*J. exp. Biol.* **146**, 229–253 (1989)
*Printed in Great Britain* © *The Company of Biologists Limited 1989*



# SENSORY CODING AND COROLLARY DISCHARGE EFFECTS IN MORMYRID ELECTRIC FISH

BY CURTIS C. BELL

*Robert S. Dow Neurological Sciences Institute, Good Samaritan Hospital and Medical Center, 1120 NW 20th Avenue, Portland, OR 97209, USA*

## Summary

Weakly electric fish use their electrosensory systems for electrocommunication, active electrolocation and low-frequency passive electrolocation. In electric fish of the family Mormyridae, these three purposes are mediated by separate classes of electroreceptors: electrocommunication by Knollenorgan electroreceptors, active electrolocation by Mormyromast electroreceptors and low-frequency passive electrolocation by ampullary electroreceptors. The primary afferent fibres from each class of electroreceptors terminate in a separate central region. Thus, the mormyrid electrosensory system has three anatomically and functionally distinct subsystems.

This review describes the sensory coding and initial processing in each of the three subsystems, with an emphasis on the Knollenorgan and Mormyromast subsystems. The Knollenorgan subsystem is specialized for the measurement of temporal information but appears to ignore both intensity and spatial information. In contrast, the Mormyromast subsystem is specialized for the measurement of both intensity and spatial information. The morphological and physiological characteristics of the primary afferents and their central projection regions are quite different for the two subsystems and reflect the type of information which the subsystems preserve.

This review also describes the electric organ corollary discharge (EOCD) effects which are present in the central projection regions of each of the three electrosensory subsystems. These EOCD effects are driven by the motor command that drives the electric organ to discharge. The EOCD effects are different in each of the three subsystems and these differences reflect differences in both the pattern and significance of the sensory information that is evoked by the fish's own electric organ discharge. Some of the EOCD effects are invariant, whereas others are plastic and depend on previous afferent input.

The mormyrid work is placed within two general contexts: (a) the measurement of time and intensity in sensory systems, and (b) the various roles of motor command (efferent) signals and self-induced sensory (reafferent) signals in sensorimotor systems.

## Introduction

Weakly electric fish are nocturnal animals, and this nocturnal life is made

Key words: electrosensory, electroreception, efference copy, central expectation, plasticity, timing, intensity.

possible by their electrosensory system. The electrosensory system has a motor side, the electric organ, and a sensory side, the electroreceptors. The electric organ discharge (EOD) of weakly electric fish is too weak to use as a weapon and the system has three other roles: *active electrolocation*, in which nearby objects are sensed by the way they affect the pattern of current flow from the fish's own EOD; *electrocommunication*, in which EODs are emitted and received as a means of communication between electric fish; and *low-frequency passive electrolocation,* in which the low-frequency electric fields that all animals generate in water are sensed. Echolocating bats are also nocturnal animals and use their non-visual sensory system in three very similar ways: for echolocation of objects, for auditory communication with other bats, and for sensing the general sounds of the environment.

In electric fish of the family Mormyridae each role of the electrosensory system is mediated largely or exclusively by a separate class of electroreceptors and its associated central structures (Bennett, 1965; Szabo & Fessard, 1974; Bell, 1986*b*). The three classes of electroreceptors are: Mormyromasts, which mediate active electrolocation; Knollenorgans, which are involved in electrocommunication; and ampullary electroreceptors, which mediate low-frequency passive electrolocation. The Mormyromasts and ampullary electroreceptors may also play some role in electrocommunication, but such a role has not been established.

Primary afferent fibres from electroreceptors terminate centrally in the electrosensory lateral line lobe (ELL) (Maler *et al.* 1973; Bell & Russell, 1978*b*). Mormyromast and ampullary afferents terminate in separate parts of the cerebellum-like cortex of ELL, whereas Knollenorgan afferents terminate in a histologically simpler region, the nucleus of ELL (NELL).

Afferents from all three types of electroreceptors respond to the fish's own EOD (Szabo & Hagiwara, 1967; Bell & Russell, 1978*a*; Bell, 1986*b*). Each region of ELL is therefore affected at the time of the EOD by self-induced afferent activity. (Such self-induced activity was termed 'reafferent' by von Holst & Mittelstaedt, 1950.) Each region of ELL is also affected at the time of the EOD, however, by corollary discharge signals associated with the motor command that drives the electric organ (Bennett & Steinbach, 1969; Zipser & Bennett, 1976*b*; Bell, 1982). The electric organ corollary discharge (EOCD) and reafferent signals are shown diagrammatically in Fig. 1. The EOCD signals have different time courses and effects in each region. Moreover, some of the EOCD signals are invariant, whereas others are modified by previous sensory experience.

*The first goal* of this review is to describe what is known about the sensory coding and initial stages of central processing in each of the three electrosensory subsystems of mormyrid fish, with an emphasis on the time-measuring Knollenorgan and the intensity-measuring Mormyromast subsystems. The morphological and physiological specializations in each subsystem are compared with each other and with the time- and intensity-measuring parts of other sensory systems.

*The second goal* of this review is to describe the corollary discharge effects on sensory input which occur in each region of the mormyrid ELL. The general roles

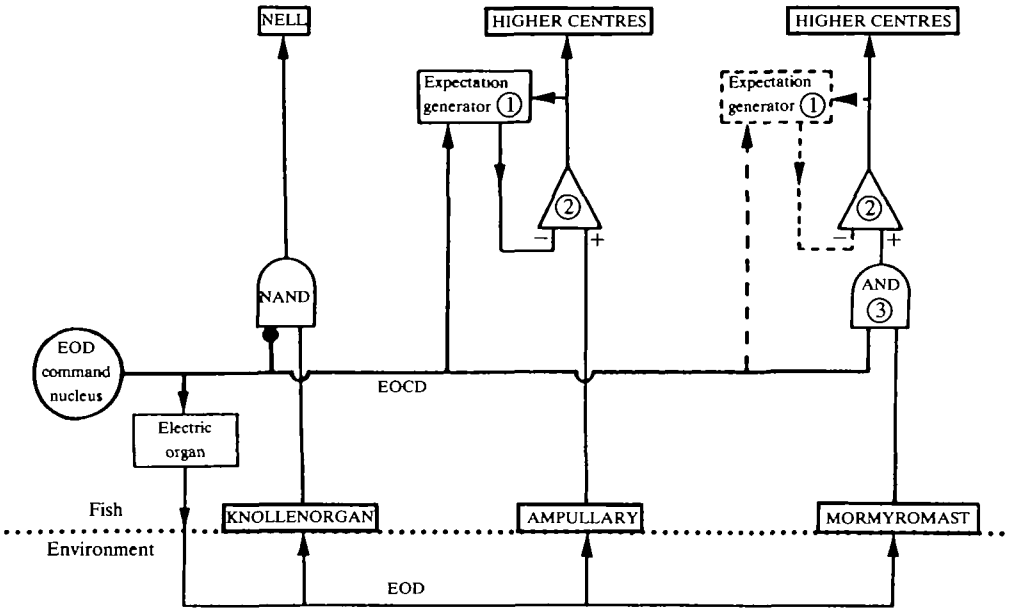



Fig. 1. Diagram showing the interactions between electric organ discharge (EOD)-evoked reafferent input and electric organ corollary discharge (EOCD) signals for all three electroreceptor systems. The EOD command nucleus on the left elicits both EOCD and EOD signals. The EOD is generated by the electric organ and evokes reafferent responses in all three types of electroreceptor afferents. In the Knollenorgan region, reafferent input is blocked by the EOCD (NAND gate). In the ampullary region, a central expectation about reafferent input (modifiable EOCD), that is based on past input, is stored in an 'expectation generator' and is released from storage by an EOCD signal. The expectation is subtracted from actual input in the electrosensory lateral line lobe (ELL) (2) and is updated by the output of ELL. A similar process has now been identified in the Mormyromast region. This adaptive process in the Mormyromast region is shown preceded by a fixed facilitation (AND gate) (from Bell, 1986*a*).

of corollary discharge signals or efferent feedback in comparison to reafferent feedback are also discussed.

## Mormyrid electrosensory system

### *Electrocommunication and the Knollenorgan subsystem*

The amplitude and waveform of an individual fish's EOD do not vary so long as the electrical load on the electric organ does not change (Bell *et al.* 1976). The waveform of the EOD is different, however, in different species and in the two sexes of some species (Bennett, 1971*a*; Hopkins, 1986). Both the waveform of single EODs and the sequence of intervals between successive EODs appear to convey information between fish (Hopkins, 1986; Hopkins & Bass, 1981; Kramer, 1979; Moller & Bauer, 1970; Bell *et al.* 1974).

Behavioural studies by Hopkins & Bass (1981), for example, indicate that sex discrimination may be based on the duration of the EOD in some mormyrid species. In the species which they studied, *Brienomyrus brachyistius (triphasic)*, the EOD of the female is 0·4 ms in duration whereas the EOD of the male is 1·6 ms in duration. Hopkins & Bass found that the male responds to a simple square wave of 0·4 ms as if a female were present but responds much less or not at all to square waves of 0·1 or 1·6 ms. Hopkins (1986) has suggested that the leading and trailing edges of other fishes' EODs activate afferents on opposite sides of the fish or on opposite ends, and that the interval between the leading and trailing edges is computed centrally. Such temporal discriminations would have to be made over a wide range of stimulus intensities to be useful, and the responsible sensory system would have to be able to disregard the effects of changes in stimulus intensity. The sensory system would also have to transmit very accurately the critical temporal features of the stimulus.

*Coding and preservation of temporal information in the Knollenorgan subsystem*

Timing information about the stimulus is efficiently encoded at the electroreceptor and is well-maintained centrally, owing to various specializations of the Knollenorgan pathway. In comparison, intensity information about the stimulus appears to be largely ignored at the level of the Knollenorgan electroreceptor. Finally, spatial information about the stimulus, although present in the primary afferents, appears to be only poorly maintained centrally. The poor maintenance of spatial information suggests that the Knollenorgan system might not be very good at localizing stimuli, but this has not been tested behaviourally.

Knollenorgan electroreceptors and primary afferents are well suited for the encoding of temporal information. Knollenorgans are phasic receptors and respond only to transients. The primary afferent response has a very low threshold (0·1 mV across the skin) and is usually a single spike at a short fixed latency (Bennett, 1965). Increasing stimulus intensity to many times threshold has surprisingly little effect on the response – no additional spikes are added and there is only a small reduction in latency, of 0·2–0·4 ms, for near-threshold stimuli (Steinbach & Bennett, 1971).

Primary Knollenorgan afferents are large (6–8 $\mu$m in diameter) and branch only a few times within the nucleus of the ELL (NELL; see Fig. 5, right side) where they terminate. The branches remain both thick (1–4 $\mu$m) and myelinated right up to the terminals on NELL cells (Szabo *et al.* 1983; Mugnaini & Maler, 1987). The afferent terminals are large and electron microscopy shows that they are of a mixed chemical–electrical morphology (Szabo *et al.* 1983; Mugnaini & Maler, 1987). Somatotopy is present in the mapping of the skin onto the nucleus but it is only very rough (Bell & Russell, 1978*b*; Bell & Grant, 1989).

The cells of NELL are rounded and adendritic and their axons project to the mesencephalon (Enger *et al.* 1976). There are no recurrent collaterals or interneurones in NELL, and thus no anatomical indication of lateral inhibition. The long initial segment of the axon and that part of the cell body not covered by

primary afferent terminals are densely covered with small chemical synaptic boutons. These boutons contain glutamic acid decarboxylase (GAD) (Mugnaini & Maler, 1987; Denizot *et al.* 1987) and are probably responsible for a corollary discharge inhibition in NELL (Bell & Grant, 1989).

Intracellular recordings from NELL cells reveal two types of synaptic potentials: (1) brief all-or-none excitatory postsynaptic potentials (EPSPs) that are evoked by stimulation of individual electroreceptors, and (2) electric organ corollary discharge (EOCD) inhibitory postsynaptic potentials (IPSPs) that are driven by the EOD motor command (Bell & Grant, 1989). The synaptic potentials are caused by inputs to NELL cells, but are also observed in intracellular recordings from Knollenorgan afferent fibres near NELL because of the electrical synapses which act as a kind of electrical window between pre- and postsynaptic elements (Fig. 2). A large afferent spike is also observed inside the fibre, of course (Fig. 2Biii).

The peripherally evoked EPSPs are electrotonic and represent the arrival of an impulse at the terminals of a Knollenorgan afferent. The latencies of these EPSPs to suprathreshold stimuli show almost no discernible variation and the EPSPs follow repetitive stimulation up to frequencies as high as 500 Hz (Fig. 2C). This reliability of transmission results from the properties of the Knollenorgan electroreceptor, the axonal arbor of the primary afferent and the electrical synapses onto NELL cells. The thickness and myelination of the preterminal fibres in the axonal arbor ensure minimal variability in conduction time and minimal refractory effects on impulse propagation (Paintal, 1966). Similarly, electrical transmission shows little variability and refractoriness in comparison with chemical transmission (Bennett, 1977).

The peripherally evoked EPSPs in NELL are large and rise rapidly from the baseline, ensuring that time to threshold will be minimally affected by noise, and thus less variable. The size and rapid rise time of the EPSP are consequences, presumably, of strong current sources in the large terminals and preterminal fibres, and of the rounded adendritic postsynaptic cell bodies. Such cell bodies will yield minimal electrotonic delays and maximal rise times.

The physiological findings are consistent with the anatomical finding of poor somatotopy in indicating that the Knollenorgan subsystem does not maintain and analyse detailed spatial information. Selective stimulation of any one of two or three different Knollenorgan electroreceptors can evoke a postsynaptic spike in a NELL cell (Bell & Grant, 1989). This indicates a loss of spatial information, since such cells would not discriminate among electroreceptors at different locations. Furthermore, stimulation of electroreceptors near the ones giving rise to EPSPs does not reveal any sign of lateral inhibition, a finding consistent with the lack of anatomical evidence for such inhibition. Thus, the Knollenorgan subsystem, unlike sensory systems where spatial information is critical, does not make use of local contrast enhancement.

The Knollenorgan subsystem from electroreceptor to medulla is highly specialized for the encoding and transmission of information about the timing of brief electrical transients, such as those which occur in the EODs of electric fish.

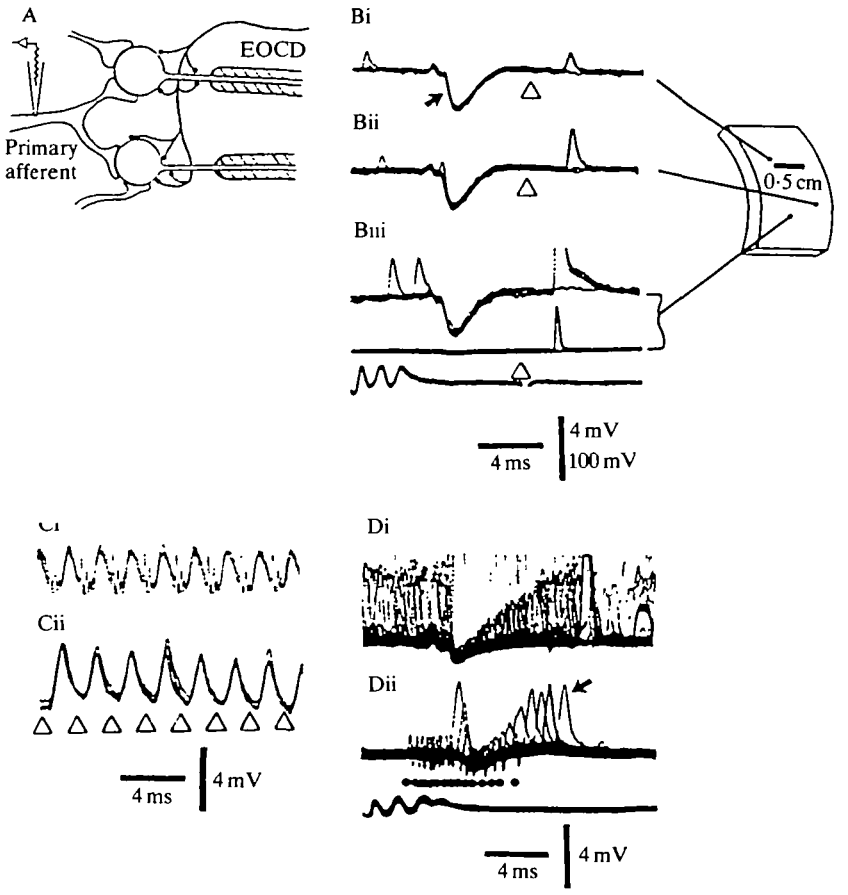



Fig. 2. Intracellular recordings from Knollenorgan afferents. (A) Schematic drawing. Primary Knollenorgan afferents and fibres responsible for EOCD inhibition (EOCD) end on NELL cells. (B) Two electrotonic EPSPs (i and ii) and the large afferent spike (iii) evoked by stimulation of different skin regions (as indicated in drawing on right). Arrow points to EOCD IPSP. Sweeps are superimposed and triggered by command signal (bottom trace). (C) High following frequency of electrotonic EPSPs in response to local electrosensory stimuli. Two EPSPs from two different fibres (i and ii) each follow the stimulus to 500 Hz. Time of stimulus is shown by shock artefacts in i and by open triangles in ii. (D) Superimposed traces of EPSPs show time course of inhibition. The top trace shows spontaneous EPSPs, whereas the middle trace shows evoked EPSPs (time of stimuli indicated by black dots and small shock artefacts). Large afferent spikes are visible as vertical rows of fine dots in the top trace and are not inhibited. The effects of electrosensory stimuli are visible on the right of the same trace. Arrow in ii points to EPSP. Sweeps are triggered by command signal (from Bell & Grant, 1989).

Intensity and spatial information about such stimuli is ignored or poorly maintained, however. NELL cells appear to act as simple relays of timing information rather than as feature detectors. The analysis of pulse duration and

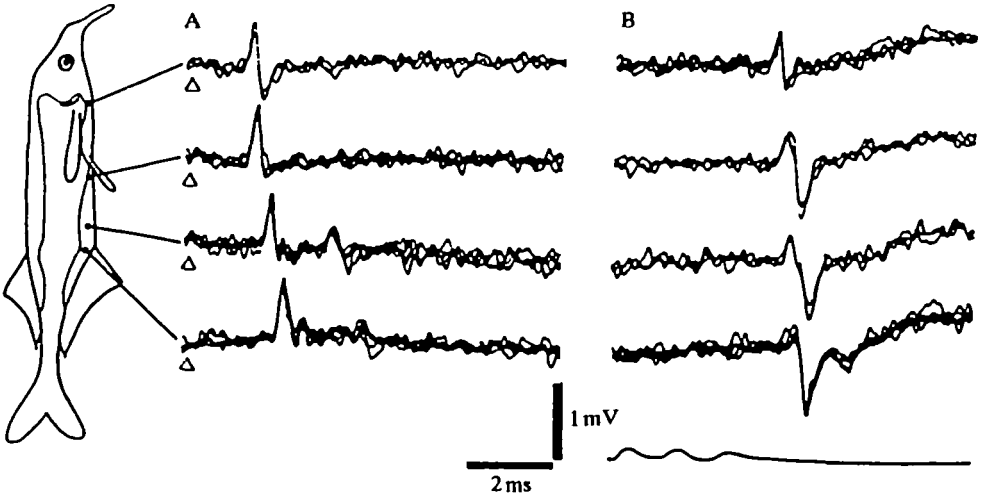



Fig. 3. Corollary discharge and electrosensory evoked field potentials in NELL. The most rostrally recorded potentials are at the top and the most caudally recorded ones are at the bottom. (A) Potentials evoked by local electrosensory stimuli at the sites indicated in the drawing on the left. Sweeps are initiated by the stimuli. (B) Corollary discharge potentials recorded at the same NELL sites as the potentials in A. Sweeps are triggered by the EOD command signal shown in the bottom trace. Vertical calibration bar is for evoked potential traces only. EOD command signal is about 150 $\mu$V in amplitude (from Bell & Grant, 1989).

other stimulus features must occur at mesencephalic and higher levels (Bell, 1986*b*; Mugnaini & Maler, 1987), but has not yet been examined.

*Corollary discharge effects in the Knollenorgan system*

Most Knollenorgan afferents respond to the fish's own EOD with a single impulse at a short, fixed latency of a few milliseconds (Szabo & Fessard, 1965; Bell, 1986*b*). The fish's own EOD is a strong stimulus and each occurrence of the EOD probably evokes responses from most or all of the sensitive Knollenorgan afferents. This large reafferent response will occur several times per second and could greatly interfere with the detection and measurement of weak signals from other fish. The problem is solved by a brief and precisely timed EOCD-driven inhibition which appears to block completely the reafferent response (Bennett & Steinbach, 1969; Zipser & Bennett, 1976*b*; Russell & Bell, 1978; Szabo *et al.* 1979; Bell & Grant, 1989). The EOCD inhibition of Knollenorgan reafference is shown as a NAND gate on the left of Fig. 1.

Such corollary discharge effects are examined in fish in which the effect of the motor command on the electric organ is blocked and in which the motor command ('command signal') continues to occur spontaneously, in isolation from the normally consequent EOD (examples of the command signal are shown in the bottom traces of Figs 2B,D, 3B, 7B,C). The EOD occurs at a fixed latency of

about 2 ms following the motor command in normal fish where the effect of the motor command is not blocked.

The cellular basis for the EOCD inhibition is an EOCD-driven IPSP in NELL cells (Bell & Grant, 1989). The IPSP is also observed inside primary Knollenorgan afferents because of the electrical synapses (Fig. 2B), as mentioned in the previous section. The latencies are such that reafferent input evoked by the EOD arrives during the peak of the EOCD inhibition, as required for a blockade. The EOCD blockade has been confirmed in discharging fish by recording in the mesencephalic nucleus where axons from NELL terminate (Szabo *et al.* 1979). The blockade of the reafferent response to the EOD is one important argument for concluding that Knollenorgans are not involved in active electrolocation.

The duration of complete blockade is remarkably brief, only 1–2 ms, and confined to the peak of the IPSP in NELL cells (Fig. 2D). This duration appears to be sufficient to block the reafferent response, however, because of the brevity and fixed latency of the Knollenorgan response.

The latency of the EOCD effect is remarkably constant for a given cell or a given location in NELL (see superimposed traces in Fig. 2B). The latency of the EOCD effect is about 1 ms shorter at the rostral end of NELL than at the caudal end, however (Fig. 3B). This variation in latency corresponds roughly to a similar variation in latency for the Knollenorgan afferent response (Fig. 3A). The variation in afferent response latency occurs because afferents from the head terminate rostrally, whereas afferents from the tail terminate caudally, and conduction times are less for afferents from the head. Thus, the spatial distribution of EOCD latencies in NELL shows a rough correspondence to the spatial distribution of EOD-evoked reafferent latencies (Bell & Grant, 1989).

The covariation in latency between the EOCD inhibition and the reafferent response allows the inhibition to be as brief as possible and still block the reafferent response. A brief EOCD inhibition means minimal interference with the task of the Knollenorgan system, which is to detect external stimuli.

The systematic rostrocaudal increase in latency of the EOCD effect is probably due to central conduction time. The fibres responsible for the EOCD inhibition descend from a small sublemniscal nucleus rostral to ELL (Bell *et al.* 1981; Mugnaini & Maler, 1987). The difference in central conduction time to the rostral and caudal NELL, for these fine fibres which conduct over a short distance, appears roughly to match the difference in peripheral conduction time for the much larger primary Knollenorgan afferents which conduct over a long distance.

The EOCD inhibition in NELL matches the reafferent EOD response in latency, in duration and, roughly at least, in the spatial distribution of latencies. The EOCD inhibition appears to be relatively invariant or 'hard-wired', since it could not be modified during the course of electrophysiological experiments lasting several hours (Bell & Grant, 1989). Neither extensive pairing with an electrosensory stimulus nor lack of pairing produced any noticeable effect. This invariance is in marked contrast to modifiable EOCD effects which have been observed in the ampullary and Mormyromast systems.

*Low-frequency passive electrolocation and the ampullary system*

All aquatic animals generate electric fields in their near environment. The most important of these fields in terms of strength or spatial extent are low-frequency fields in the range 2–20 Hz (Kalmijn, 1974). The fields may be near direct current at their source but are converted to low frequencies by movement, including respiratory movement, of the animals. Many groups of fishes and amphibians have specialized electroreceptors, known as ampullary electroreceptors, for measuring these electric fields (Kalmijn, 1974). Afferents from ampullary electroreceptors discharge tonically and the discharge frequency is modulated up and down by external electrical fields. One species of mammal, the platypus, has also been shown to be electroreceptive (Scheich *et al.* 1986).

Afferents from ampullary electroreceptors in mormyrids terminate centrally in the ventral lateral zone of the cortex of ELL (see Fig. 5, right side; Bell, 1982). Central processing of information from the ampullary type of electroreceptor has been studied more extensively in non-electric fish, such as catfish (McCreery, 1977) and elasmobranchs (Montgomery, 1984), than in electric fish. A modifiable EOCD has been identified, however, in the ampullary region of the mormyrid ELL (Bell, 1982).

The fish's EOD evokes a reafferent response in its own ampullary afferents, usually an acceleration followed by a deceleration in the tonic discharge rate (Bell & Russell, 1978*a*). The ampullary reafferent response, unlike the Mormyromast reafferent response, is little affected by nearby objects and cannot be used, therefore, for active electrolocation (Bell & Russell, 1978*a*). The ampullary reafferent response should be viewed, like that of the Knollenorgan reafferent response, as a potentially disruptive signal that could interfere with the detection of external signals of interest.

The potentially disruptive effects of the ampullary reafferent response are nullified or minimized by the modifiable EOCD in the ampullary region of ELL (Bell, 1982). A simple EOCD inhibition of the reafferent response, such as occurs in the Knollenorgan region, would not be appropriate in the ampullary region because the response lasts about 100 ms. A blockade of that duration, occurring with each EOD, would make the sensory system useless since EODs are often emitted at rates higher than 10 Hz. Instead, the EOD motor command elicits a kind of negative image of the reafferent response that has occurred in the recent past. This negative image of the expected reafferent response is summed with the actual reafferent response in cells of the ampullary region of ELL, reducing the potentially disruptive effects of the reafferent response. The process is illustrated in the centre of Fig. 1.

The most striking feature of the EOCD in the ampullary region is its modifiability. When the sensory input that follows the motor command (i.e. the reafferent input) changes, the EOCD also changes and in a corresponding manner. The EOD command alone does not usually elicit any response from ELL ampullary cells as long as no electrosensory stimuli have been given for several minutes (Fig. 4, top). Pairing an electrosensory stimulus that affects the cell with

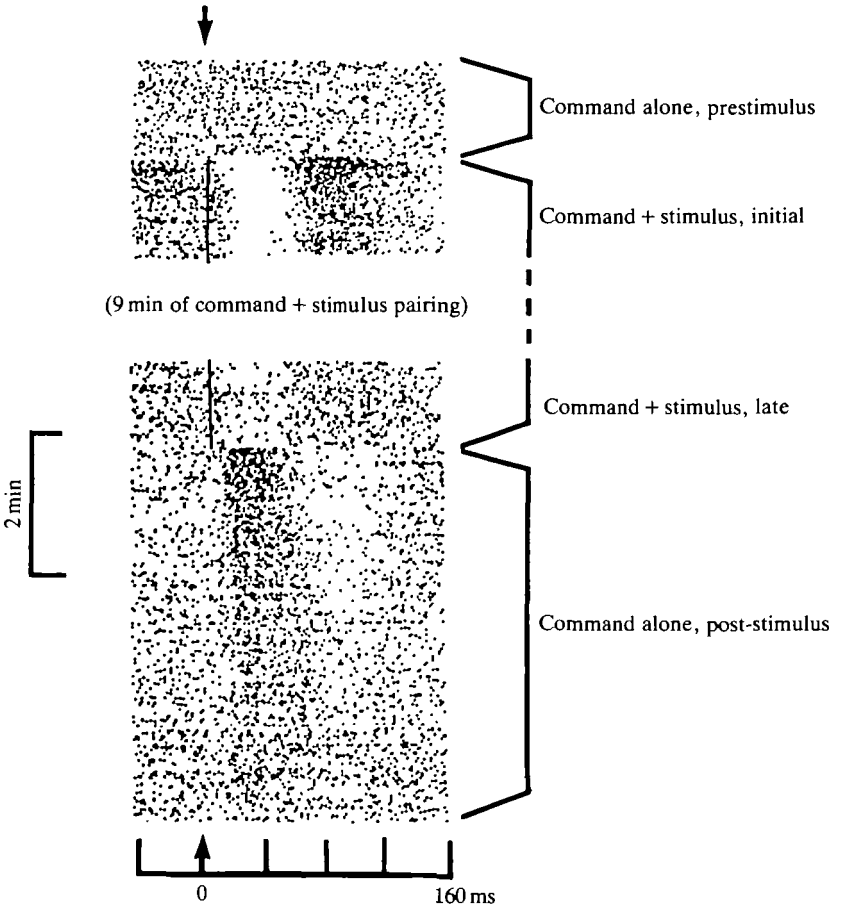



Fig. 4. Raster display showing the development and subsequent disappearance of a response to command alone for a cell in the ampullary region of ELL. Downward arrow at top of figure and upward arrow at the bottom indicate the time of occurrence of the EOD motor command. The presence of a stimulus is indicated by a vertical black line in the raster display. The effect of command alone before pairing with a stimulus, the initial effect of command plus stimulus, the effect of command plus stimulus after 11 min of pairing and the effect of command alone after pairing with a stimulus are shown (from Bell, 1986*b*).

the EOD motor command for several minutes leads to a reduction of the effect of the stimulus plus command (Fig. 4, middle). This reduction is due to the development of a new response to the command which is opposite to the effect of the stimulus. The effect of the command alone can be seen in isolation by simply turning off the stimulus (Fig. 4, bottom).

The modified EOCD is a faithful negative image of the temporal and spatial pattern of sensory input that has been associated with the EOD motor command. Alterations in the amplitude, polarity (acceleration or deceleration in discharge

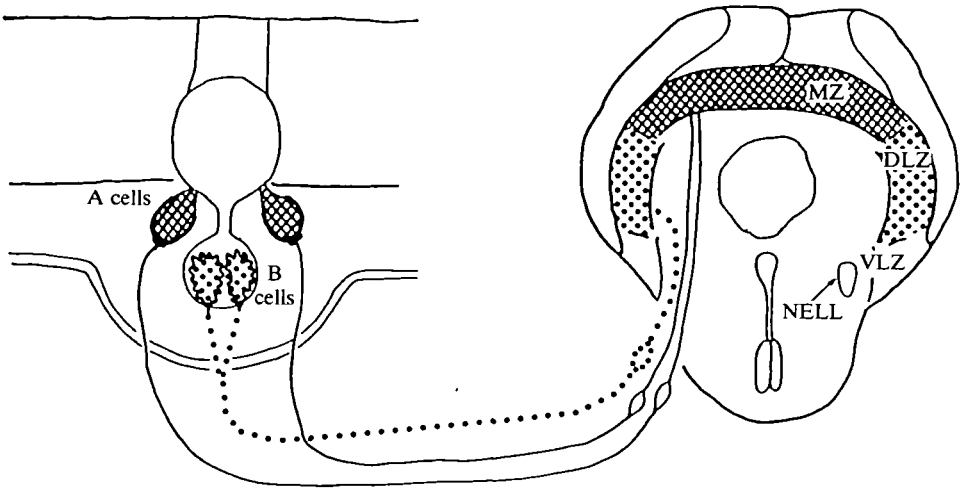



Fig. 5. Diagram illustrating the relationship between the peripheral cell of origin and the central zone of termination for the two types of Mormyromast afferents. The different regions of ELL are indicated: DLZ, dorsolateral zone of cortex; MZ, medial zone of cortex; VLZ, ventrolateral zone of cortex; NELL, nucleus of ELL (from Bell *et al.* 1989).

rate), time course and spatial distribution of the paired sensory input result in corresponding changes in the modifiable EOCD.

The newly developed effect of the command disappears within a few minutes in the absence of sensory input (Fig. 4). This disappearance is not due to a simple passive decay of a stored pattern, but is instead due to the active rematching of the new (and flat) pattern of afferent input which is present after turning off the stimulus. The modified EOCD does not disappear if active rematching is prevented for 30 min by injecting local anaesthetic into the command nucleus (Bell, 1986*a*). Nothing is known at present about the site and mechanism of storage of the modifiable EOCD.

Although small objects do not have much effect on the responses of ampullary afferents to the fish's own EOD, major environmental changes, such as changes in water conductivity or proximity of large non-conducting surfaces, will affect these reafferent responses. Modifiability of the EOCD ensures a match between the reafferent response pattern and the EOCD pattern, so that the effect of the reafferent response will continue to be minimized in spite of environmental changes.

### *Active electrolocation and the Mormyromast system*

The pattern of current flow through the skin that is caused by the fish's own EOD is influenced by nearby objects with impedances that are different from that of water. The task of the active electrolocation system is to measure this two-dimensional pattern of current flow and to construct from it a three-dimensional

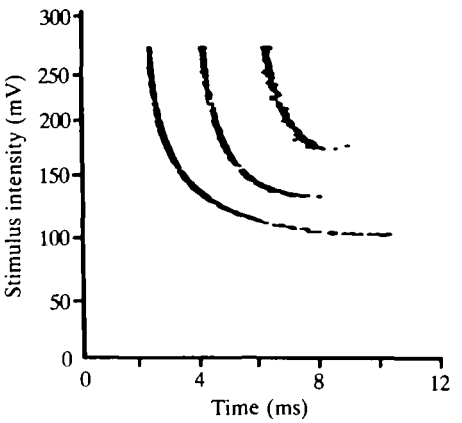



Fig. 6. Response of a Mormyromast afferent fibre as a function of stimulus intensity. Raster display in which each dot represents a spike in the response to an electrosensory stimulus given at time zero. Positions on the abscissa show the times of the different spikes in a response (1, 2 or 3 spikes per response in this fibre). Positions on the ordinate show the stimulus intensities, in millivolts across the skin, at which the responses were evoked. Note the smooth change in latency of the first spike as stimulus intensity is increased. The stimulus was a square wave of 10 ms duration.

world of objects in the near environment. The critical stimulus features, therefore, are stimulus intensity and its spatial distribution.

*Coding of stimulus intensity in Mormyromast afferents*

Mormyromast electroreceptors are well suited for measuring the local intensity of self-induced current flow in active electrolocation. Unlike Knollenorgan afferents, Mormyromast afferents show a smoothly graded responsiveness to stimuli of different intensities (see Fig. 6). Moreover, the responses of Mormyromast afferent fibres to the fish's own EOD are markedly affected by the presence of nearby objects (Szabo & Hagiwara, 1967; Bell & Russell, 1978*a*).

The Mormyromast is unique among electroreceptors in having two types of sensory cells, the A and B sensory cells of Szabo & Wersall (1970). The two cell types are distinct in morphology, location within the electroreceptor organ and primary afferent innervation (Fig. 5). Recent anatomical work has shown that primary afferents from type A cells project to the medial zone of ELL cortex, whereas afferents from type B cells project to the dorsolateral zone of ELL cortex (Fig. 5; Bell *et al.* 1989). Both projections have a precise somatotopic organization. These anatomical results indicate the presence of two Mormyromast submodalities which are separate at the electroreceptor, primary afferent and ELL levels. Anatomical connections between the two ELL zones (Bell *et al.* 1981) indicate that information from the two types of sensory cells is partially integrated at the level of ELL, but the mechanism and utility of this integration is not known.

Physiological recordings indicate some clear differences between the two types of afferents in threshold, maximum number of spikes per response, strength–duration curves, recovery following subthreshold stimuli and tuning curves (C. C. Bell, in preparation). But which, if any, of these differences are critical for the system is not known.

The variations in afferent response between threshold stimulus intensities and stimulus intensities which yield maximum responses are quite similar for the two types of afferents, although the threshold levels are different. The responses at threshold are single spikes at latencies of 9–12 ms. Increases in stimulus intensity cause smooth decreases of 7–9 ms in the latency of the first spike as well as the addition of more spikes to the response (Fig. 6). Afferents from type A cells have a maximum of 2–4 spikes and afferents from type B cells have a maximum of 4–8 spikes (C. C. Bell, in preparation). In each type of afferent, the maximum responses are obtained at intensities that are 2–3 times the intensity at threshold. The marked latency shifts with small changes in stimulus intensity make the Mormyromast response a poor measure of stimulus timing.

Szabo & Hagiwara (1967) suggested some years ago that latency might be the critical means of coding stimulus intensity in Mormyromast afferents, and several factors support this suggestion for both types of afferents.

(1) Stimulus intensity maps onto the latency of the first spike with great precision and without discontinuities.

(2) The alternative codes of spike number and spike frequency are discontinuous measures of stimulus intensity, changing abruptly with each additional spike. Moreover, spike number or spike frequency could not be used to measure intensities below the threshold for a second spike, a range which includes as much as one-third of the total dynamic range and within which first-spike latency varies continuously (Fig. 6).

(3) The alternative of a multifibre code, in which stimulus intensity is measured by the number of active fibres, is probably used by the system, at least in part. But Mormyromast electroreceptors on the trunk are rather far apart (1–2 mm), and complete reliance on a multifibre code would bring with it a significant degradation in spatial resolution. In contrast, a latency code would give a very accurate measure of stimulus intensity at a single point on the skin surface.

(4) Two recent results from intracellular recording of Mormyromast afferents near their central terminals (see next section) support the possibility of first-spike latency as a critical code. (a) Such recordings indicate that spikes which follow a preceding spike by less than 5 ms do not arrive at all the terminals of the axon, because of refractoriness in fine branches of the axonal arbor. Intervals between spikes in the Mormyromast response are less than 5 ms, however. Thus, for some postsynaptic cells, only the first spike of the response would be available. (b) A fixed latency EOCD EPSP is present in some of the postsynaptic cells on which Mormyromast afferents terminate. This EPSP could serve to decode first-spike latency by summing with the EPSP produced by the afferent spike (C. C. Bell, in preparation).

*Central axonal arbors and initial processing in the Mormyromast system*

Primary Mormyromast afferents are large (6–9 $\mu$m in diameter) and remain large up to a few hundred micrometres from their terminals in the granule and intermediate layers of ELL cortex. They then branch repeatedly to form a dense arbor with fine preterminal branches. Axonal swellings are strung like beads along the finer branches, with several hundred such swellings in each axonal arbor. Electron microscopy of labelled afferents shows myelinated preterminal fibres as fine as 0·3 $\mu$m and that the axonal swellings are sites of synaptic contact. Electron microscopy also shows that the synaptic contacts on some granule cells are morphologically mixed, i.e. with a gap junction/chemical synapse morphology (Bell *et al.* 1989).

Two morphological features of the afferent axon, remaining large up to the terminal arbor and retaining myelin into the fine branches of the arbor, suggest that the peripherally established timing of the first spike of a Mormyromast response, which is a good measure of stimulus intensity but not of stimulus timing, is preserved by the Mormyromast afferent up to its terminals in ELL.

Characteristic synaptic potentials are recorded inside Mormyromast afferents in ELL, in addition to the large afferent spike. Zipser & Bennett (1976*a*,*b*) observed these potentials in the mormyrid ELL, but interpreted them as recordings from intrinsic 'principal cells' of ELL. More recent studies which used intracellular staining for morphological identification show that the recordings are from Mormyromast afferents (Slesinger & Bell, 1985; C. C. Bell, in preparation). As with Knollenorgan afferents, the best interpretation of these synaptic potentials is that they are caused by inputs to postsynaptic cells and are observed inside the afferents because of the electrotonic synapses which the afferents make on postsynaptic cells. Three types of synaptic potentials are recorded: electrosensory EPSPs evoked by stimulation of electroreceptors near the one from which the recorded afferent originates, electrosensory IPSPs evoked by stimulation of more distant electroreceptors, and EOCD EPSPs associated with the EOD motor command (Fig. 7).

The electrosensory EPSPs can often be shown to be composed of all-or-none unitary EPSPs that are evoked by stimulation of electroreceptors near the one which gives rise to the recorded afferent (C. C. Bell, in preparation). The threshold, latency and shift in latency with stimulus intensity of the unitary EPSPs are quite similar to those of Mormyromast afferent spikes, and the unitary EPSPs are, therefore, interpreted as electrotonic EPSPs caused by impulses in other Mormyromast afferents that synapse on some of the same cells as the recorded afferent.

The electrotonic EPSPs follow suprathreshold stimuli with great accuracy so long as the interval between stimuli is longer than 10 ms. The EPSPs become smaller at interstimulus intervals less than 10 ms, however, and disappear completely at intervals of less than 5 ms. The failure of a second closely spaced impulse to evoke an electrotonic EPSP is probably due to refractoriness in the fine branches of the Mormyromast's terminal arbor. This result suggests that only the

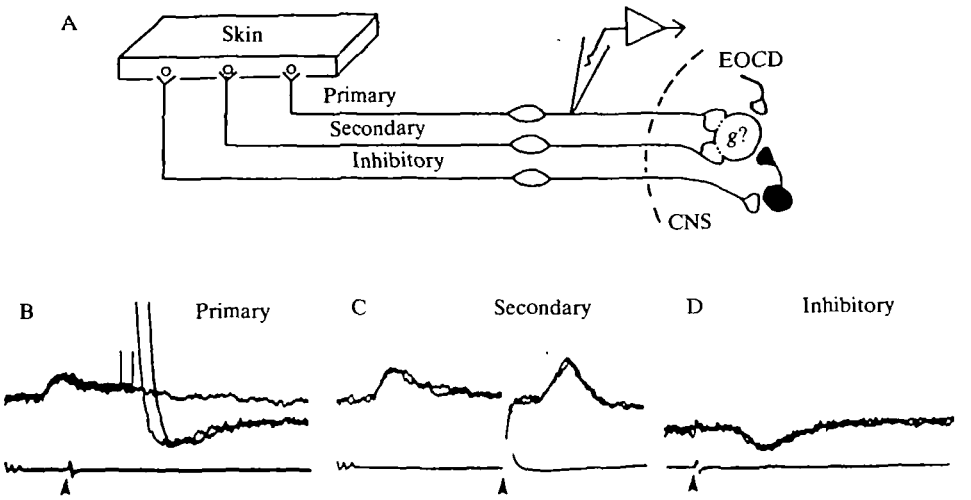



Fig. 7. Intracellular recordings from Mormyromast afferents. (A) Hypothesized connections. The recorded afferent is denoted as primary and other afferents which converge on some of the same granule cells as secondary. The set of granule cells upon which both afferents converge is symbolized by a single granule cell (*g*). Granule cells are also contacted by synapses which convey the EOCD EPSP and by inhibitory interneurones. The inhibitory interneurones (indicated by a small black cell) are excited by more distant electroreceptors and are responsible for the lateral inhibition. (B) Sweeps are initiated by command signal shown in the bottom trace. A threshold stimulus (upward arrowhead) to the primary electroreceptor elicits a large afferent spike that arises directly from the baseline. Note the EOCD-driven EPSP at the start of the sweep. (C) Sweeps are again initiated by the command signal. A stimulus to a secondary electroreceptor (upward arrowhead) elicits an EPSP. (D) A stimulus to more distant electroreceptors (upward arrowhead) elicits an IPSP (from Slesinger & Bell, 1985).

first spike in the normal burst response to the fish's EOD arrives at all the terminals of the axonal arbor.

The electrosensory IPSP evoked by stimulation of more distant electroreceptors indicates that a well-developed lateral inhibitory system is present at the initial stages of processing. The presence of such inhibition in the Mormyromast region of ELL is in contrast to the absence of lateral inhibition in the Knollenorgan region of ELL.

The EOCD EPSP occurs at a short latency, fixed with respect to the EOD motor command (Fig. 7B,C). The peak of the EOCD EPSP occurs at the time when an EOD-evoked reafferent input of minimum latency would arrive in ELL. As with the EOCD IPSP in the Knollenorgan region, the EOCD EPSP in Mormyromast afferents is not affected by pairing or lack of pairing with an electrosensory stimulus, at least during the course of electrophysiological experiments lasting several hours. Thus, an invariant or hard-wired type of match between the timing

of the EOCD effect and the timing of reafferent input is present in both the Knollenorgan region and the initial stages of the Mormyromast region.

Two possible functions may be suggested for the EOCD EPSP that is present in some of the cells contacted by Mormyromast afferents. One possible function would be selectively to enhance the afferent responses that are evoked by the fish's own EOD in relation to responses evoked by other types of stimuli. Only responses to the fish's own EOD are significant for active electrolocation and there is behavioural evidence for corollary discharge-driven gating of the active electrolocation system (Meyer & Bell, 1983). Such an EOCD-driven gate is symbolized by an AND gate in Fig. 1. A second possible function of the EOCD EPSP would be to serve as a means of decoding latency, as described above. The higher the stimulus intensity, the shorter the latency and the greater the interaction with the EOCD EPSP in the postsynaptic cells. The two possible functions are not mutually exclusive.

The histology and central connections of the two Mormyromast zones of ELL cortex are very similar to those of the ampullary zone, suggesting that similar events occur in both Mormyromast and ampullary regions, in spite of the marked differences in afferent signals and analytical tasks. One might expect, therefore, that the modifiable EOCD effects which are prominent in the ampullary zone might also be present in the Mormyromast zones. Recent preliminary results indicate the presence of modifiable EOCD effects in the Mormyromast zones, but these have not yet been studied in detail (C. C. Bell & K. Grant, unpublished observations).

The function of the modifiable EOCD in the Mormyromast region would not be to nullify reafferent input, as in the Knollenorgan and ampullary regions, since such reafferent input is the essential signal for active electrolocation. There are behavioural suggestions that with each EOD the fish compares the present reafferent input with the reafferent input of the recent past (Szabo & Fessard, 1965; Harder *et al.* 1967; Heiligenberg, 1976). The same circuitry that is used to nullify reafferent input in the ampullary zone could also be the basis of such a comparison process in the Mormyromast zones.

## Comparison of the mormyrid electrosensory system with other sensory and sensorimotor systems

### *Subsystems for the measurement of time and intensity*

The Knollenorgan and Mormyromast subsystems are markedly different in morphology and physiology. These morphological and physiological specializations are all consistent with the measurement, preservation and analysis of timing information by the Knollenorgan system and of spatially distributed intensity information by the Mormyromast subsystem (Szabo & Fessard, 1974; Bell, 1986*b*).

The possibility that latency or timing of an impulse is critical for the measurement of stimulus intensity in the Mormyromast subsystem would seem at first to blur the distinction between the two subsystems and to be likely to result in

morphological and physiological similarities between them. But this is not the case. The two systems are similar only in the large size of the primary afferents and in the retention of this large size up to the terminal arbor.

Time and intensity are treated separately in sensory systems of other vertebrate species also, and several parallels are present among the different systems. Three such systems have been studied. (1) Wave-type gymnotoid electric fish which have two kinds of separately innervated electroreceptors, T (for timing) electroreceptors which are very sensitive to the time or phase of the stimulus and P (for probability) electroreceptors which are very sensitive to the intensity of the stimulus (Heiligenberg, 1989; Scheich *et al.* 1973; Zakon, 1986). (2) Pulse-type gymnotoid electric fish which also have two types of electroreceptor afferents, 'pulse markers' and 'burst duration coders' that appear to measure time and intensity, respectively (Szabo & Fessard, 1974; Bastian, 1976; Zakon, 1986). (3) Barn owls which have primary auditory afferents that branch as they enter the brain. One branch conveys timing or phase information and the other conveys amplitude information. The two branches terminate in separate parts of the cochlear nucleus complex (Konishi *et al.* 1988; Takahashi, 1989).

The T or time-measuring afferents in wave-type gymnotoid fish terminate on the spherical cells of ELL which are found in a separate layer beneath the granule layer in which the P or intensity-measuring fibres terminate (Maler *et al.* 1981). The spherical cells are widely spaced, implying that the somatotopic map is not fine-grained, and no evidence exists for lateral inhibition among spherical cells. The projection of T afferents onto spherical cells also appears to be characterized by extensive convergence (Carr *et al.* 1986), although it is not known whether impulses in different individual T fibres can cause the same spherical cell to discharge as in mormyrid NELL cells. Thus, the T system in gymnotoid fish, like the Knollenorgan system in mormyrid fish, does not appear to maintain and analyse detailed spatial information.

Carr (1986) has pointed out that the subsystems which are specialized for the preservation and analysis of temporal information in the barn owl auditory system and in the electrosensory system of wave-type gymnotoid fish have several morphological features in common. These common features are essentially the same as those described above for the Knollenorgan subsystem and include: large afferent fibres, minimal branching in the axonal arbor, large preterminal fibres, large terminals and rounded adendritic or paucidendritic postsynaptic cells. Some of these features are also found in the part of the mammalian anteroventral cochlear nucleus which appears to be responsible for interaural phase comparisons (Smith & Rhode, 1987).

Parallels are also present in the intensity-measuring subsystems of different species. For example, the projections to ELL of the P system in gymnotoid fish and the Mormyromast system in mormyrid fish are both characterized by fine somatotopy and lateral inhibition. Furthermore, the terminal arbors of Mormyromast afferents, P type afferents in gymnotoid fish and the intensity-measuring branch of primary auditory afferents in owls are all characterized by extensive

branching, fine preterminal axons and multiple synaptic contacts (Bell *et al.* 1989; Maler *et al.* 1981; Mathieson *et al.* 1987; Konishi *et al.* 1988).

The morphological differences in afferent terminal arbors between time and intensity subsystems are consistent and would be expected to have physiological consequences. Stimulus following or phase-locking is known to occur at much higher frequencies in the time subsystems than in the intensity subsystems in the electrosensory systems of mormyrid and gymnotoid fish and in the auditory system of owls (Szabo & Fessard, 1974; Bell & Grant, 1989; C. C. Bell, in preparation; Carr *et al.* 1986; Heiligenberg, 1989; Konishi *et al.* 1988). Such following-frequency differences are presumably due to differences in axonal arbors, synapses and postsynaptic cells. The specific contribution of axonal arbors can be examined in mormyrid electrosensory afferents because of the electrical synapses of these afferents (Bell & Grant, 1989; C. C. Bell, in preparation). Most neural systems have purely chemical synapses, and in such systems it is difficult to separate the effects of impulse propagation failure from transmitter release failure in determining synaptic transmission. As might be expected, and as described in previous sections, the axonal arbors of Knollenorgan afferents with thick preterminal axons follow much higher impulse frequencies than the axonal arbors of Mormyromast afferents with very thin preterminal axons.

The similarities between the different sensory systems are clear, but there is also an important difference between the mormyrid system, on the one hand, and the gymnotoid and owl auditory systems on the other. The time and intensity subsystems in the mormyrid are well separated within the central nervous system at medullary, mesencephalic and higher levels. The two subsystems remain parallel with minimal interaction. In contrast, both anatomy and physiology indicate that intensity and time information are integrated centrally in the gymnotoid electrosensory system and in the auditory systems of birds to yield new information that is important for jamming avoidance or object location in gymnotoid fish and for sound localization in the auditory system (Heiligenberg, 1989; Konishi *et al.* 1988; Takahashi, 1989). Gymnotoid wave-type fish, which integrate phase and amplitude information, may be able to discriminate impedances which have the same effect on stimulus amplitude but are different in the relative contribution of resistive and capacitative elements, whereas mormyrid fish may not be able to make such discriminations.

The central conduction times in the Knollenorgan EOCD path were found roughly to match the peripheral conduction times in Knollenorgan afferents. The use of axonal conduction times to achieve an integrative purpose has been described in a number of other sensory and motor systems including: the electric organ discharge control system and the phase-measuring system of gymnotoid fish, in which synchrony is achieved by variation in conduction velocity to compensate for differences in conduction distance (Bennett, 1971*b*; Heiligenberg & Dye, 1982); the mammalian retinal ganglion cells, in which variations in optic nerve conduction velocity compensate for variations in intraretinal conduction time (Stanford, 1987); and the owl auditory system, in which conduction time

comparisons yield measurements of interaural time delays (Konishi *et al.* 1988; Takahashi, 1989; Carr & Konishi, 1988).

In general, close control over conduction time would be necessary within any system in which temporal measurements are critical. The need for such control is particularly clear in those sensory systems where temporal acuity in the microsecond range has been shown, as in the phase-comparison system of gymnotoid fish (Rose & Heiligenberg, 1985) or in the detection of moving targets by the echolocation system of bats (Simmons, 1979). The mechanisms by which the results of an information-processing task might control conduction velocity or conduction distance are unknown.

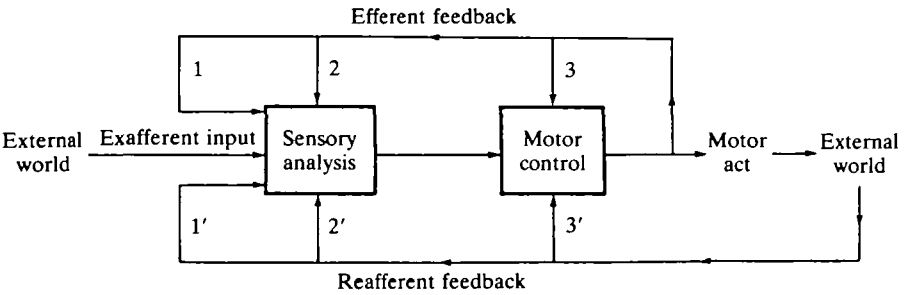
### *General uses of efferent and reafferent feedback*

The mormyrid results illustrate two properties of corollary discharge signals that may be quite general. (a) The temporal and spatial pattern of a corollary discharge signal will depend on and match the pattern of the reafferent signal with which it is associated. 'Pattern' includes such features as: latency with respect to the motor command, duration and spatial distribution. Pattern may also include amplitude and time course, as in the ampullary region. Optimal interaction between corollary discharge and reafferent signals would seem to require such a match. (b) The effect of the corollary discharge signal will depend on the significance of the reafferent signal with which it is associated. Reafferent signals that are uninformative and potentially disruptive will be blocked or minimized, whereas those which are informative will be enhanced and interpreted.

Modifiable corollary discharge signals, such as those which have been studied in the ampullary region (Bell, 1982) and identified in the Mormyromast region of the mormyrid ELL (C. C. Bell & K. Grant, unpublished observations) are of particular interest and may occur in other systems. The reafferent input evoked by a motor command will sometimes change, either because of factors internal to the organism such as growth, injury or fatigue, or because of environmental changes such as muscle loading. If the corollary discharge is to continue to interact with and match the reafferent input, then it may be useful to modify the corollary discharge in accord with the changes in reafferent input. In a more general sense, the modifiable EOCD is an expectation concerning the sensory consequences of a motor command. If the sensory consequences change, then the expectation should also change.

The term 'corollary discharge' has been used with various degrees of specificity. It is used most commonly, perhaps, to refer to any type of feedback from an efferent command path, i.e. any use of an efferent command signal other than the driving of an effector organ. Some restrict the term, however, to the effect of a motor command on a sensory system (McCloskey, 1981; Bell, 1984) and that is how the term has been used in the previous sections of this review. [See McCloskey (1981), Bell (1984), and Bullock (1986) for discussion of the term 'corollary discharge' and the related term 'efference copy'.]

Three very general uses of efferent feedback from a motor command path may,




*Uses of efferent feedback*

(1) Substitute for sensory information.

(2) Modulating or interpreting re- or exafferent input.

(3) Motor control (sequencing, coordination, etc.).

*Uses of reafferent feedback*

(1') Sensory information about external world (active sensory systems).

(2') Modulating or interpreting re- or exafferent input.

(3') Motor control (sequencing, coordination, etc.).

Fig. 8. Block diagram illustrating different uses of efferent and reafferent feedback. Efferent feedback signals are derived from the motor command path before it reaches the effectors. Reafferent feedback is derived from sensory receptors affected by the commanded motor act. Exafferent input is derived from sensory receptors that are driven by stimulus sources in the external world.

in fact, be distinguished (Fig. 8). (1) Efferent feedback may be used as a substitute for sensory input in many systems [Fig. 8 (1)]. Thus, skeletal motoneurone activity may indicate the weight of an object (McCloskey, 1981), ocular motoneurone activity may indicate eye position (Guthrie *et al.* 1983), and efferent activity to the lens of the eye may indicate the distance of an object when the object is in focus (Collett, 1977; Harkness, 1977). (2) Efferent feedback may be used to modulate or interpret re- or exafferent input, as in the mormyrid electrosensory system [Fig. 8 (2)]. ['Exafferent' input is the term introduced by von Holst & Mittelstaedt (1950) to refer to sensory input of purely external origin.] There are, of course, many other examples of this use including the blockade of lateral line activity during active movements (Roberts & Russell, 1972) and the modulation of primary afferent terminals during fictive locomotion (Stehouwer & Farel, 1981; Dubuc *et al.* 1988). (3) Finally, efferent feedback may be used in motor control to sequence or coordinate different parts of a motor act [Fig. 8 (3)]. Ventral spinocerebellar activity, for example, is strongly modulated during fictive locomotion, and appears to help coordinate descending motor commands with spinal locomotor commands (Lundberg, 1971; Arshavsky *et al.* 1972, 1983).

Reafferent feedback is sensory input that results from an animal's own motor activity and has uses which parallel the uses of efferent feedback. In many systems, in fact, it remains an open question as to whether efferent or reafferent feedback is the most important. In some cases, such as active sensory systems, the reafferent feedback is strongly affected by events in the external world. In other cases,

however, the reafferent feedback is hardly affected by the external world and provides accurate information about the motor act alone.

The three uses of reafferent feedback which parallel those of efferent feedback are as follows (Fig. 8). (1) Reafferent feedback is a type of sensory input and provides information about the environment in active sensory systems [Fig. 8 (1′)]. (2) Reafferent feedback in one set of afferents can be used to modulate or interpret re- or exafferent input in another set of afferents [Fig. 8 (2′)]. In the active sensory systems of pulse-type gymnotoid fish and echolocating bats, for example, the time of the emitted signal appears to be given by a reafferent mechanism, i.e. by a class of receptors that are especially sensitive to the emitted signal, rather than by a corollary discharge mechanism as in mormyrid fish (Szabo & Fessard, 1974; Bastian, 1976; Suga, 1989). Similarly, the position of the head must be known for the correct interpretation of vestibular signals (Nashner & Wolfson, 1974), of auditory localization cues (Takahashi, 1989) and of retinal position (Sparks, 1989). Reafferent feedback from the neck is a likely source of such information (Cohen, 1961). (3) Finally, reafferent feedback may be used like efferent feedback to sequence or coordinate different parts of a motor act, as in Sherrington's (1947) concept of reflex chaining [Fig. 8 (3′)].

Efferent and reafferent feedback have complementary advantages and disadvantages. Efferent feedback is very fast, since it occurs before the motor command leaves the central nervous system. Thus, it allows a sensory receiving area to be prepared well in advance of an expected reafferent input, and allows rapid sequencing and coordination of motor commands. Efferent feedback only provides information about the commanded act, however, and not about the act which actually occurs. Reafferent feedback is slow but provides accurate information about the act which actually occurs. It may also provide information about the interaction between the motor act and the environment. In general, efferent feedback may have the advantage when the coupling between the commanded motor act and the actual motor act is very tight, whereas reafferent feedback may have the advantage when such coupling is more variable.

Funds for the studies on the mormyrid electrosensory system were provided by the National Institutes of Health. The figures were made by Andrea Frost. Fig. 8 and the general comments on efferent and reafferent feedback owe much to discussions with Drs James Houk and David Sparks. Drs Charles Russell and Randy Zelick provided helpful criticisms of the text.

## References

ARSHAVSKY, Y. I., BERKINBLIT, M. B., FUKSON, O. I., GELFAND, I. M. & ORLOVSKY, G. N. (1972). Origin of modulation in neurones of the ventral spinocerebellar tract during locomotion. *Brain Res.* **43**, 276–279.

ARSHAVSKY, Y. I., GELFAND, I. M. & ORLOVSKY, G. N. (1983). The cerebellum and control of rhythmical movements. *Trends Neurosci.* **6**, 417–422.

BASTIAN, J. (1976). Frequency response characteristics of electroreceptors in weakly electric fish (Gymnotoidei) with a pulse discharge. *J. comp. Physiol.* **112**, 165–189.

BELL, C. C. (1982). Properties of a modifiable efference copy in electric fish. *J. Neurophysiol.* **47**, 1043–1056.

BELL, C. C. (1984). Effects of motor commands on sensory inflow, with examples from electric fish. In *Comparative Physiology: Sensory Systems* (ed. L. Bolis, R. D. Keynes & S. H. P. Maddrell), pp. 636–647. Cambridge: Cambridge University Press.

BELL, C. C. (1986*a*). Duration of plastic change in a modifiable efference copy. *Brain Res.* **369**, 29–36.

BELL, C. C. (1986*b*). Electroreception in mormyrid fish, central physiology. In *Electroreception* (ed. T. H. Bullock & W. Heiligenberg), pp. 423–452. New York: John Wiley & Sons, Inc.

BELL, C. C., BRADBURY, J. & RUSSELL, C. J. (1976). The electric organ of the mormyrid as a current and voltage source. *J. comp. Physiol.* **110**, 65–88.

BELL, C. C., FINGER, T. E. & RUSSELL, C. J. (1981). Central connections of the posterior lateral line lobe in mormyrid fish. *Expl Brain Res.* **42**, 9–22.

BELL, C. C. & GRANT, K. (1989). Corollary discharge inhibition and preservation of temporal information in a sensory nucleus of mormyrid electric fish. *J. Neurosci.* **9**, 1029–1044.

BELL, C. C., MYERS, J. P. & RUSSELL, C. J. (1974). Electric organ discharge patterns during dominance-related behavioral displays in *Gnathonemus petersii*. *J. comp. Physiol.* **92**, 201–228.

BELL, C. C. & RUSSELL, C. J. (1978*a*). Effect of electric organ discharge on ampullary receptors in a mormyrid. *Brain Res.* **145**, 85–96.

BELL, C. C. & RUSSELL, C. J. (1978*b*). Termination of electroreceptor and mechanical lateral line afferents in the mormyrid acousticolateral area. *J. comp. Neurol.* **182**, 367–382.

BELL, C. C., ZAKON, H. & FINGER, T. E. (1989). Mormyromast electroreceptor organs and their afferent fibers in mormyrid fish. I. Morphology. *J. comp. Neurol.* (in press).

BENNETT, M. V. L. (1965). Electroreceptors in mormyrids. *Cold Spring Harb. Symp. quant. Biol.* **30**, 245–262.

BENNETT, M. V. L. (1971*a*). Electric organs. In *Fish Physiology* (ed. W. S. Hoar & D. J. Randall), pp. 347–491. New York: Academic Press.

BENNETT, M. V. L. (1971*b*). Electroreception. In *Fish Physiology* (ed. W. S. Hoar & D. J. Randall), pp. 493–574. New York: Academic Press.

BENNETT, M. V. L. (1977). Electrical transmission: a functional analysis and comparison to chemical transmission. In *Handbook of Physiology* section I, vol. I *Cellular Biology of Neurons*, part I (ed. J. M. Brookhart, V. B. Mountcastle, E. R. Kandel & S. R. Geiger), pp. 357–416. Bethesda: American Physiological Society.

BENNETT, M. V. L. & STEINBACH, A. B. (1969). Influence of electric organ control system on electrosensory afferent pathways in mormyrids. In *Neurobiology of Cerebellar Evolution and Development* (ed. R. Llinas), pp. 207–214. Chicago: American Medical Association.

BULLOCK, T. H. (1986). The comparative neurobiology of expectation: stimulus acquisition and the neurobiology of anticipated and unanticipated input. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. Fay, A. Popper & W. Tavolga). New York: Springer-Verlag.

CARR, C. E. (1986). Time coding in electric fish and barn owls. *Brain Behav. Evol.* **28**, 122–133.

CARR, C. E., HEILIGENBERG, W. & ROSE, G. J. (1986). A time-comparison circuit in the electric fish midbrain. I. Behaviour and physiology. *J. Neurosci.* **6**, 107–119.

CARR, C. & KONISHI, M. (1988). Axonal delay lines for time measurement in the owl's brainstem. *Proc. natn. Acad. Sci. U.S.A.* **85**, 8311–8315.

COHEN, L. A. (1961). Role of eye and neck proprioceptive mechanisms in body orientation and motor coordination. *J. Neurophysiol.* **24**, 1–11.

COLLETT, T. (1977). Depth perception in toads based on measurement of efference to lens accommodation muscle. *Nature, Lond.* **267**, 349.

DENIZOT, J. P., CLAUSSE, S., ELEKES, K., GEFFARD, M., GRANT, K., LIBOUBAN, S., RAVAILLE-VERON, M. & SZABO, T. (1987). Convergence of electrotonic club endings, GABA- and serotoninergic terminals on second order neurons of the electrosensory pathway in mormyrid fish, *Gnathonemus petersii* and *Brienomyrus niger* (Teleostei). *Cell Tiss. Res.* **249**, 301–309.

DUBUC, R., CABELGUEN, J. M. & ROSSIGNOL, S. (1988). Rhythmic fluctuations of dorsal root potentials and antidromic discharges of primary afferents during fictive locomotion in the cat. *J. Neurophysiol.* **60**, 2014–2036.

ENGER, P. S., LIBOUBAN, S. & SZABO, T. (1976). Rhombo-mesencephalic connections in the fast conducting electrosensory system of the mormyrid fish, *Gnathonemus petersii*. An HRP study. *Neurosci Letts* **3**, 239–243.

GUTHRIE, B. L., PORTER, J. D. & SPARKS, D. L. (1983). Corollary discharge provides accurate eye position information to the oculomotor system. *Science* **212**, 1193–1195.

HARDER, W., SCHIEF, A. & UHLEMANN, H. (1967). Zur Empfindlichkeit des schwachelektrischen Fisches *Gnathonemus petersii*, (Gthr. 1862) (Mormyriformes, Teleostei) gegnuber electrischen Feldern. *Z. vergl. Physiol.* **54**, 89–108.

HARKNESS, L. (1977). Chameleons use accommodation cues to judge distance. *Nature, Lond.* **267**, 346–349.

HEILIGENBERG, W. (1976). Electrolocation and jamming avoidance in the mormyrid fish *Brienomyrus*. *J. comp. Physiol.* **109**, 357–372.

HEILIGENBERG, W. (1989). The processing of electrosensory information. *J. exp. Biol.* **146**, 255–275.

HEILIGENBERG, W. & DYE, J. (1982). Labeling of electroreceptive afferents in a gymnotoid fish by intracellular injection of HRP: the mystery of multiple maps. *J. comp. Physiol.* **148**, 287–296.

HOPKINS, C. D. (1986). Behavior of mormyridae. In *Electroreception* (ed. T. H. Bullock & W. Heiligenberg), pp. 527–571. New York: John Wiley & Sons, Inc.

HOPKINS, C. D. & BASS, A. H. (1981). Temporal coding of species recognition signals in an electric fish. *Science* **212**, 85–87.

KALMIJN, A. J. (1974). The detection of electric fields from inanimate and animate sources other than electric organs. In *Handbook of Sensory Physiology: Electroreceptors and Other Specialized Receptors in Lower Vertebrates* (ed. A. Fessard), pp. 147–200. Berlin: Springer Verlag.

KONISHI, M., TAKAHASHI, T. T., WAGNER, W., SULLIVAN, W. E. & CARR, C. E. (1988). Neurophysiological and anatomical substrates of sound localization in the owl. In *Auditory Function: Neurobiological Basis of Hearing* (ed. G. M. Edelman, W. E. Gall & W. M. Cowan), pp. 721–745. New York: John Wiley & Sons Inc.

KRAMER, B. (1979). Electric and motor responses of the weakly electric fish, *Gnathonemus petersii* (Mormyridae) to playback of social signals. *Behav. Ecol. Sociobiol.* **6**, 67–69.

LUNDBERG, A. (1971). Function of the ventral spinocerebellar tract – a new hypothesis. *Expl Brain Res.* **12**, 317–330.

MCCLOSKEY, D. I. (1981). Corollary discharges: motor commands and perception. In *Handbook of Physiology, The Nervous System* (ed. V. B. Brooks), pp. 1415–1447. Bethesda, MD: American Physiological Society.

MCCREERY, D. B. (1977). Two types of electroreceptive lateral lemniscal neurons of the lateral line lobe of the catfish *Ictalurus nebulosus*; connections from the lateral line nerve and steady-state frequency response characteristics. *J. comp. Physiol.* **113**, 317–339.

MALER, L., KARTEN, H. J. & BENNETT, M. V. L. (1973). The central connections of the posterior lateral line nerve of *Gnathonemus petersii*. *J. comp. Neurol.* **151**, 57–66.

MALER, L., SAS, E. K. B. & ROGERS, J. (1981). The cytology of the posterior lateral line lobe of high frequency weakly electric fish (Gymnotidae): Dendritic differentiation and synaptic specificity in a simple cortex. *J. comp. Neurol.* **195**, 87–140.

MATHIESON, W. B., HEILIGENBERG, W. & MALER, L. (1987). Ultrastructural studies of physiologically identified electrosensory afferent synapses in the gymnotiform fish, *Eigenmannia*. *J. comp. Neurol.* **255**, 526–537.

MEYER, J. H. & BELL, C. C. (1983). Behavioral measurements of sensory gating by a corollary discharge. *J. comp. Physiol.* **151**, 401–406.

MOLLER, P. & BAUER, R. (1970). "Communication" in weakly electric fish *Gnathonemus niger* (Mormyridae). I. Variation of electric organ discharge (EOD) frequency elicited by controlled electric stimuli. *Animal Behav.* **18**, 768–786.

MONTGOMERY, J. C. (1984). Noise cancellation in the electrosensory system of the thornback ray;

common mode rejection of input produced by the animal's own ventilatory movement. *J. comp. Physiol.* A **155**, 103–111.

MUGNAINI, E. & MALER, L. (1987). Cytology and immunohistochemistry of the nucleus of the lateral line lobe in the electric fish *Gnathonemus petersii* (Mormyridae) brain. Evidence suggesting that GABAergic synapses mediate an inhibitory corollary discharge. *Synapse* **1**, 1–25.

NASHNER, L. M. & WOLFSON, P. (1974). Influence of head position and proprioceptive cues on short latency postural reflexes evoked by galvanic stimulation of the human labyrinth. *Brain Res.* **67**, 255–268.

PAINTAL, A. S. (1966). The influence of diameter of medullated nerve fibres of cats on the rising and falling phases of the spike and its recovery. *J. Physiol., Lond.* **184**, 791–811.

ROBERTS, B. L. & RUSSELL, I. J. (1972). The activity of lateral line efferent neurones in stationary and swimming dogfish. *J. exp. Biol.* **57**, 435–448.

ROSE, G. & HEILIGENBERG, W. (1985). Temporal hyperacuity in the electric sense of fish. *Nature, Lond.* **318**, 178–180.

RUSSELL, C. J. & BELL, C. C. (1978). Neuronal responses to electrosensory input in the mormyrid valvula cerebelli. *J. Neurophysiol.* **41**, 1495–1510.

SCHEICH, H., BULLOCK, T. H. & HAMSTRA, R. H. (1973). Coding properties of two classes of afferent nerve fibers: high-frequency electroreceptors in the electric fish, *Eigemannia*. *J. Neurophysiol.* **36**, 39–60.

SCHEICH, H., LANGNER, G., TIDEMAN, C., COLES, R. & GUPPY, A. (1986). Electroreception and electrolocation in platypus. *Nature, Lond.* **319**, 401–402.

SHERRINGTON, C. S. (1947). *The Integrative Action of the Nervous System.* New Haven: Yale University Press.

SIMMONS, J. (1979). Perception of echo phase information in bat sonar. *Science* **204**, 1336–1338.

SLESINGER, P. & BELL, C. C. (1985). Primary afferent fibers conduct impulses in both directions under physiological stimulus conditions. *J. comp. Physiol.* A **157**, 15–22.

SMITH, P. H. & RHODE, W. S. (1987). Characterization of HRP labeled globular bushy cells in the cat anteroventral cochlear nucleus. *J. comp. Neurol.* **266**, 360–375.

SPARKS, D. L. (1989). Constraints on sensory coding and processing imposed by the format of motor commands. *J. exp. Biol.* **146**, 195–207.

STANFORD, L. R. (1987). Conduction velocity variations minimize conduction time differences among retinal ganglion cell axons. *Science* **238**, 358–360.

STEHOUWER, D. J. & FAREL, P. B. (1981). Sensory interactions with a central motor program in anuran larvae. *Brain Res.* **218**, 131–140.

STEINBACH, A. B. & BENNETT, M. V. L. (1971). Effects of divalent ions and drugs on synaptic transmission in phasic electroreceptors in a mormyrid fish. *J. gen. Physiol.* **58**, 580–598.

SUGA, N. (1989). Cortical computational maps for auditory imaging. *J. exp. Biol.* **146**, 277–286.

SZABO, T., ENGER, P. S. & LIBOUBAN, S. (1979). Electrosensory systems in the mormyrid fish, *Gnathonemus petersii*: Special emphasis on the fast conducting pathway. *J. Physiol., Paris* **75**, 409–420.

SZABO, T. & FESSARD, A. (1965). Le fonctionnement des electrorécepteurs étudies chez les Mormyres. *J. Physiol., Paris* **57**, 343–360.

SZABO, T. & FESSARD, A. (1974). Physiology of electroreceptors. In *Handbook of Sensory Physiology: Electroreceptors, Other Specialized Receptors in Other Vertebrates* (ed. A. Fessard), pp. 59–124. Berlin: Springer-Verlag.

SZABO, T. & HAGIWARA, S. (1967). A latency-change mechanism involved in sensory coding of electric fish (mormyrids). *Physiol. Behav.* **2**, 331–335.

SZABO, T., RAVAILLE, M., LIBOUBAN, S. & ENGER, D. S. (1983). The mormyrid rhombencephalon. I. Light and EM investigations on the structure and connections of the lateral line lobe nucleus with HRP labeling. *Brain Res.* **266**, 1–19.

SZABO, T. & WERSALL, J. (1970). Ultrastructure of an electroreceptor (mormyromast) in a mormyrid fish, *Gnathonemus petersii*. *J. Ultrastruct. Res.* **30**, 473–490.

TAKAHASHI, T. T. (1989). The neural coding of auditory space. *J. exp. Biol.* **146**, 307–322.

VON HOLST, E. & MITTELSTAEDT, H. (1950). Das Reafferenzprinzip. *Naturwissenschaften* **37**, 464–476.

ZAKON, H. H. (1986). The electroreceptive periphery. In *Electroreception* (ed. T. H. Bullock & W. Heiligenberg), pp. 103–156. New York: John Wiley & Sons, Inc.

ZIPSER, B. & BENNETT, M. V. L. (1976*a*). Responses of cells of the posterior lateral line lobe to activation of electroreceptors in a mormyrid fish. *J. Neurophysiol.* **39**, 693–712.

ZIPSER, B. & BENNETT, M. V. L. (1976*b*). Interaction of electrosensory and electromotor signals in the lateral line lobe of a mormyrid fish. *J. Neurophysiol.* **39**, 713–721.