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INSIGHTS INTO NEURAL MECHANISMS AND EVOLUTION OF BEHAVIOUR FROM ELECTRIC FISH

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Abstract | Both behaviour and its neural control can be studied at two levels. At the proximate level, we aim to identify the neural circuits that control behaviour and to understand how information is represented and processed in these circuits. Ultimately, however, we are faced with questions of why particular neural solutions have arisen, and what factors govern the ways in which neural circuits are modified during the evolution of new behaviours. Only by integrating these levels of analysis can we fully understand the neural control of behaviour. Recent studies of electrosensory systems show how this synthesis can benefit from the use of tractable systems and comparative studies.

Behaviour, although multifaceted and diverse, also seems to be convergent across taxa. Even distantly related organisms can show similar behaviours, involving sensory pattern recognition, locomotion and experience-dependent changes in sensory processing and motor output. In neuroscience, the prevalent use of particular systems as models for understanding the function of the human nervous system rests on this functional overlap and structural homology. However, we are only beginning to understand whether similarities in behaviour are paralleled by similarities in control mechanisms, neural circuitry and processing. This gap in knowledge is not surprising; the identification of the neural control of any particular behaviour or function can be a formidable challenge. As we learn more about how neural circuits control behaviour, we hope to gain a greater understanding of why particular solutions have developed[1]. Integration of information at these two levels will be essential for revealing the uniqueness of particular neural circuits[2] and mechanisms, as well as for understanding the roles of historical forces in determining the final architecture of neural circuits and processing.

Electrosensory systems (BOX 1) are well suited to addressing these questions. In addition to their established utility for investigating receptor[3] and ion channel[4] function, electric fish have increasingly been used for studying the neural circuits that control behaviour[5]. Some fish are purely electroreceptive, whereas others can both sense and produce electric fields. Most species of the latter type continue to produce discharges of their electric organs (EODs, electric organ discharges) when prepared for *in vivo* neurophysiological recording. Furthermore, changes in these EODs produce a variety of electrosensory behaviours, permitting investigators to study the entire neural circuit for the control of these behaviours[5,6]. The fish's intended signals can be monitored and replaced by substitute signals, thereby opening the loop between behaviour and its sensory consequences[6,7]. The jamming avoidance responses (JARs) of 'wave-type' gymnotiform fishes have been particularly well studied. As I will discuss, comparative studies of JARs and the adaptive cancellation of expected sensory information[8] have increased our understanding of the neural control of behaviour and its evolution.

Jamming avoidance responses

Behaviour. Wave-type electric fish generate electric fields (FIG. 1a) by periodically discharging their electric organs. They can 'electrolocate' objects[9] in their environment by sensing perturbations of these fields — that is, by sensing changes in the timing and amplitude of the signals caused by the presence of nearby objects — with

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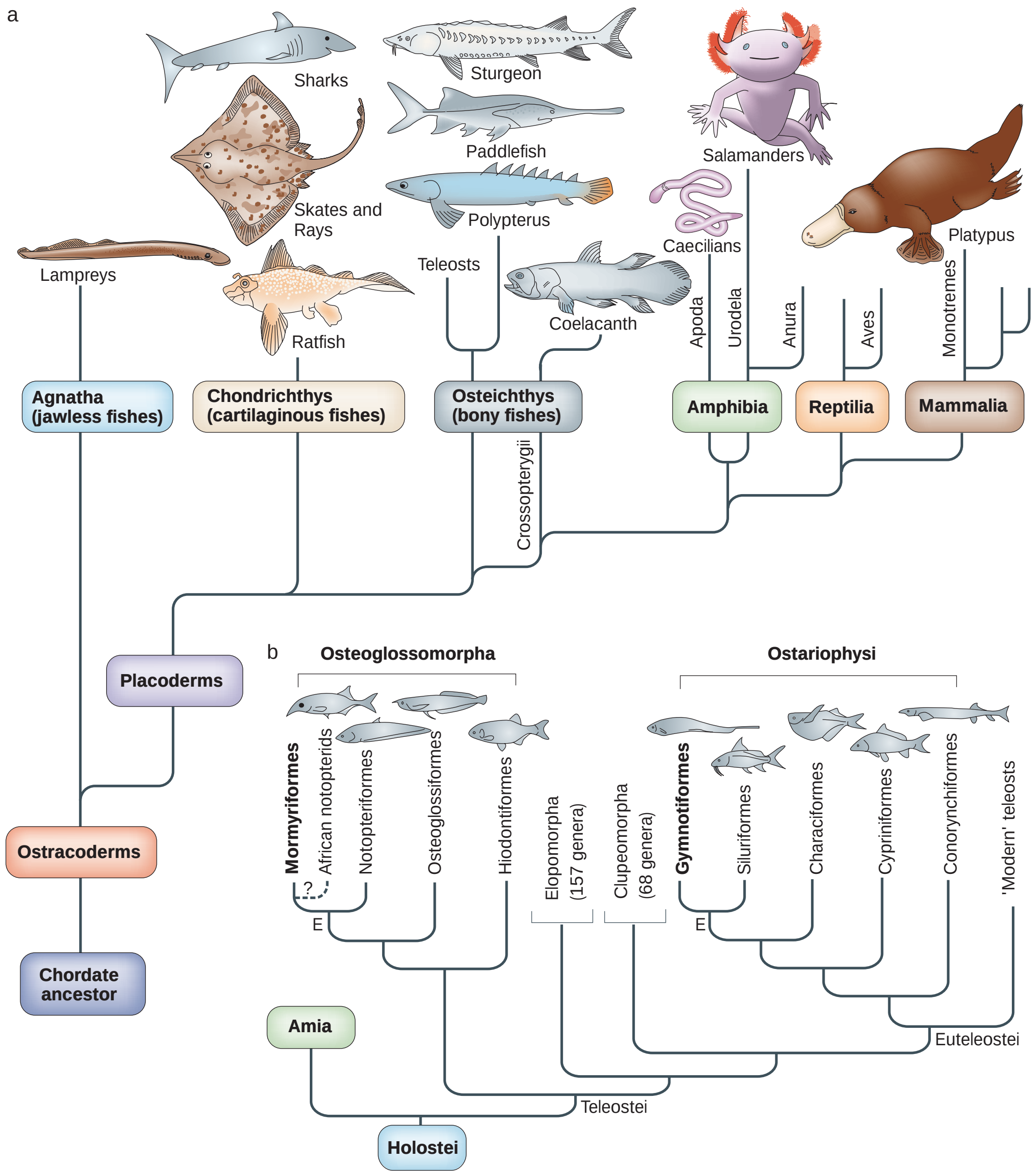
Box 1 | Electroreception



Electroreception, which is the detection of weak electric fields, is widespread among vertebrates, with cases in all classes of fishes, two orders of amphibians and even mammals (the duck-billed platypus). This 'exotic' sense seems to be an ancestral vertebrate trait, as it is present in lampreys and cartilaginous fishes. Its spotty presence in particular vertebrate groups indicates that electroreception has evolved (been 'reinvented') a number of times during vertebrate evolution. Particularly compelling evidence for the independent evolution of this sense is its presence in mormyriforms (African) and gymnotiforms (South American), two distantly related (Osteoglossomorpha versus Ostariophysi) orders of teleost (modern, bony) electric fishes, and in the duck-billed platypus, a monotreme mammal. In all cases, electroreception does not seem to be the ancestral condition. Modern holostean (the lineage that gave rise to teleosts) fishes are not electroreceptive. Similarly, electroreception in the duck-billed platypus is probably a derived trait because it is not characteristic of reptilians (from which mammals evolved). Electroreceptors vary in sensitivity (from 0.005 µV cm^{-1} to >0.1 mV cm^{-1}) and frequency sensitivity (near DC (direct current) to >15 kHz). All electroreceptive animals have ampullary receptors, which are highly sensitive and best excited by very low frequencies (less than 30 Hz). Other electroreceptor types are found in most electrogenic species. Electrogenic fish produce electric signals by discharging their electric organs, which consist of columns of modified muscle cells (electrocytes)[57]. Some organs generate strong discharges (hundreds of volts) that are useful for stunning prey, whereas others produce weak discharges (millivolts) that are used for social communication and electrolocation. Species that have electric organs of the latter type produce either intermittent (pulse species) or periodic (wave species) discharges. Both types of weakly-electric fish also have electroreceptors that are tuned to the species-specific higher frequencies found in their discharges. **b** reproduced, with permission, from REF.19 © (1999) Company of Biologists.

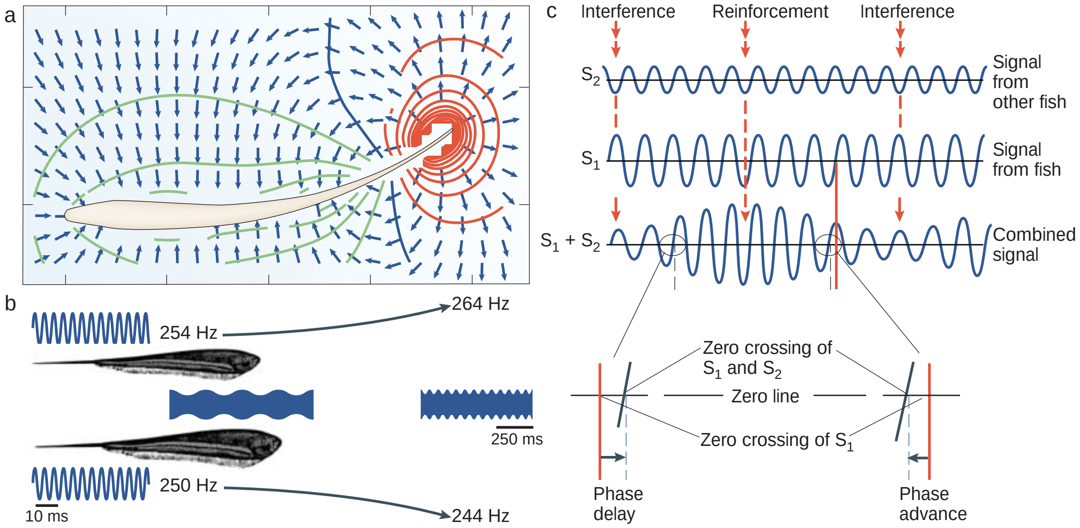


Figure 1 | **The jamming avoidance response. a** | Diagram of the electric field of a wave-type electric fish (shown in outline). Current vectors (blue arrows) and isopotential lines in 1-mV contours (green, red) are for the head-negative phase of the electric organ discharge (EOD). Reproduced, with permission, from REF. 58 © (1999) Company of Biologists. **b** | Representation of jamming avoidance responses (JARs) of two wave-type fish (*Eigenmannia*). The EODs of these fish are normally emitted at a highly regular frequency (250 Hz for one fish, 254 Hz for the other) and generate a quasi-sinusoidal signal. These two signals summate to produce the 'beating' waveforms (centre), wherein the peak-to-trough amplitude fluctuates over time at a rate equal to the frequency difference of the EODs of the two fish (4 Hz in this example). During the JAR, fish change their EOD frequency so as to increase the frequency difference; the higher frequency fish raises its EOD frequency and the lower frequency fish decelerates its signal. **c** | Sinusoidal representations of the EODs of two fish, and the signal that results from the addition of these signals ($S_1 + S_2$). The signal of the neighbour (S_2) is smaller and of a higher frequency than that of the focal fish. The amplitude and phase of the combined signal fluctuates over time as the two signals slowly and regularly move in and out of phase. The amplitude peak of the combined signal corresponds to the point in time when S_1 and S_2 are in phase (reinforcement); at the beat minimum, the two signals are in antiphase (interference). The timing of zero-crossings of the combined signal, relative to those of S_1, are delayed as the amplitude rises, and advanced as the amplitude falls; this relation between amplitude and phase modulations is reversed when the frequency of S_2 is lower than that of S_1 (phase advance accompanies increases in amplitude).

specialized electroreceptors that are distributed over the body surface. This use of the electric field to 'image' objects can be compromised if a neighbouring fish is producing EODs at a slightly different frequency (FIG. 1b), because the two signals add constructively and destructively over time (FIG. 1). This results in a 'beating' waveform, in which the amplitude and timing of the resulting signal is modulated at a rate equal to the difference in frequency between the two EODs. Relatively slow changes in signal amplitude and timing 'mask' those created by relative motion between the fish and its environment, and can impair electrolocation[10,11]. When confronted with this jamming situation, some species of electric fish change their EOD frequency so as to increase the difference in frequency between their own EOD and that of a neighbouring fish[12,13]. These JARs restore, and can even enhance, the fish's ability to electrolocate in the presence of the EODs of a neighbouring fish. Although there will still be interference between the two signals, the larger frequency difference means that the resulting fluctuations in signal amplitude and timing occur at a much higher rate (that is, a faster temporal frequency). As in the visual systems of various species, central temporal filtering processes largely eliminate the steady-state sensory information that results from these fast fluctuations[14,15].

At least three types of jamming avoidance conditions have been found in closely related families of South American electric fish (gymnotiforms)[13]. *Eigenmannia* has a robust JAR, in which it can either increase or decrease its EOD frequency (in response to a lower or higher frequency jamming neighbour, respectively). Fish of the closely related family, Apteronotidae, also produce JARs, but only increase their EOD frequency. However, the 'basal' gymnotiform fish *Sternopygus*[16–19] entirely lacks a JAR. The taxonomic distribution of this trait is made even more interesting by the presence of a JAR in the African mormyriform electric fish *Gymnarchus niloticus*[13], which is distantly related to the South American gymnotiforms[19]. Like *Eigenmannia*, *Gymnarchus* can either increase or decrease its EOD frequency when it detects interference by a neighbour. Interestingly, these orders of fishes do not share an electroreceptive or electrogenic ancestor (BOX 1). Therefore, the African and South American electric fish evolved their electric signalling and sensing capabilities independently, and their JARs are an example of convergent evolution. This distribution of the trait offers an excellent opportunity for comparative analyses of these behaviours and their neural control. Conversely, elucidating the neural mechanisms that underlie these behaviours provides further support for convergent evolution of this trait, as we will see.

Extensive mechanistic studies of the JAR of *Eigenmannia* have shown that these fish use a complex algorithm to determine whether to increase or decrease their EOD frequency[5–7]. They detect the concurrent modulations of signal amplitude and timing (FIG. 1c) in body surface regions that detect foreign EODs, and compare them to signals sensed by a 'reference' area — a part of the body surface that is minimally affected by the foreign signal. For example, a concurrent rise in signal amplitude and timing advance, relative to the reference signal, indicates that the foreign signal is lower in frequency than the fish's own EOD. Although, theoretically, there are several techniques that fish could use to determine the correct direction in which to change their EOD frequency, *Gymnarchus* (the African fish) also uses this complex algorithm[20]. This convergence of solution is surprising, considering that African electric fish can evaluate sensory input with regard to their EOD motor commands (see below). It is likely that this algorithm, although complex, is the most desirable solution to the problem. What factors or forces promoted the 'selection' of this strategy? This complex analysis of amplitude and timing relations might be functionally superior to other solutions. Alternatively, the existing architecture of the electrosensory system might have made this the most straightforward solution.

Behavioural studies of the gymnotiform *Sternopygus*, which lacks a JAR, support the idea that preadaptations promoted the 'selection' of this strategy. *Sternopygus* seems to reflect ancestral gymnotiform traits, and is largely immune to jamming[11]. Despite lacking a JAR, *Sternopygus* can discriminate whether a foreign signal is higher or lower in frequency than its own EODs[21]. The experiments that showed this took advantage of the natural inclination of these fish to move in synchrony with movements of their local environment. The fish's tracking responses to movements of its hiding (surround) tube were conditioned by preceding movement of the surround with delivery of a signal of either higher or lower frequency than that of its own EOD. After conditioning, the fish would make particular movements in response to the external signal alone. These results indicate that this sensory discriminative ability might be an ancestral electrosensory trait that predated and served as a preadaptation for the evolution of the JAR. It is likely that discriminating relative frequency has been important in the social behaviour of these fish[22]. *Sternopygus*, like other gymnotiform genera, might establish dominance hierarchies based on the EOD frequencies of conspecifics. Males produce EODs of increasing frequency in response to females. During the breeding season, females discharge at frequencies approximately twice that of males, and males produce more complex frequency increases in response to those females that discharge at frequencies greater than twice that of their own EOD frequency, compared to those females that discharge at lower frequencies[23]. These behavioural findings indicate that *Sternopygus*, despite lacking a JAR, has the neural circuitry and mechanisms required for evaluating relations between modulations of signal amplitude and timing differences.

Neural correlates. Neurophysiological studies of both *Sternopygus* and *Eigenmannia* have shown that the convergence of amplitude modulation and timing difference information occurs in neurons of the torus semicircularis[24,25] (FIG. 2a), the homologue of the inferior colliculus. In *Eigenmannia*, the discrimination of relative frequency is then completed and interfaced with motor control circuits in the diencephalic target of the torus, the nucleus electrosensorius (NE)[26,27]. Unlike the torus, there is no clear somatotopic organization in the NE. Instead, NE neurons seem to receive convergent information from across the body surface. Recordings from single neurons in the NE of *Eigenmannia* show that they respond selectively to the 'sign' of the frequency difference (Df); some respond best when the frequency of an external (jamming) signal is several Hz higher than the fish's own EOD, others when it is several Hz lower. The NE contains a simple 'motor map' (FIG. 2b), and stimulation of specific regions of the NE (NE↑ or NE↓) by glutamate iontophoresis can produce slow increases or decreases, respectively, in the frequency of the EOD[28,29]. These changes in EOD frequency are mediated through the prepacemaker (PPn) and sublemniscal prepacemaker (SPPn) motor control regions[30,31]; lesions of these areas eliminate increases or decreases in frequency, respectively.

Cytologically, the NE of *Sternopygus* is similar in organization to that of *Eigenmannia*, with the same subnuclei[32]. Moreover, sign-selective neurons have been recorded from each of the subdivisions of the NE of *Sternopygus*[32]. Consistent with the fact that *Sternopygus* does not produce a JAR, however, changes in the frequency of the EOD cannot be elicited by glutamate iontophoresis in any NE region in this fish (R. L. Green and G. J. R., unpublished data). *Sternopygus* does have the PPn and SPPn motor control regions and, when stimulated, these elicit frequency increases and interruptions, respectively[33]. So it seems that *Sternopygus* has the sensory capacity to make the discrimination required for the JAR, but lacks the necessary coupling at the sensory–motor interface.

These findings show that 'sign selectivity' is not uniquely associated with the presence of a JAR, and, historically, probably served other functions, such as electrolocation and social behaviour. If this assumption is correct, then the basic mechanisms used to evaluate relations between amplitude modulation and timing differences might be an ancestral trait, which served as a preadaptation for the evolution of JARs. The validity of this hypothesis would be challenged if jamming avoidance was present in a common ancestor, and subsequently lost in *Sternopygus*. However, further comparative studies of the premotor circuitry indicate that this is not the case, as fish in different gymnotiform families seem to have evolved their JARs independently. For example, *Eigenmannia* uses the NE↑–PPn pathway to raise its EOD frequency (FIG. 2b), whereas *Apteronotus* produces similar frequency increases through the NE–SPPn circuit[34], which *Eigenmannia* uses to generate frequency decreases[30] (by $GABA_A$ (γ-aminobutyric acid type A)-mediated inhibition of the tonically active SPPn).

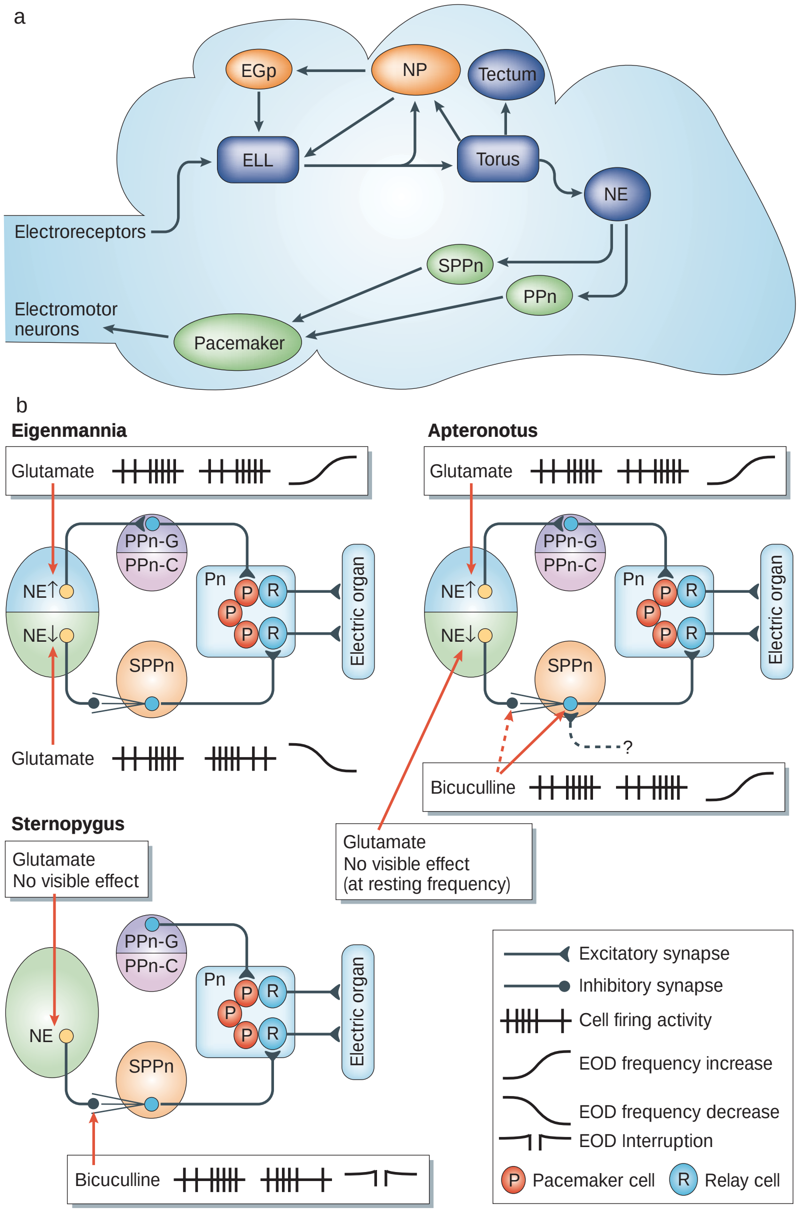


Figure 2 | **Electrosensory circuits. a** | Electrosensory pathway in *Eigenmannia*: ELL, electrosensory lateral line lobe; EGp, eminentia granularis pars posterior; NP, nucleus praeeminentialis; NE, nucleus electrosensorius; SPPn, sublemniscal prepacemaker nucleus; PPn, prepacemaker nucleus. Orange structures are involved in feedback; green structures represent descending control pathways. **b** | Premotor–motor circuits for controlling electric organ discharge (EOD) modulations in three genera of gymnotiform fishes. NE↑ and NE↓ regions of the NE, when stimulated by iontophoresis of glutamate in *Eigenmannia*, cause slow increases or decreases in the EOD frequency. When active, PPn-G (gradual) and PPn-C (chirp) (subdivisions of the PPn) elicit slow, smooth increases in EOD frequency or abrupt cessations of EODs, respectively. Cells in the NE↓ area make inhibitory contacts with the dendrites of SPPn neurons. Blocking inhibition at the SPPn (with bicuculline) causes EOD frequency increases in *Apteronotus* or large EOD frequency increases that culminate in interruptions in *Sternopygus*. Prepacemaker neurons project to the pacemaker nucleus (Pn), where they synapse with either pacemaker (P) or relay (R) cells.

How *Apteronotus* controls the function of its SPPn to raise its EOD frequency during JARs is unclear. These comparative findings support the hypothesis that sign-selectivity is an ancestral trait, which served as a preadaptation for the evolution of JARs.

Evaluations of relationships between amplitude modulation and timing differences might be fundamental for electrolocation and communication in all fish that produce periodic EODs, thereby providing a ready-made solution for the relative-frequency discrimination that is required to generate JARs. This hypothesis is supported by the finding that the African electric fish *Gymnarchus* also produces a JAR, and uses the same algorithm for discriminating relative EOD frequency as do the South American electric fish. Fish in these two orders evolved their active electric sensory systems, and therefore their JARs, independently. Consistent with this hypothesis of convergent evolution of JARs, the neural control of this behaviour in *Gymnarchus* is different from that of South American electric fish. For example, timing difference computations are carried out in lamina 6 of the 12-layered torus semicircularis of the gymnotiform midbrain[35], whereas in *Gymnarchus* similar comparisons occur in the inner-cell layer of the electrosensory lateral line lobe (ELL)[36,37], a medullary structure.

Together, these comparative data show that particular algorithms for the control of behaviour can be favoured across multiple cases of evolution of that behaviour, even though the selected algorithms are complex. This convergence or parallelism, and the evolution of the behaviour itself, might have been promoted by the presence of the mechanisms for evaluating amplitude modulation and timing difference information. Ultimately, therefore, the reasons why these fish use complex algorithms for the control of behaviour become clear when we consider the roles of historical forces (essential preadaptations) in the evolution of behaviour. Comparative studies can also reveal the diverse ways in which particular computations can be performed by neural circuits. Identifying the factors that govern why particular neural circuits are used is an important and interesting area of research.

Adaptive cancellation of sensory input

Another example of convergent processes in electrosensory systems is the adaptive cancellation of expected sensory input. All animals are faced with the problem of dissociating sensory information about their environment (exafference) from sensory information that results from their own motor activity (reafference)[38]. In electric fish, voluntary or involuntary movements and EODs cause expected self-stimulation of electroreceptors. External sensory input that is predictable because of its regularity of association with other input can also represent expected information. To attend selectively to unexpected exafferent signals, animals must eliminate the expected sensory components from the incoming stream[39]. Across three groups of fishes that have independently evolved electrosensory systems — Rajidae, Mormyridae and Apteronotidae — adaptive cancellation of expected sensory information is mediated by a common plasticity mechanism involving a parallel-fibre interface between primary sensory and cerebellar structures[8] (FIG. 3a,b).

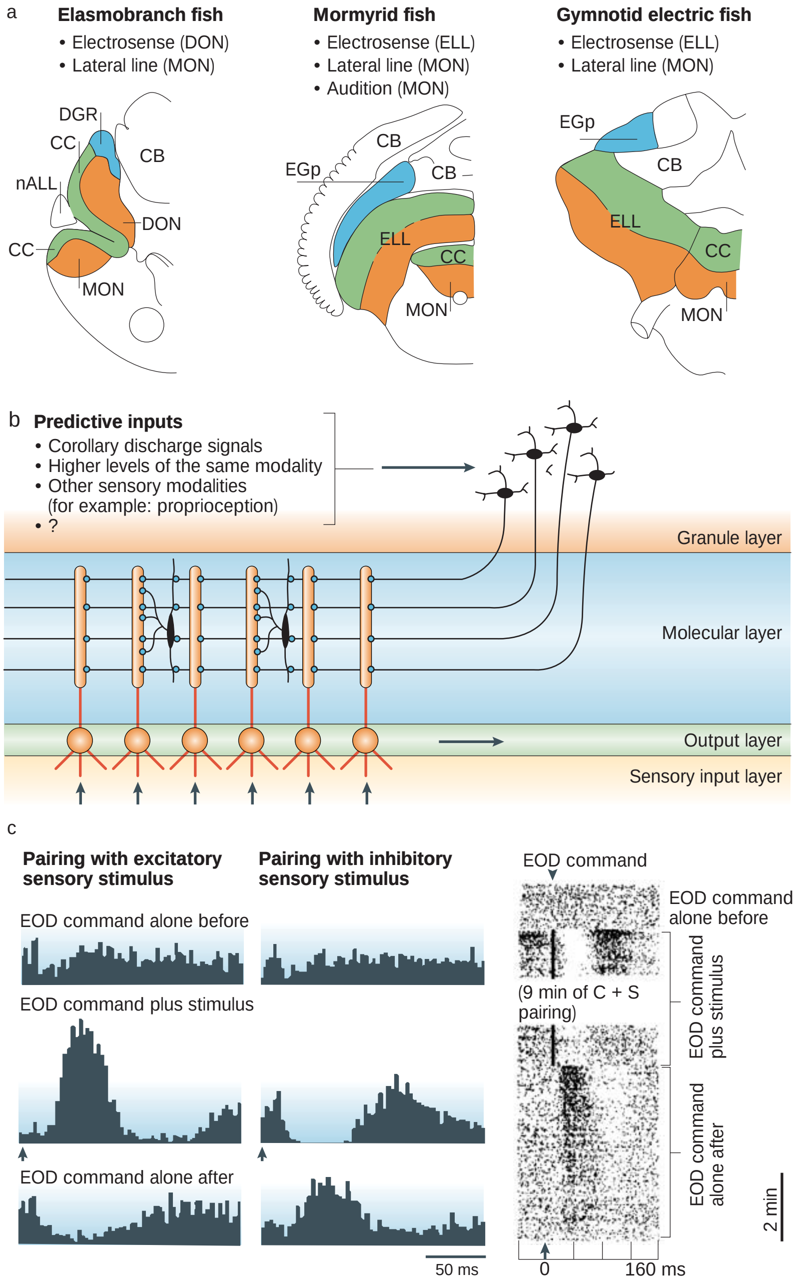


Figure 3 | **Adaptive filtering in electrosensory systems. a** | Schematic diagrams to show the boundaries of the electrosensory, lateral line/auditory and cerebellar structures in the hindbrains of skates (elasmobranch fish), mormyrid and gymnotid electric fish. Conventional cerebellum: CC, corpus cerebellum; CB, cerebellum. Sensory-associated cerebellum: EGp, eminentia granularis posterior; DGR, dorsal granular ridge. Primary central sensory structures: DON, dorsal octavolateral nucleus; ELL, electrosensory lateral line lobe; MON, medial octavolateral nucleus. **b** | The granule cells of sensory-associated cerebellar regions send parallel fibres to the 'molecular layer' of the sensory structures, where they synapse with the apical dendrites of sensory neurons and interneurons (such as stellate cells and Golgi cells). **c** | Right, raster plots of the spike activity of an ampullary-type neuron in a mormyrid fish; changes in activity over time (repeated trials shown as individual rows on the vertical dimension) reveal cancellation of expected electrosensory information. The timing of the central command for electric organ discharges (EODs) is marked by arrows; the electric organ itself was 'silenced' pharmacologically. An electrosensory stimulus that decreased the activity of this cell was paired (followed, vertical line) by EOD commands for 9 min. The sensory stimulus was then withheld, revealing command-related activity. Left, histograms of the activity of two neurons before pairing (top), during the beginning of pairing (middle) and in response to the EOD command alone directly following termination of the pairing (bottom). Sensory stimulation (arrow) increased the activity of one cell (far left), and decreased the activity of the other. **a** and **b** modified, with permission, from REF. 52 © (1999) Company of Biologists; panels in **c** provided by C. Bell.

Reafferent sensory activity in mormyrids. Cancellation of expected reafferent sensory information was first discovered in pulse-type mormyriform fish, which are useful for studying this process[40]. A modifiable cancellation process was later found in the ELL (FIG. 3a) of these fish[41,42]. Normally, each EOD activates several types of electroreceptor. These discharges can be blocked by neuromuscular antagonists, which allows investigators to control the timing and magnitude of sensory stimulation. In addition, information concerning the command for each EOD — a 'corollary discharge' — is sent by way of the paratrigeminal command-associated nucleus to the granule cell zone of the electrosensory cerebellum (FIG. 3b), which overlays the ELL (in the medulla). This corollary discharge input is used to generate a 'negative image' of the expected reafferent activity. If sensory stimulation is consistently paired with the EOD command for a period of time, the response of an ampullary-type ELL cell to the stimulus is progressively attenuated (FIG. 3c). Removing the sensory stimulus then reveals a command-associated response, which is the mirror image of the original sensory response, and negative images can cancel out either excitatory or inhibitory sensory input (FIG. 3c, left and central panels). Over time, if the command is not paired with the sensory stimulus, this response of the cell to the command also fades[43]. Therefore, the negative image of the sensory response represents a memory that is used quantitatively to eliminate the expected effects of the sensory stimulus, but still allows the cell to respond to unpredictable exafferent input.

Sensory activity arising from EODs is one form of reafferent information. Electroreceptors can also be activated as a consequence of movements of the animal[44]. As discussed below for skates, reafference stemming from respiration can also be adaptively cancelled.

Reafferent sensory activity in skates. Unlike the mormyriform and gymnotiform electric fish, skates (elasmobranches) rarely produce EODs. However, small currents that flow from the body through the gills, and that are modulated by the fish's respiratory movements, can modulate the activity of electroreceptors[45,46]. These electroreceptors are highly sensitive to the small, low-frequency electric signals that are emitted by the skates' prey. The respiration-related activity of electroreceptors represents self-induced noise that could obscure this exafferent information.

Over time, skates can construct a negative image of the reafference that is expected to result from respiratory movements[47,48]. In the dorsal octavolateral nucleus (DON) of the medulla (FIG. 3a), corollary discharge information concerning the respiratory motor commands is integrated with temporally correlated sensory activity. Importantly, the strength of the sensory input to each neuron is unaffected; only sensory activity that is time-locked to the ventilatory cycle is cancelled. As in mormyrids, neuromuscular antagonists can be used to block the sensory consequences of motor commands; in this case, gill movements are abolished, and the corollary discharge-driven negative image of the expected reafference can be recorded in isolation. Corollary discharges of motor commands have been recorded extracellularly in the dorsal granular ridge, which forms a cap over the DON. This granule cell region is the source of parallel fibre input to the apical dendrites of the principal cells in the DON, consistent with the hypothesis that adaptive changes in the strength and sign of command-related negative images result from plasticity at the synapses between parallel fibres and the DON cells.

These examples show that corollary discharges of motor commands can be used to adaptively cancel temporally correlated sensory input to medullary neurons. The negative (activity) image that is constructed can be adaptively adjusted to precisely cancel the expected reafference. In addition to motor commands, however, certain types of sensory activity can be used to cancel out other sensory input. Examples of this form of adaptive cancellation are seen in skates and gymnotiform electric fish.

Within and across-modality sensory input. Skates and gymnotiforms can use sensory input from the electrosensory or proprioceptive systems to predict, and therefore to cancel, the activation of electroreceptors[48–50]. For example, if focal electrosensory stimulation is paired with externally controlled movements of the fins or tail, over time the electrosensory responses of principal cells will gradually become smaller. These fin or tail flexions induce proprioceptor activity that can be measured in parallel fibre responses[51], and can predict associated electroreceptor activation. Similarly, focal electrosensory stimulation can be paired with more diffuse, broad-field modulations of the amplitude of an applied electric field. After several tens of minutes of pairing, the global stimulation alone elicits a pattern of activity that is inverted (negative image) with respect to that elicited by the previously paired focal stimulation. Because the predictive signal, manifested as parallel fibre activity, is in this case under the control of the experimenter (unlike EODs or respiration, which are initiated by the fish), it can be stopped once the negative image, resulting from the pairing regimen, has been formed. Under these conditions, where no updating of the negative image is required, the memory (negative image) persists for at least several hours.

Why would broad-field electrosensory or proprioceptive information be useful as a predictive signal for adaptive plasticity? One possibility is that this process continually equalizes the sensitivity of the cells in the first-order array. Gymnotiform fish, for example, regularly ‘wag’ their tails, thereby modulating the electric field strength and the activity of electroreceptors. If particular electroreceptors are more strongly excited by these modulations than their neighbours, over time this should be counterbalanced by the strengthening of a negative image input through the parallel fibre inputs (direct and indirect) to the dendrites of the ‘over-active’ neurons; a maintained ‘hot spot’ of activity is, in most cases, best interpreted as an inherent imbalance in the system that should be corrected.

In all three systems, adaptive cancellation of expected sensory input is believed to result from plasticity at the parallel fibre synapses onto the dendrites of first-order central neurons. Electrophysiological support for this model comes from studies that paired direct stimulation of parallel fibres with intracellular current injection and recorded the resulting excitatory postsynaptic potentials (EPSPs)[52,53]. When EPSPs from parallel fibre stimulation (the predictive input) preceded the depolarizing current injection, EPSP amplitude was depressed.

The evolution of adaptive cancellation. As shown above, investigators have made considerable progress in identifying how electric fish adaptively cancel expected sensory input. We can now ask why particular neural implementations of such cancellation have evolved. Skates, gymnotiforms and mormyriforms independently evolved their electric senses and organs. Considering the universal importance of tasks such as dissociating between exafferent and reafferent sensory information, and calibrating receptor sensitivity, it is understandable that these fish have convergently evolved adaptive cancellation mechanisms. However, it is remarkable that in all three cases the adaptive cancellation process seems to be mediated through plasticity at parallel fibre synapses onto cells in the primary central electrosensory areas. Why should this neural solution to the adaptive cancellation problem have been uniquely favoured? A likely explanation for this convergence is that cerebellar circuits are both phylogenetically very old and highly conserved in their properties. It seems that plasticity at cerebellar synapses has historically been important for adjusting the gain of neural responses. Because this role of cerebellar circuits predated the evolution of most electrosensory systems, it seems likely that it was an ideal and ready-made neural solution. Adaptive plasticity in the lateral line systems of fish provides further support for this idea[8].

Implications and future directions

The comparative study of the neural control and evolution of behaviour in electric fish has just begun. For example, only one study has addressed the issue of sign selectivity in the diencephalon of *Sternopygus*, and none has been done in *Apteronotus*. The details of the comparative circuitry between NE areas and prepacemaker regions can be addressed by intracellular recording and labelling studies. This investigation is in its infancy, and will be essential for determining the changes in physiology and microcircuitry that were required for the evolution of JARs. To complete this understanding we must also investigate the constraints on this evolution. For example, why did *Aperonotus* not use its PPn region to control the smooth increases in EOD frequency that characterize its JAR? And why did *Sternopygus* fail to evolve a JAR? It will also be important to determine whether the mechanisms for sign selectivity are similar in *Gymnarchus*[54] and the gymnotiforms — are there integrative mechanisms that are favoured for performing computations of this general class? Such information could have widespread importance for understanding brain function.

To date, only one study of the responses of premotor neurons (PPn and SPPn) to sensory stimuli has been made[55]. These extracellular recordings from the PPn of *Eigenmannia* showed that single neurons respond highly selectively to negative Df stimuli, regardless of the orientation of the external jamming field. The capacity of these cells to differentiate in their firing rate between negative and positive Df stimuli is similar to the discriminative abilities of the fish itself[55]. Further neurophysiological studies of these premotor regions in other species are required. Recordings from the SPPn region in *Eigenmannia* and in *Apteronotus* should reveal whether there are other 'recognition units'.

Comparative studies of adaptive cancellation in electric fish have enhanced our understanding of how predictive information is used in conjunction with sensory afference to generate memories that permit expected input to be excluded. Future work in these systems will provide an excellent opportunity for us to understand how cerebellar circuits participate in these processes. Many questions still remain. In addition to direct parallel fibre input to first-order central sensory cells, there is indirect, presumably inhibitory, input. It remains to be seen whether inhibitory synapses onto these central neurons, for example from stellate cells, are also plastic. If they are, then inhibition stemming from parallel fibre activity might also contribute to the modifiable cancellation signal. Another important systems-level question is what information the individual parallel fibres are carrying. The specificity of adaptive cancellation indicates that the activity of individual granule cells is likely to represent highly specific information — that is, they should use a sparse code. It is also important to know the level of spontaneous activity in these cells and whether activity related to predictive inputs changes over time. Only recently, with the development of 'whole-cell' intracellular recording with patch-type pipettes, has it been possible to record intracellularly from granule cells *in vivo*[56]. Preliminary findings indicate that there is a sparse coding of predictive signals in the granule cell population (D. Bodznick and G. J. R., unpublished observations). Finally, the synaptic plasticity that underlies adaptive cancellation is known to be Ca^{2+} dependent[44], but further work is needed to identify the mechanisms that are responsible for adjusting synaptic efficacy.

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The author declares no competing financial interests.

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