform analysis (Lyons-Warren et al., 2012b; Xu-Friedman and Hopkins, 1999). The ELa sends its only outputs to the adjacent ELp, where the first stages of IPI analysis occur (Carlson, 2009). ELp projects to the isthmic granule nucleus (IG), which in turn projects back to the ELp and to the valvula cerebellum (Finger et al., 1981; Haugede-Carre, 1979). The role of the feedback projection from the IG to the ELp is not yet understood. The IG–valvula connection is thought to be the main pathway by which electrocommunication information reaches the cerebellum (Russell and Bell, 1978). Horseradish peroxidase injections into ELp also retrogradely labeled small perilemniscal neurons in the caudal midbrain and neurons in the rostral midbrain in an area ventral to the torus longitudinalis (Finger et al., 1981), although the functions of these putative inputs to ELp are not known.

ELp also projects bilaterally to the subpræeminential nucleus and ipsilaterally to the inferior olive and the MV (Haugede-Carre, 1979). The MV therefore receives a direct projection from the nELL, as well as an indirect projection *via* the EL (Fig. 2). The MV projects to the optic tectum (Wullimann and Northcutt, 1990), homolog of the mammalian superior colliculus (Nieuwenhuys et al., 1998). The function of the MV–optic tectum pathway is currently unknown; however, the optic tecta of many taxa contain spatial maps of multiple sensory modalities. Therefore, one hypothesis is that the MV plays a role in localizing signaling fish (Friedman and Hopkins, 1998). The MV may also provide a minor projection to the KO region of the valvula cerebellum (Finger et al., 1981). Responses to electrosensory stimuli can be recorded in the telencephalon (Prechtl et al., 1998), and at least some of these responses are likely to be mediated by the KO pathway. It remains unknown how electrosensory information from KOs may reach the telencephalon, although a projection from the valvula cerebellum has been described (Wullimann and Rooney, 1990). Clearly, much remains to be learned about the processing of electrocommunication signals after the ELp.

The KO pathway contains several anatomical specializations characteristic of time-coding circuits. First, the channel for processing communication signals is dedicated to this task and it remains segregated from other electrosensory pathways. Second, the timing of sensory events is encoded by precisely time-locked spikes in KO receptors, nELL axons and ELa large cells (Amagai et al., 1998; Bennett, 1965; Friedman and Hopkins, 1998). Third, both the nELL and the ELa contain large adendritic neurons (Amagai et al., 1998; Szabo and Ravaille, 1976). Larger neurons are required to maintain axons with large diameters, which conduct impulses with greater velocity than axons of smaller diameter (Waxman, 1980). The heavy myelination of nELL axons further aids in increasing conduction velocity. In addition, larger neurons have lower input resistance and greater ability to generate current, thereby resulting in neurons that are less susceptible to voltage fluctuations caused by stray currents (Carr and Friedman, 1999). However, larger neurons require a larger synaptic current, which is achieved by large synaptic terminals and gap junctions onto the large cells of both the nELL and the ELa (Bell and Russell, 1978; Mugnaini and Maler, 1987a; Mugnaini and Maler, 1987b; Szabo and Ravaille, 1976; Szabo et al., 1983). Larger synaptic endings also transmit with lower temporal jitter (Trussell, 2008), and electric coupling through gap junctions further helps preserve timing information by reducing transmission time. Another, although less well understood, specialization common to time-coding pathways is an abundance of calcium-binding proteins (Carr and Friedman, 1999). These proteins may decrease presynaptic levels of calcium soon after synaptic transmission to shorten postsynaptic potentials, or to prevent the buildup of harmful loads of calcium as a byproduct of large synaptic currents (Friedman and Kawasaki, 1997). The large cells of the nELL and the ELa are immunoreactive to the calcium-binding proteins calretinin and calbindin, with precise staining patterns varying across species (Friedman and Kawasaki, 1997). Additional

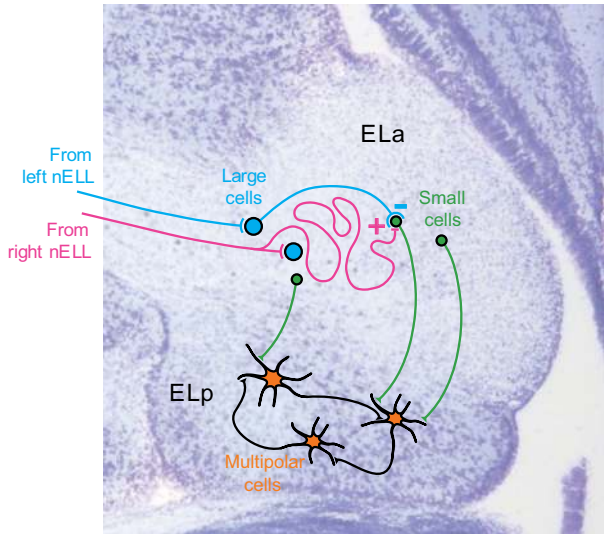

Fig. 5. ELa and ELp microcircuitry overlaid on a horizontal Nissl section through the midbrain of *Brienomyrus brachyistius* (schematic cells are not to scale). As nELL axons enter the ELa, they synapse directly onto adendritic large cells before following a convoluted path to synapse onto adendritic small cells. Large cells are entirely intrinsic to the ELa, providing inhibitory input onto small cells *via* a large calyx-like terminal. Small cells are hypothesized to act as time comparators that integrate inhibition from one side of the body with excitation from the opposite side of the body to recode the peripheral spike timing differences that code for EOD waveform. ELa small cells project to multipolar cells in the ELp. The microcircuitry within the ELp is less well understood, although there are extensive excitatory and inhibitory interactions among the multipolar cells. Temporal filtering of small cell outputs by the circuit in the ELp establishes tuning to the peripheral spike timing differences that code for IPIs.

specializations that contribute to timing preservation in auditory pathways include AMPA-receptor splice variants with exceptionally fast kinetics and high calcium permeability, voltage-gated potassium channels, and large, fast inhibitory postsynaptic currents (Trussell, 1997), although similar features have not yet been found in the KO pathway.

Sensory filtering and temporal sharpening

Sensory-evoked spikes are relayed by KO afferents to the ipsilateral nELL (Fig. 2), where they terminate with large club endings onto large, adendritic, spherical neurons *via* mixed chemical–electrical synapses (Bell and Grant, 1989; Bell and Russell, 1978; Denizot et al., 1987; Mugnaini and Maler, 1987b; Szabo and Ravaille, 1976; Szabo et al., 1983). Each KO afferent contacts three to 11 nELL cells, and an estimated three to four afferents converge onto each nELL cell (Bell and Grant, 1989).

In addition to excitation from KO afferents, nELL cells receive GABAergic inhibitory input from the slem *via* small boutons that terminate on the soma and axon initial segment (Bell et al., 1981; Denizot et al., 1987; Mugnaini and Maler, 1987b; Szabo et al., 1983). The slem receives input from MCA and thereby mediates corollary discharge-driven inhibition of nELL neurons (Fig. 2), which blocks sensory responses for a brief window of time immediately after production of the fish's own EOD (Zipser and Bennett, 1976). The effects of this corollary discharge-driven inhibition can be seen downstream of the nELL, as stimuli delivered during a period of approximately 3 ms starting immediately after the production of each EOD do not elicit electrosensory responses in the EL or KO region of the valvula (Amagai, 1998; Bennett and Steinbach, 1969; Russell and Bell, 1978; Szabo et al., 1979; Zipser and Bennett, 1976). Behavioral studies have confirmed that fish are less sensitive to electrosensory stimuli occurring up to 1.5 ms after the fish's own EOD (Moller, 1970).

Broad somatotopy is evident in the KO projections to the nELL, such that afferents arising from the dorsal surface of the skin terminate ventrally, and those from the ventral surface terminate dorsally (Bell and Russell, 1978; Maler et al., 1973a; Maler et al., 1973b). Further, afferents from the head project to the rostral nELL, and those from the tail project to the caudal nELL. Accordingly, the latency of potentials in response to sensory stimulation is shortest in the rostral nELL and longest in the caudal nELL. A matching latency gradient is present in the corollary discharge potentials recorded at different locations within the nELL (Bell and Grant, 1989). Thus, the corollary discharge is effective at blocking KO responses to the fish's own EOD, with anatomical adjustments accounting for differences in conduction time from KOs on different parts of the body. The duration of mormyrid EODs spans a wide range across species (Fig. 1), and it remains to be determined whether the window of corollary discharge-driven inhibition varies in relation to species differences in EOD duration. Another open question is whether nELL projections to the midbrain incorporate compensatory delays to account for the differences in latency from KOs on the tail compared with those on the head.

The nELL has been considered to simply relay spike times from peripheral receptors to the midbrain. However, comparing the microcircuitry within the nELL with other sensory pathways suggests that the temporal codes established by KOs may be sharpened in the nELL. First, the convergence of multiple time-locked inputs has been proposed to enhance temporal precision by reducing jitter in the postsynaptic neuron (Carr et al., 1986a; Kawasaki et al., 1988). Such a mechanism has been implicated in the sharpening of phase-locking in auditory pathways (Joris et al., 1994; Sullivan and Konishi, 1984). When n correlated inputs converge onto a single neuron, the jitter of the response of the postsynaptic neuron should be reduced by $1/\sqrt{n}$ (Calvin, 1983). This hypothesis was tested in the mouse auditory brainstem by Xu-Friedman and Regehr (Xu-Friedman and Regehr, 2005), who found that convergence of multiple inputs onto single postsynaptic neurons reduces jitter, with the degree of jitter reduction determined by the number, strength and timing of inputs. The spherical soma and long, thin initial segment of nELL cells may also contribute to enhancing their temporal precision. An electron-dense undercoating thought to represent the spike-initiation zone occurs distally on the initial segment (Mugnaini and Maler, 1987b). Thus, synaptic currents must traverse a region of low input resistance (large adendritic soma) followed by a region of high input resistance ('uncoated' proximal initial segment) before reaching the spike initiation zone. This may provide a mechanism to 'discard' synaptic inputs not arriving in sufficient synchrony with other inputs (Maler et al., 1981). Neurons with similar morphology have been found in the time-coding pathways of multiple, distantly related species of wave-type weakly electric fish (Carr et al., 1986b; Kawasaki and Guo, 1996; Maler et al., 1981). Further, convergence of multiple synaptic inputs onto such neurons is associated with postsynaptic reductions in temporal jitter (Carr et al., 1986a). Thus, convergence of multiple inputs onto spherical somas with long initial segments and distal spike-initiation zones could represent a general adaptation for temporal coding.

Determining sender identity: a circuit for processing submillisecond spike timing differences

In species with an ELa/ELp, the axons of nELL cells project bilaterally to the ELa (Figs 2, 5), with ~60% of the axons arising contralaterally and ~40% arising ipsilaterally (Amagai et al., 1998; Bell et al., 1981; Bell and Grant, 1989; Enger et al., 1976b; Friedman and Hopkins, 1998; Szabo et al., 1983). At least some of the nELL cells bifurcate, giving rise to bilateral ELa projections (Friedman and Hopkins, 1998). The nELL–ELa projections show no obvious somatotopy (Bell and Maler, 2005; Friedman and Hopkins, 1998). In addition to incoming nELL axons, the ELa contains large GABAergic inhibitory interneurons and small projection neurons (Friedman and Hopkins, 1998; Mugnaini and Maler, 1987a). The large cells of *B. brachyistius* are adendritic, measure 9–18 μm in diameter, and are predominately located in the medial portion of the ELa, where incoming nELL axons enter the nucleus (Friedman and Hopkins, 1998; George et al., 2011). Interestingly, the large cells of *G. petersii* have dendrites (Mugnaini and Maler, 1987a), indicating important species differences in ELa microcircuitry. In both species, small cells are adendritic, measure 3–7 μm in diameter, and are distributed throughout the ELa (Amagai et al., 1998; Friedman and Hopkins, 1998; George et al., 2011; Mugnaini and Maler, 1987a).

As nELL axons enter the ELa, they first contact one to three large cells with large, cup-like endings giving rise to mixed chemical–electrical synapses (Mugnaini and Maler, 1987a; Szabo et al., 1983). Each nELL axon then follows a long and tortuous path, traveling for up to an additional 7 mm after the first synapse onto a large cell (Friedman and Hopkins, 1998). As a nELL axon winds through the ELa, it makes small *en passant* mixed chemical–electrical excitatory endings onto dozens of small cells, although the majority of these endings are made by the last 1–2 mm of the axon (Friedman and Hopkins, 1998; Xu-Friedman and Hopkins, 1999). Large cells project directly to small cells with a more restricted terminal field, giving rise to large GABAergic calyceal synapses that envelop the small cell somas (Friedman and

Hopkins, 1998; George et al., 2011; Mugnaini and Maler, 1987a). Sensory stimulation elicits a time-locked action potential in both nELL axons and large cells at a latency of ~2.5–3 ms and with low jitter following a stimulus edge, reflecting the 'on' or 'off' responses of KOs (Amagai et al., 1998; Friedman and Hopkins, 1998). Taken together, these findings suggest that small cells receive delayed excitatory input *via* a nELL axon, and time-locked inhibitory input *via* a large cell (Fig. 5).

ELa small cells are hypothesized to perform analysis of the small spike timing differences between peripheral receptors that represent EOD waveform. Several lines of evidence support this hypothesis. First, the ELa is the first station in the KO pathway where information from opposite sides of the body converges (Szabo et al., 1983), and small cells appear to be the only cells in the ELa that receive inputs from different receptive fields (Friedman and Hopkins, 1998; Xu-Friedman and Hopkins, 1999). Second, small cells are adendritic, and time comparator neurons in other circuits are typically adendritic or have minimally branching dendritic arbors (Carr et al., 1986a; Carr and Konishi, 1990; Grothe, 2003; Matsushita and Kawasaki, 2004). Third, variation in nELL axon lengths to small cells function as delay lines (Friedman and Hopkins, 1998), similar to the delay lines found in certain sound localization circuits (Carr, 1993). Fourth, the large calyceal ending onto small cells presumably makes the inhibitory transmission fast and reliable, as seen in the excitatory calyx of Held in the mammalian auditory system (Nicol and Walmsley, 2002). Fifth, anatomical specializations for preserving timing information disappear at small cells (Friedman and Kawasaki, 1997; Xu-Friedman and Hopkins, 1999). Finally, ELp neurons that receive input from small cells are tuned to pulse waveform (Amagai, 1998).

These various lines of evidence led Friedman and Hopkins (Friedman and Hopkins, 1998) to propose a delay-line anti-coincidence detection mechanism for small cell encoding of stimulus duration. In this model, each small cell receives inhibition elicited by one edge of a stimulus pulse and delayed excitation elicited by the other edge (Fig. 6). A given small cell will respond only if the excitatory and inhibitory inputs are not coincident, i.e. if the two inputs are separated in time. The relative timing of these inputs is determined by the duration of the stimulus pulse as well as the length of the axonal delay to the small cell. For short stimulus durations, inhibition in response to the trailing stimulus edge will block the delayed excitation in response to the leading edge, but for longer durations, the delayed excitation will arrive before the inhibition (Fig. 6). Therefore, this model predicts that each small cell will only respond to stimuli longer than a certain minimum duration, and variation in axonal delay across the population of small cells will establish variation in this minimum duration (Fig. 6). Under this model, then, small cells would recode peripheral timing differences into a population code, with the number of responding small cells increasing with increasing stimulus pulse duration.

Unfortunately, small cells are extremely difficult to record from, so direct tests of this model have not yet been possible (Amagai et al., 1998; Friedman and Hopkins, 1998; Xu-Friedman and Hopkins, 1999). However, we recently developed a novel fluorescence-based method for obtaining targeted extracellular recordings from small cell axons (Lyons-Warren et al., in press). Preliminary results suggest that variably delayed excitation and precisely timed inhibition in response to different stimulus edges are indeed important in establishing small cell responses, but that multiple excitatory inputs to small cells, as well as relatively short axonal delays to some cells, make for more complicated patterns of tuning than predicted by the Friedman–Hopkins model (Lyons-Warren et al., 2012b). This

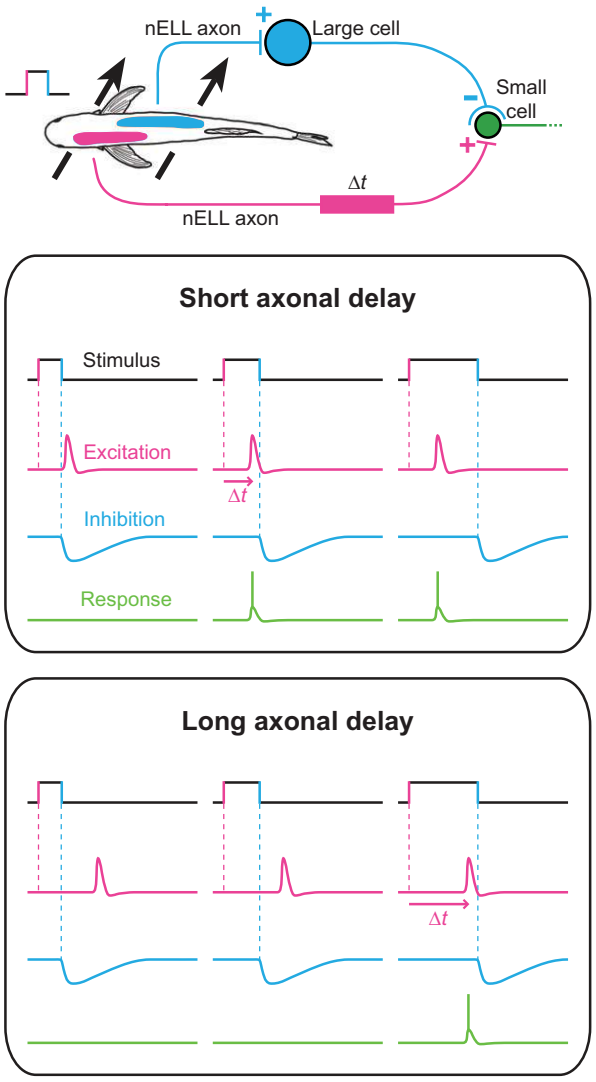

Fig. 6. Friedman–Hopkins model for small cell duration tuning (modified from Xu-Friedman and Hopkins, 1999). Knollenorgans on one side of the body surface (pink) respond to the upward edge of a square pulse, and this gives rise to an excitatory input to a small cell *via* a nELL axonal delay line (Δ*t*). Knollenorgans on the other side of the body surface (blue) respond to the downward edge, and this gives rise to an inhibitory input to the small cell *via* an ELa large cell. This is just one example of many possible receptive field organizations of the excitatory and inhibitory inputs to small cells. The responses of small cells to stimuli of different durations are determined by the length of the excitatory axonal delay (below). For short-duration stimuli, inhibition in response to stimulus offset blocks the delayed excitation in response to stimulus onset. For pulses that are longer than the excitatory delay, however, the delayed excitation arrives before the inhibition, and the small cell responds. Different small cells receive excitatory input with different delays, establishing variation in the minimum pulse duration that can elicit a response. As a result, increasing pulse duration leads to the progressive recruitment of small cells with longer axonal delays, and pulse duration is reflected in the total number of responding cells.

scenario would result in a distributed population code, with the identity of responsive small cells, and not just total number, reflecting EOD waveform (Fig. 7). This would represent a novel mechanism for recoding submillisecond timing differences, distinct from avian sound localization pathways that use delay-line coincidence detection to convert a temporal code into a place code,

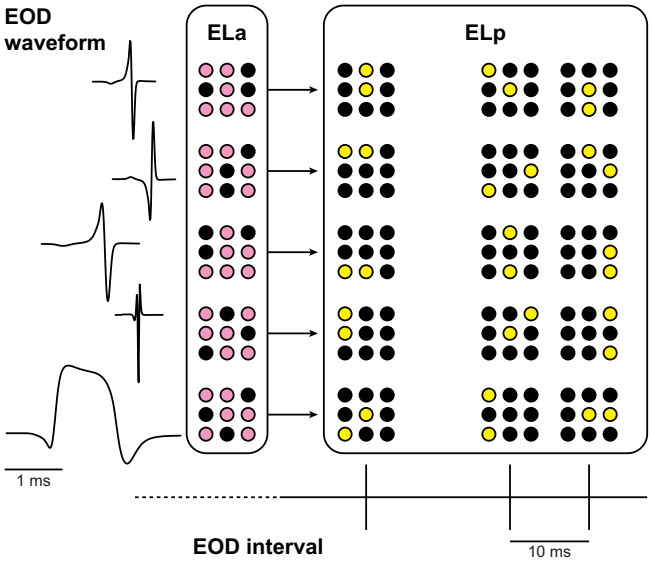

Fig. 7. Multiplexed temporal codes are converted into distributed population codes in the ELa and the ELp. EOD waveform is represented by the pattern of responsive neurons across the population of small cells in the ELa, and both EOD waveform and EOD interval are represented by the pattern of responsive neurons across the population of multipolar cells in the ELp. Five different EOD waveforms are shown, from top to bottom: *Brienomyrus brachyistius* EOD, reversed polarity *B. brachyistius* EOD, elongated *B. brachyistius* EOD, *Stomatorhinus ivindoensis* EOD and *Paramormyrops* sp. 'VAD' EOD. Nine model small cells are shown and for each of the five EOD waveforms, pink indicates responding cells and black indicates non-responding cells. Each EOD waveform results in a unique pattern of responsiveness across the population of small cells. This information is sent to the ELp, where multipolar cells respond selectively to EOD waveform as well as EOD interval. Nine model multipolar cells are shown and for the five EOD waveforms and three different EOD intervals (from left to right: long, medium and short), yellow indicates responding cells and black indicates non-responding cells. Each possible combination of EOD waveform and EOD interval results in a unique pattern of responsive neurons across the population of multipolar cells.

as well as mammalian sound localization pathways that use binaural excitation combined with monaural inhibition to convert a temporal code into a rate code (Köppl, 2009; Schnupp and Carr, 2009).

Small cell axons project topographically to the ELp, with medial small cells projecting medially and lateral small cells projecting laterally (Friedman and Hopkins, 1998). The anatomy of the ELp indicates that it is a region of substantial local processing. First, ELp neurons, with somatic diameters of 6–14 µm, exhibit widely branching dendritic arbors spanning up to 200 µm in diameter (George et al., 2011; Xu-Friedman and Hopkins, 1999), suggesting extensive synaptic integration. Second, the ELp contains inhibitory GABAergic interneurons (George et al., 2011). Third, in addition to their extrinsic projections, the axons of individual ELp neurons give rise to collaterals that project throughout the nucleus (George et al., 2011; Xu-Friedman and Hopkins, 1999). Fourth, ELp neurons exhibit a range of response latencies to sensory stimulation: some neurons respond in a time-locked manner 7–9 ms after a stimulus, whereas others respond with variable latencies of 12–20 ms, longer than would be expected from a direct excitatory input from the ELa (Amagai, 1998). Fifth, multiple phases of excitation and inhibition can often be seen in intracellular recordings from ELp neurons (Carlson, 2009; George et al., 2011; Xu-Friedman and Hopkins, 1999). Finally, paired whole-cell recordings *in vitro* reveal extensive synaptic connections among ELp neurons (Ma et al., 2013).

Extracellular single unit recordings in ELp suggest two cell types based on responses to single pulses (Amagai, 1998). Type I cells respond with high probability at latencies of 7–9 ms and their responses increase with increasing stimulus duration, being minimally affected by stimulus polarity or amplitude. In contrast, Type II cells have a low response probability, weaker time-locking, latencies >12 ms, selectivity for a limited range of stimulus durations and intensities, and strong preferences for stimulus polarity. The sensitivity of ELp neurons to stimulus pulse duration, amplitude and polarity reveals that the information necessary for identifying signaling fish as well as determining their distance, location and orientation is present in the spike timing differences of KOs.

Determining the behavioral state of the sender: multiple mechanisms for temporal filtering of interspike intervals

In addition to pulse waveform, ELp neurons are also tuned to IPI (Fig. 8), owing to temporal filtering of incoming small cell spike trains (Carlson, 2009; George et al., 2011). Thus, stimulus information encoded into interspike intervals in the periphery is retained during the processing of spike timing differences in the ELa. Low-pass tuning describes preferential responses to long intervals (low frequencies), high-pass tuning describes preferential responses to short intervals (high frequencies), band-pass tuning describes preferential responses to intermediate intervals, and band-stop tuning describes preferential responses to short and long, but not intermediate, intervals. Low-pass and high-pass tuning curves vary widely in shape, and band-pass and band-stop tuning curves vary widely in best/worst interval and bandwidth (Carlson, 2009; George et al., 2011). As a result, diversity of interval tuning across the population of ELp neurons results in the recoding of IPIs into a distributed population code in which IPI is reflected in the identity of responsive neurons, much like the population code of EOD waveform in the ELa. Thus, both temporal codes – spike timing differences that code for EOD waveform and interspike intervals that code for IPI – are sequentially converted into distributed population codes in this circuit. The resulting sensitivity of ELp neurons to EOD waveform and IPI means that both components are represented in the identities of responsive neurons (Fig. 7).

Some ELp neurons are also responsive to changes in IPI, with response magnitude depending on whether IPIs are increasing or decreasing (Carlson, 2009). This preference arises from hysteresis, or the degree to which responses to particular IPIs are affected by preceding IPIs. Some neurons in each tuning class exhibit a large amount of hysteresis, whereas others exhibit little to none. Thus, the responses among ELp neurons can provide information about the direction of IPI change as well as the specific IPI sequence, resulting in selective responses to communication signals such as scallops, rasps and accelerations (Carlson, 2009).

GABAergic inhibition plays an important role in IPI tuning. Blocking $GABA_A$, but not glycine, receptors caused increases in the amplitude, latency to maximum depolarization, and duration of synaptic responses to single pulse stimulation (George et al., 2011). These effects occurred regardless of the neurons' IPI tuning, demonstrating that neurons of all tuning classes receive inhibition. Furthermore, blocking inhibition caused a general shift towards high-pass tuning: the majority of low-pass, band-pass and band-stop neurons switched to high-pass tuning, and most high-pass neurons experienced a sharpening of their high-pass tuning. Therefore, the interaction of excitation and inhibition is essential in establishing IPI tuning diversity among ELp neurons.

Similar selectivity of central neurons to temporal patterns of sensory stimulation has been documented in several auditory and

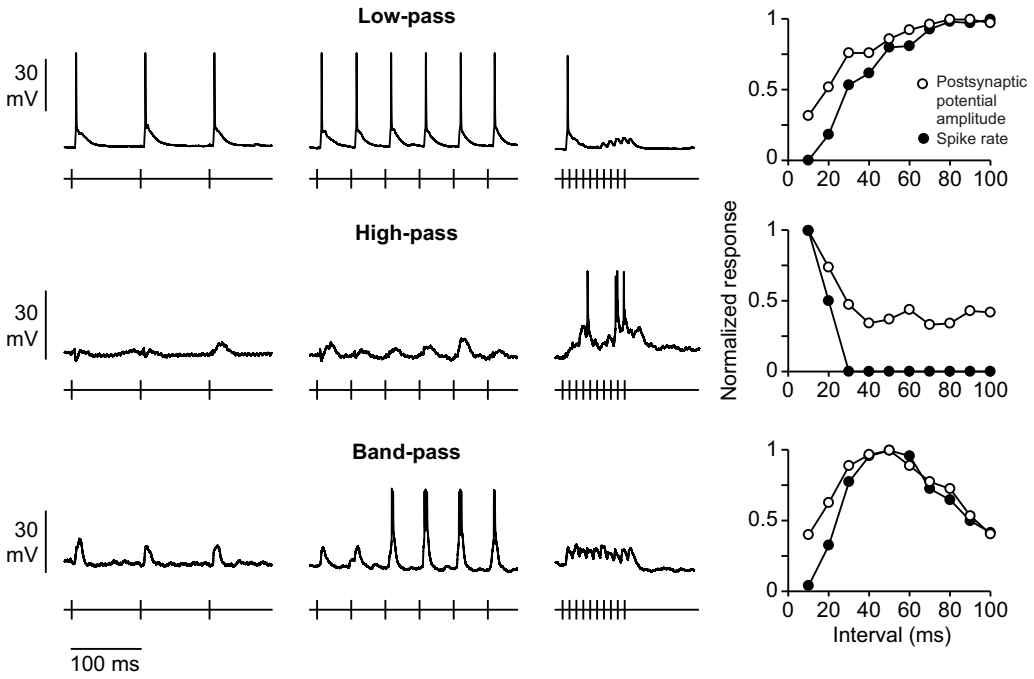

Fig. 8. IPI tuning of ELp neurons in response to electrosensory stimulation *in vivo*. Data from three different neurons are shown (data from Carlson, 2009). Intracellular recordings show responses to, from left to right, 100, 50 and 10 ms IPIs, with stimulus trains shown underneath each recording trace. On the far right, tuning curves show the normalized average spike rate and postsynaptic potential amplitude as a function of stimulus IPI in response to 10 repetitions of each stimulus [details on stimulus presentation and tuning curve generation can be found in Carlson (Carlson, 2009)].

electrosensory pathways (Edwards et al., 2002; Fortune and Rose, 1997b; Grothe, 1994; Huetz et al., 2009; Marsat and Maler, 2010; Pluta and Kawasaki, 2010; Rose and Capranica, 1983). Given the prevalence of temporal coding across sensory systems, an understanding of central mechanisms for temporal filtering in these systems should provide fundamental insight into general issues in sensory processing. A variety of synaptic mechanisms have been proposed to give rise to temporal filtering properties in single neurons (Fig. 9). Temporal summation, in which responses evoked by successive stimuli overlap in time, has been hypothesized to produce interval tuning (Edwards et al., 2007; Rose et al., 2011). Temporal summation of excitation can cause increased responses to short intervals, whereas temporal summation of inhibition can cause decreased responses to short intervals (Fig. 9). Short-term synaptic plasticity, or a change in synaptic strength with repeated stimulation, has also been implicated in interval tuning (Buonomano, 2000; Edwards et al., 2007; Edwards et al., 2008; Fortune and Rose, 2000; Klyachko and Stevens, 2006; Rose and Fortune, 1999; Zucker and Regehr, 2002). Short-term synaptic plasticity occurs on the timescale of tens of milliseconds to several minutes, and can result in increases or decreases in synaptic strength, called facilitation and depression, respectively (Zucker and Regehr, 2002). Facilitation of excitation or depression of inhibition at short stimulation intervals could produce high-pass responses, whereas facilitation of inhibition or depression of excitation could produce low-pass responses (Fig. 9). Finally, differences in the relative timing of excitatory and inhibitory inputs has also been hypothesized to underlie interval tuning (Edwards et al., 2008; Grothe, 1994). If inhibition is delayed with respect to excitation, then repeated stimulation at short intervals could cause excitation to overlap with inhibition evoked by previous stimuli, resulting in an attenuation of response characteristic of low-pass tuning (Fig. 9). This scenario requires the latency of excitation and inhibition to be fixed during repeated stimulation. By contrast, high-pass tuning could result if the latency to excitation or inhibition changes with repeated stimulation. For instance, if excitation and inhibition occur near-simultaneously in response to a single pulse, the resulting synaptic response would be small. If, however, repeated stimulation increased inhibitory latency, then larger responses giving rise to high-pass tuning could result (Fig. 9).

In the ELp, *in vitro* whole-cell recordings have revealed that temporal summation of excitation and inhibition plays a major role in establishing single-neuron tuning to temporal patterns of presynaptic input, and computational modeling reveals that all major classes of IPI tuning can be established by just this one mechanism (George et al., 2011). However, this study also revealed that the IPI tuning of a small subset of ELp neurons may be influenced by short-term synaptic depression (George et al., 2011). Somewhat surprisingly, *in vivo* and *in vitro* studies currently underway have uncovered widespread short-term depression in both excitatory and inhibitory pathways to ELp neurons (Baker et al., 2012). Differences in the relative magnitude and time course of depression in excitatory and inhibitory pathways may contribute to interval tuning as well as directional sensitivity to changes in interval. Short-term depression is also prevalent in avian and mammalian auditory time-coding pathways (MacLeod, 2011).

In addition to synaptic mechanisms, intrinsic membrane properties of postsynaptic neurons can contribute to temporal filtering (Hutcheon and Yarom, 2000; Mehaffey et al., 2008b). First, the membrane itself passively filters high-frequency fluctuations in membrane potential. In the ELp, membrane time constants are widely distributed between 5 and 25 ms (Kohashi et al., 2012), suggesting that short IPIs within the behaviorally relevant range are differentially filtered. Further, neurons with longer time constants would be more affected by temporal summation, and they would

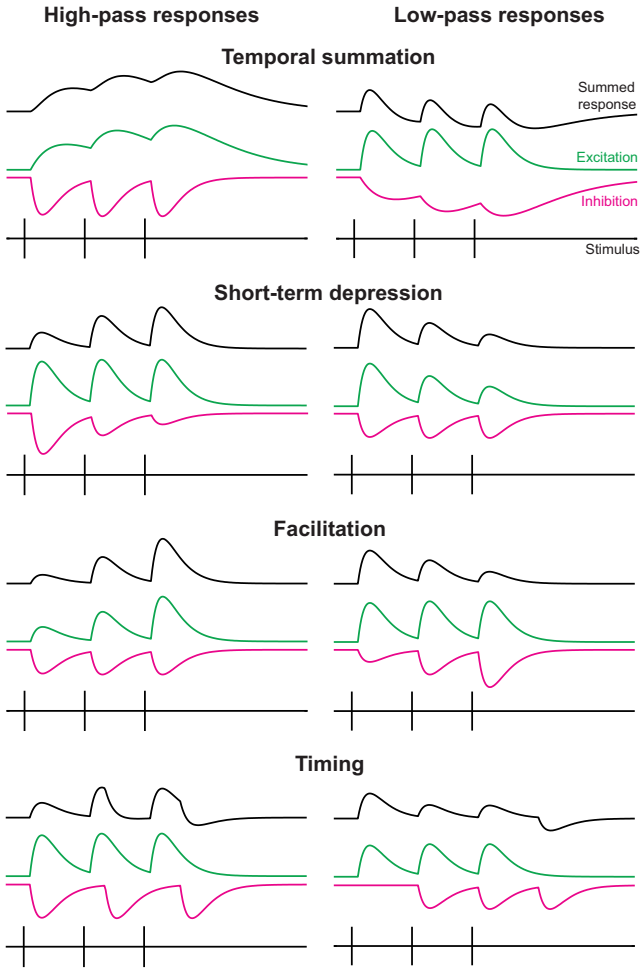

Fig. 9. Multiple synaptic mechanisms can establish IPI tuning. Different excitatory (green) and inhibitory (magenta) responses to short-interval stimulation (ticks) can give rise to different summated synaptic responses (black). In this simple model, summed responses are determined by subtracting the inhibitory response from the excitatory response. Temporal summation, in which synaptic responses to successive stimuli overlap in time, can establish IPI tuning. When excitation lasts longer than the stimulation interval, temporal summation leads to an increase in response characteristic of high-pass tuning. Conversely, temporal summation of inhibition occurs when inhibition lasts longer than the stimulation interval, causing a decrease in response characteristic of low-pass tuning. Short-term synaptic depression, or a decrease in synaptic strength with repeated stimulation, of inhibition can produce high-pass tuning, and depression of excitation can produce low-pass tuning. Facilitation, or an increase in synaptic strength with repeated stimulation, of excitation can result in high-pass tuning, whereas facilitation of inhibition can result in low-pass tuning. Finally, the relative timing of excitation and inhibition can establish interval-tuned responses. If excitation and inhibition occur near-coincidently, the response to a single stimulus would be small. Increasing latency of inhibition with repeated stimulation could result in high-pass tuning. In contrast, if the latencies of excitation and inhibition were fixed, and inhibition was delayed with respect to excitation, stimulation at short intervals could cause excitation to coincide with inhibition elicited by previous stimuli, resulting in low-pass tuning.

be able to integrate over multiple non-coincident inputs. Such a scenario could give rise to the longer latency and more highly variable responses of the Type II ELp neurons described by Amagai (Amagai, 1998). Second, voltage-gated channels in the postsynaptic cell can shape synaptic responses (O'Donnell and Nolan, 2011). The significance of low-threshold voltage-sensitive channels in temporal coding is particularly well described in auditory brainstem neurons where timing information is highly preserved (Brown and Kaczmarek, 2011; Kuba, 2007; Trussell, 1999). Calcium-activated potassium channels (Ellis et al., 2007) as well as voltage-sensitive channels (Carlson and Kawasaki, 2006; Fortune and Rose, 1997a; Fortune and Rose, 2003; Mehaffey et al., 2008a) are suggested to shape frequency tuning and stimulus selectivity in response to electrosensory stimuli in wave-type electric fish. Current studies are investigating the contribution of similar mechanisms to interval tuning in the ELp (e.g. Kohashi et al., 2012). The diversity of interval tuning and hysteresis among ELp neurons is likely due to complex interactions between temporal summation, short-term synaptic plasticity, and intrinsic membrane properties. Having multiple such 'free parameters' may establish a higher dimensionality of 'coding space' in which to represent multiple behaviorally relevant stimulus features in a single circuit.

Finally, although current evidence points to extensive processing of communication signals within ELp, many questions about the nature of these local circuit interactions remain. Excitatory and inhibitory network interactions among IPI-tuned neurons could act in several ways to shape IPI tuning (Fig. 10). For example, combining inputs from one low- and one high-pass neuron onto a single postsynaptic neuron can establish band-pass, band-stop or all-pass tuning, depending on the excitatory/inhibitory nature of the inputs. Furthermore, sharpening of low- or high-pass tuning can result when excitatory and inhibitory inputs converge.

Sensory multiplexing and the evolution of signals and species

Evolutionary change in nervous systems can have profound effects on processes that influence species diversification (Carlson, 2012; Carlson and Arnegard, 2011). Communication signals play an essential role in mate choice. As a result, signal divergence can establish reproductive isolation between populations, thereby reinforcing this divergence and promoting speciation (Hoskin and Higgie, 2010). For signal divergence to result in reproductive isolation, however, receivers must have the perceptual ability to detect signal variation. The evolution of novel perceptual abilities can therefore open up new dimensions of signal variation for mate choice, which can drive increased rates of species diversification and signal evolution (Carlson, 2012; Carlson and Arnegard, 2011). For example, if two populations of the same species become geographically isolated, their mating signals may diverge over time due to processes such as genetic drift, local adaptation to different environments, or reproductive character displacement. If receivers can detect the difference, then members of the two populations will be less likely to mate if they later come into contact, and selection may then act to drive further signal divergence to prevent hybridization. Indeed, the evolution of distributed KOs and ELa/ELp in clade A (Fig. 3) established the novel ability to discriminate temporal variation in EOD waveform, which fueled dramatic increases in the rates of species diversification and EOD evolution (Carlson et al., 2011). A similar process may have resulted from evolutionary change in the auditory system of frogs (Ryan, 1986) and the visual system of cichlid fishes (Seehausen et al., 2008; Terai et al., 2006). Importantly, the evolution of EOD waveform coding established temporal multiplexing in the KO electrosensory system (Fig. 4), thereby adding increased dimensionality to electrocommunication. This evolutionary change and its effects on mormyrid diversity underscore a primary advantage of temporal

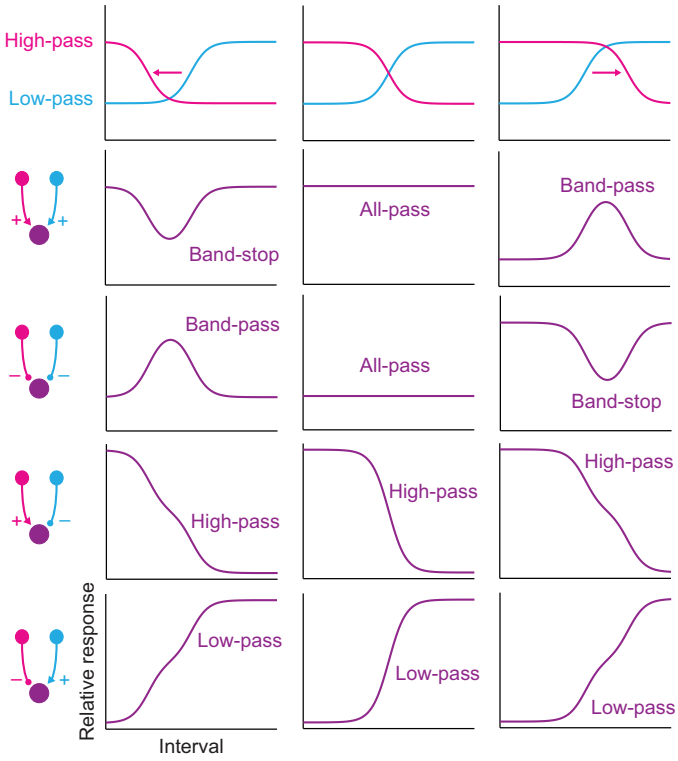

Fig. 10. Convergence of high- and low-pass tuning can establish diverse temporal filters. The tuning curves of model neurons (purple) that receive synaptic inputs from one high-pass (magenta) and one low-pass (blue) neuron are shown. Excitatory connections are indicated by '+' and inhibitory connections are indicated by '–', and the tuning of each postsynaptic neuron is determined by a simple addition of '+' tuning curves and subtraction of '–' tuning curves. A variety of different types of interval tuning, including high-pass, low-pass, band-pass, band-stop and all-pass, can be created by different combinations of high-pass and low-pass excitation and inhibition.

multiplexing: increased information transmission within a single channel.

Future directions

Evolutionary change in nervous systems provides a powerful tool for employing comparative approaches to study neural mechanisms of behavior, as it allows for a direct comparison between differences in behavior with differences in neural circuitry (Carlson, 2012). However, we have only scratched the surface in understanding evolutionary change in the KO sensory system. How do the rosette KOs of non-clade-A species encode electric signals? How does the EL process these signals? Does the EL have the large cells and small cells of the ELa, the multipolar cells of the ELp, or completely different cell types? Are there axonal delay lines in the EL?

Many important questions remain about the coding of electrocommunication signals in clade A species. For example, how is information about signaler location and orientation (Schluger and Hopkins, 1987) extracted from the spatiotemporal pattern of KO responses? How are signals from multiple fish differentiated? How is signal coding affected by changes in the relative positions of sender and receiver? What are the roles of the MV and the ELp–IG feedback loop in processing communication signals? How do downstream targets, including the cerebellum and optic tectum, process information from the ELp and the MV, and how do they modulate the fish's own EOD production? The answers to these questions will contribute to our understanding of not only mormyrid electrocommunication, but also sensory processing of temporally coded information in general.

List of abbreviations

AMPA	2-amino-3-(3-hydroxy-5-methyl-isoxazol-4-yl)propanoic acid
BCA	bulbar command-associated nucleus
CN	command nucleus
DP	dorsal posterior thalamic nucleus
EL	exterolateral nucleus
ELa	anterior exterolateral nucleus
ELL	electrosensory lateral line lobe
ELp	posterior exterolateral nucleus
EMN	electromotor neuron
EOD	electric organ discharge
GABA	γ-aminobutyric acid
IG	isthmic granule nucleus
IPI	interpulse interval
KO	knollenorgan
MCA	mesencephalic command-associated nucleus
MRN	medullary relay nucleus
MV	medioventral nucleus
nELL	nucleus of the electrosensory lateral line lobe
OB	olfactory bulb
PCN	precommand nucleus
slem	sublemniscal nucleus
tel	telencephalon
val	valvula cerebellum
VP	ventroposterior nucleus

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Competing interests

No competing interests declared.

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