

The Evaluation of Electroreceptive Feedback in a Gymnotoid Fish with Pulse-Type Electric Organ Discharges

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Summary. How does a gymnotoid electric fish with pulse-type electric organ discharges (EODs) detect specific novelties in electroreceptive feedback from its own EODs if it is contaminated by EODs of a neighbor? To answer this question, experiments were performed on intact as well as on curarized animals. Specimens were curarized and their silenced EODs replaced by artificial pulses, S_1 , in order to dissociate electroreceptive afferences¹ from the activity of the electric organ pacemaker. The animal's ability to detect small, local distortions in its own EOD field as well as in a substituted S_1 -field was tested while various patterns of pulses, S_2 , mimicking EODs of a neighbor, were presented (Fig. 1). The following results were obtained:

1. The animal evaluates electroreceptive afferences without reference to the pacemaker which normally drives its EODs, the main source of electroreceptive afferences.

2. Signals interfering with the animal's EOD, or S_1 , will impair the detection of specific novelties to the extent that they cause transient alterations in electroreceptive afferences over the course of several successive EODs. Foreign pulses which coincide with or narrowly precede several successive EODs are more detrimental than noncoincident pulses (Figs. 2–5, 9).

3. The animal adapts to maintained alterations of its electroreceptive afferences in the course of seconds and thereby regains its ability to detect novelties in a maintained jamming regime which allows electroreceptive afferences to stabilize to a new state (Fig. 4).

4. Detection of novelties in curarized fish im-

proves to the extent that the EOD substitute, S_1 , is presented at a high and regular rate (Figs. 6, 7). High and regular EOD rates, which are commonly observed in novel situations, should therefore enhance the animal's ability to detect the appearance of objects in its environment.

5. The Jamming Avoidance Response (JAR) prevents successive EODs from coinciding with foreign pulses of a similar repetition rate. Such coincidences disturb electroreceptive afferences most severely. By avoiding coincidences, the JAR stabilizes these afferences and thereby enhances the detection of specific novelties in the presence of conspecifics (Fig. 10).

Introduction

Electric fish assess their environment by evaluating specific novelties in electroreceptive feedback from their own electric organ discharges (EODs). This form of electrolocation (Lissmann and Machin, 1958; Bullock, 1968; Harder, 1972) is vulnerable to electric noise, particularly to EODs generated by conspecifics, and electric fish have developed strategies to avoid or at least to minimize jamming of their signals by conspecifics (see general review in Heiligenberg, 1977). Gymnotoid fish with relatively short, i.e. pulse-type rather than continual, wave-type EODs are most vulnerable to foreign pulses which coincide with or briefly precede their own EODs (Heiligenberg, 1974). By means of a specific jamming avoidance response (JAR) these fish minimize the probability of pulse-coincidences by appropriately shifting the timing of their EODs when they drift towards coincidences with EODs of a neighbor which fires at a slightly different rate (Heiligenberg, 1974, 1977; Heiligenberg et al., 1978a; Westby, 1975, 1979; Scheich et al.,

Abbreviations: BDC, burst detection coders; EOD, electric organ discharge; JAR, jamming avoidance response

¹ The term "afferences" is used instead of the more general term "inputs" to denote the afferent neuronal activity of this sensory system

1977). An additional strategy to prevent coincidences appears to exist in *Gymnotus*: Two individuals may phase-lock their EODs and thereby fire in alternation for many EOD cycles (Westby, 1975, 1979).

Whereas feedback from the animal's own EODs yields an image of the world around the fish, sensations from EODs of other individuals influence the timing of the animal's EODs. This raises the question whether an electric fish identifies feedback from its own EODs and distinguishes this input from sensations caused by other fishes' EODs. Whereas the African pulse-type electric fish, the mormyrids, apparently gate electroreceptive feedback by a corollary discharge from the pacemaker which drives the electric organ (Bennett and Steinbach, 1969; Zipser and Bennett, 1976b; Russell and Bell, 1978), no such cycle-by-cycle identification of feedback appears to exist in the South American, i.e. the gymnotoid electric fish (Bastian, 1976; Heiligenberg et al., 1978a, b).

To address the question of how a gymnotoid pulse-species is able to detect relevant novelties in electroreceptive feedback contaminated by a conspecific's noise, experiments were performed on intact as well as curarized animals. The silenced EOD of a curarized specimen was replaced by various stimulus regimes, S_1 , which served as EOD substitutes, in order to determine EOD features relevant for electrolocation performance. The animal's EOD, or its substitute, could be jammed by various regimes of pulses, S_2 , which mimicked EODs of a neighbor. The ability to electrolocate under these conditions was studied by measuring the electric organ pacemaker's responses to small, local distortions of the animal's electric field which were generated by short circuiting narrowly spaced electrode tips in the water. Unlike the locomotory electrolocation response previously explored in *Hypopygus* (Heiligenberg, 1974), the pacemaker's response could be studied in paralysed as well as intact specimens. It emerged from these investigations that first, the animal evaluates electroreceptive feedback without reference to its own pacemaker, and second, specific novelties are detected more readily in a stationary rather than in an erratic pattern of electroreceptive afferences, and third, the main function of the JAR is to stabilize these afferences.

Methods

Experiments were performed on specimens of *Hypopomus occidentalis* which were collected in small creeks crossing the Pipeline Road near Gamboa in the Panama Canal Zone. This is the only *Hypopomus* species reported from Panama. Its EOD, as recorded by a differential pair of electrodes, with the positive electrode in front of the head and the negative electrode beyond the tip of the tail, resembles a single period sinusoid (see insert in WG

of Fig. 1) of approximately 1 ms in duration. The peak spectral power of this EOD pulse is near 800 Hz, with mean and standard deviation of this value being 810 and 53 Hz, respectively ($n=11$). Depending upon the animal's state of excitation, EODs are fired at a repetition rate between 15 and 70 Hz.

Animals were maintained in water of 4 to 10 k Ohm · cm resistivity, at a pH between 6 and 7 and at a temperature between 25 and 27 °C. All experiments were performed in water of 10 kOhm · cm resistivity in an aquarium of 55 cm × 60 cm × 20 cm deep, with the animal maintained in its center. Details of experimental procedures are shown in Fig. 1.

Intact animals were maintained in a small tube built out of plastic window screen. A pair of differential electrodes, placed near the end of the tail, recorded the animal's EOD and thus provided a pacemaker related signal, pcm, which was fed to a computer to calculate its instantaneous rate as the inverse of its interval.

Curarized animals were held in two slings, made out of soft fabric and placed around the pectoral and tail regions respectively. Aerated water was supplied at a constant rate of approx. 2 to 4 drops/s via a mouth tube. The silenced EOD was replaced by an artificial, EOD like signal, S_1 (Fig. 1). A pacemaker signal, pcm, was recorded from inside a capillary placed over the tip of the tail, much as in previous studies (Heiligenberg et al., 1978a). Particular care had to be taken to place these electrodes in such a manner as to minimize the recording of stimulus artefacts.

A pair of silver wire electrode tips, placed 1 to 2 cm apart near the animal's anterior lateral body surface, could be electrically shorted for the duration of any chosen EOD or S_1 pulse by means of an electronic switch (Intersil Analog Switch DG 200 driven via optically coupled isolator HP 4350). The resistance between these electrode tips, at a separation of 1 cm, in 10 kOhm · cm water and for a 1 kHz test signal, was 67 kOhm when the switch was open and 87 Ohm when the switch was closed. The electronic switch responded to a computer generated square pulse with a delay of 600 ns. Closing of the switch during an EOD resulted in a local distortion of the animal's electric field. Distortions which occurred over a small number of successive EODs reliably elicited pacemaker responses in the animal. Closure of the switch outside the animal's EOD had no effect, provided that activation of the switch did not cause electric artifacts strong enough to be detected by the animal. The successful elimination of such artifacts was tested in this manner.

Experiments were run under on-line computer control in the following way. The respective procedures for curarized animals are given in parenthesis.

After 60 EOD (S_1) pulses had passed, the following 4 pulses, # 61 to # 64, were locally shorted by activating the electronic switch. For each EOD (S_1) pulse, the instantaneous pacemaker rate was plotted as the inverse of the most recent interevent interval. As the animal detected the local short circuit, it briefly accelerated its pacemaker rate, and a measure of its response strength is shown in the lower half of Fig. 1. The animal's electroreceptive afferences could be jammed by simultaneous presentation of an electric stimulus, S_2 , which mimicked EODs of a distant neighbor. These pulses could be presented in various phase relations with respect to EOD (S_1) pulses, and certain jamming regimes almost abolished the animal's response to the short circuit.

To measure the extent to which the detection of novelty is hampered by a given jamming regime, experiments with and without jamming were performed in alternation. To avoid excessive habituation to the short circuit stimulus the animal was given a rest of 3 to 5 min between experiments. Since jamming causes rapid changes in pacemaker rate, small accelerations in response to a short circuit are difficult to detect in individual records. For this reason 5 to 10 experiments under either condition were averaged to yield smoothed response curves with respective "response-

areas", E (obtained in presence of jamming) and C (obtained in absence of jamming), which are indicated as shaded areas in the lower half of Fig. 1. For each jamming regime, a total of 3 to 5 pairs of such curves was obtained with respective areas, E_i and C_i , $i=1, 2, 3, \dots$. A mean relative response, R , was calculated as the mean of all E_i divided by the mean of all C_i , and a corresponding standard deviation was obtained by dividing the standard deviation of the E_i by the mean of all C_i . This normalized standard deviation is plotted as a bar to either side of the corresponding mean, R , in the figures of this paper. The response to novelty under jamming was thus normalized so that $R=1$ (i.e. mean E =mean C) implied "perfect detection" and R smaller than 1 (i.e. mean E smaller than mean C) implied "impaired detection".

Further details of experimental methods will be given with the results.

Results

1. General Features of the Response to Novelty in Electroreceptive Feedback

As can be seen in the data sample in Fig. 1, an animal raises its pacemaker rate shortly after the first in a series of EODs is locally altered by a short circuit in the water. This novelty response has been reported in many other species of electric fish with pulse-type EODs (Larimer and MacDonald, 1968; Bullock, 1968; Harder, 1972; Heiligenberg, 1974). Whereas short circuiting of a single EOD hardly elicits a response in the animal, the alteration of at least 2 to 3 EODs reliably elicits a brief acceleration in EOD rate. The latency of this response varies among individuals of *Hypopomus*. Whereas some individuals accelerate their pacemaker only after 4 to 5 EODs from the beginning of the first short circuit, other individuals will already respond after 1 to 2 EODs. An animal's response latency was never seen to change over several days of experimentation.

Brief accelerations in pacemaker rate can be elicited reliably if the prestimulatory rate is less than 40 to 50 Hz. At higher pacemaker rates, which are common in states of high general excitation, a rather smooth deceleration is commonly observed instead. Whereas brief increments in pacemaker rate decay with a time constant of approximately 0.5 s, decrements have a life time approximately 10 times longer. Similar respective time constants are observed in accelerations and decelerations of pacemaker rate during jamming avoidance maneuvers, with accelerations and decelerations being elicited as the animal's EOD is scanned by pulse trains of lower or higher frequency respectively than that of its own EOD (Heiligenberg et al., 1978a; Baker, 1980). This suggests that the respective changes of pacemaker rate in novelty and jamming avoidance response are identical processes. This assumption is supported by two further observa-

tions. First, decelerations in novelty as well as in jamming avoidance responses only occur at higher EOD rates. Second, individuals vary with regard to their ability to decelerate their pacemaker, and the magnitude of decelerations in novelty and jamming avoidance responses covaries among individuals.

In order to exclusively elicit accelerations and thus to simplify the analysis of data, and since animals very rarely fire EODs at a rate higher than 40 Hz, experiments were performed at pacemaker rates lower than 45 Hz.

Animals undisturbed by any form of stimulation fire their EODs at a fairly regular rate with the coefficient of variation of inter-EOD intervals being as small as 0.01 for hundreds of successive EOD cycles. Slight disturbances, such as faint electric pulses of a distant neighbor, will render the EOD intervals more jittery. Stronger disturbances elicit accelerations in EOD rate.

Animals readily habituate to a given short circuit stimulus if not allowed sufficiently long periods of rest between stimulus presentations, and curarized animals habituate more readily than intact animals. Habituation can at least partly be overcome by moving the short circuit electrodes to a different location or by dishabituating the animal with various forms of intermittent stimulation, such as gently stroking the fish's back.

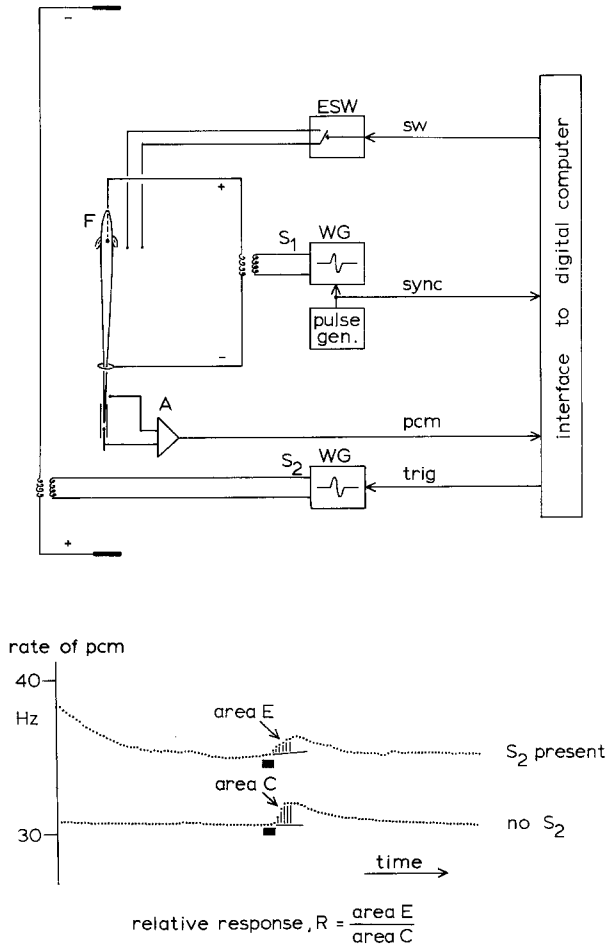
Independently of habituation, an animal's responsiveness to novelties fluctuates over the course of hours for unknown reasons. In order to compare its performance under two different experimental conditions and to eliminate any biases due to habituation and spontaneous fluctuations in responsiveness, the two experimental conditions were tested in continual alternation as described under Methods.

Curarized animals respond to novelties in afferences from a suitable EOD-substitute, S_1 , much as intact animals respond to novelties in afferences from their natural EODs. Only one out of 15 animals tested did not respond under curarization. Individuals commonly recovered from curarization and resumed normal activities. However, their responses to novelties in EOD feedback were weaker than prior to curarization. Details of experiments on curarized specimens will be given in Sect. 3.

2. The Effect of Different Jamming Regimes on Novelty Detection in Intact Animals

a) Coincident Pulses Are More Detrimental Than Noncoincident Pulses

Intact animals were exposed to stimulus pulses, S_2 , presented in a longitudinal field (see Fig. 1 and Meth-



←Fig. 1. Experimental arrangement (top) and example of averaged data records (bottom). Signal (*pcm*) of pacemaker, which normally commands the EOD, is recorded from tail tip of a curarized fish (*F*, top view, 10 to 14 cm long) and amplified by differential amplifier (*A*). An electric stimulus, S_1 , substitutes for animal's EODs, silenced by curarization. This stimulus is presented between an electrode inserted through the esophagus in the stomach and a ring-shaped electrode around the tail. The stimulus, S_1 , is produced by a single-sinusoid waveform generator, *WG*, and each sinusoid is triggered by a signal (*sync*) of a pulse generator. Period of single sinusoid is 1 ms. While occurrences of *pcm* and *sync* are continually monitored by a computer, single sinusoids, S_2 , can be triggered (*trig*) and an electronic switch (*ESW*) can be activated (*sw*) under computer control. S_2 is an electric stimulus similar to S_1 , but presented longitudinally with respect to animal's body axis, and mimics the field of a distant conspecific. Both stimuli are isolated by transformers. The electronic switch short circuits two electrode tips near animal's body surface. Same experiments can be performed on intact animals in which case no S_1 is presented and *sync* and *pcm* are provided by the EOD signal which can be recorded with a pair of differential electrodes placed near the animal's tail. Two data records at bottom of figure are plots of instantaneous rate of *pcm*, measured as the reciprocal of the interval between the current and the preceding event. Successive EOD (or S_1) events are plotted equidistantly along the abscissa with the associated *pcm* rate as a dot along the ordinate, with #1 being the first on the left. During the four successive EOD (or S_1) events, #61 to #64 (thick bar along abscissa), the electronic switch is closed. This causes an acceleration of the *pcm* rate in both instances. The areas (hatched) subtended between the initial part of the response curves (event #61 to #69) and the rate of *pcm* predicted (thin horizontal lines) from the 10 data points preceding the short circuit are measures of the animal's response. Each curve is average of 7 experiments. Relative response, *R*, under jamming is the ratio of mean areas obtained in the presence of a jamming stimulus, S_2 , and in its absence

ods) at intensities of 1, 3.1 and 10 mV/cm respectively. The stimulus pulses were presented from the beginning, i.e. EOD # 1, of each experiment, and either coincided with each EOD or were triggered 10 ms later. Coincident jamming pulses are more harmful to novelty detection than are noncoincident pulses, and their effect increases with stimulus intensity (Fig. 2). The near field intensity of *Hypopomus occidentalis* is 10 to 30 mV/cm (dependent upon the animal's size), and therefore, even nearest neighbors should only jam each other seriously if their pulses coincide. This agrees with previous results in the related species *Hypopygus lepturus* (Heiligenberg, 1974).

b) Animals Adapt to a Continual and Consistent Jamming Regime

Coincident S_2 -pulses, as described in 2a, of 10 mV/cm intensity were presented either starting at the beginning of the experiment ("temporary" jamming) or for a period starting at least 1 to 2 min prior to the

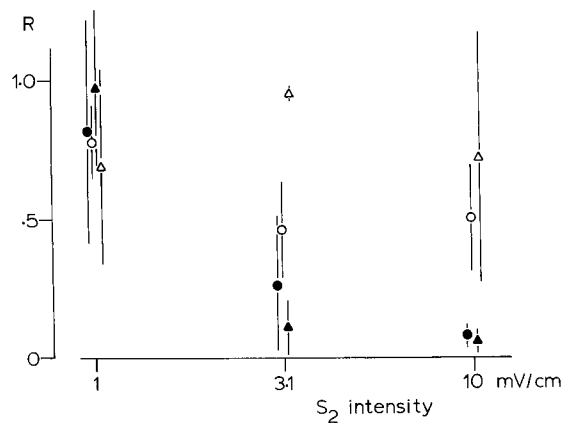


Fig. 2. Responses to novelty, *R*, deteriorate more severely if stimulus pulses, S_2 , coincide with the animal's EOD (filled symbols) than if such pulses are presented with a delay of 10 ms with regard to EODs (open symbols). Stimuli were presented from beginning of each experiment. Symbols indicate mean relative response, *R*, with its standard deviation shown by the length of the bar to either side (see Methods for definition of measures). $R=1$ means unimpaired performance. Data for 2 animals are presented by different symbols

experiment (“continual” jamming). Thus, under temporary jamming the animal had to detect a short circuit after only 60 EODs had been jammed, whereas under continual jamming many hundreds of EODs had been jammed prior to the occurrence of the short circuit. With the onset of a series of S_2 pulses of sufficient intensity, the animal regularly raises its EOD rate, much as in response to the particular novelty caused by a local short circuit. This initial increment in EOD rate has largely vanished after 60 EODs have been jammed (top record in Fig. 3, temporary-coincident S_2) at which time the short circuit is presented (thick bar). Almost no response, i.e., no separate acceleration of pacemaker rate, can be elicited by the short circuit in this case. However, if EODs are jammed for a much longer period of time (see bottom record in Fig. 3, continual-coincident S_2) the EOD rate has stabilized by the time the short circuit is presented and, although the EOD rate is still higher than in the absence of jamming (no S_2), a clear response to the short circuit stimulus can be discerned.

One may suggest at this point that in the case of the top record in Fig. 3 the animal does not detect the short circuit due to the tumultuous EOD activity which is triggered by the onset of the jamming. However, a similar EOD activity is triggered by the onset of a regime of S_2 pulses delayed by 10 ms with respect to the EODs (center record, temporary-delayed S_2), yet a clear response to the short circuit is obtained under this less harmful jamming regime. Similarly strong accelerations of pacemaker rate can be elicited by other stimuli, such as a sudden mechanical disturbance, and again distinct responses, i.e. separate accelerations in pacemaker rate, riding on top of the base line acceleration, can be elicited by a short circuit stimulus. This demonstrates that detection of a specific novelty in electroreceptive afferences is not hampered by an elevation of EOD rate. Instead, it is a short series of coincident pulses which is most detrimental to novelty detection.

The data from 4 different individuals (Fig. 4) demonstrate in all cases that temporary, coincident jamming is more detrimental than continual, coincident jamming (left diagram) and that temporary, coincident jamming is also more detrimental than temporary, noncoincident jamming (right diagram). The fact that detection of novelty improves if jamming pulses are presented for a sufficiently long period of time suggests that, with the onset of a new pattern of stimulation, the animal needs a certain minimal period of time to stabilize and update a central state or “template” of electroreceptive afferences on the background of which local novelties can be more readily discerned. This assumption will be supported by further evidence.

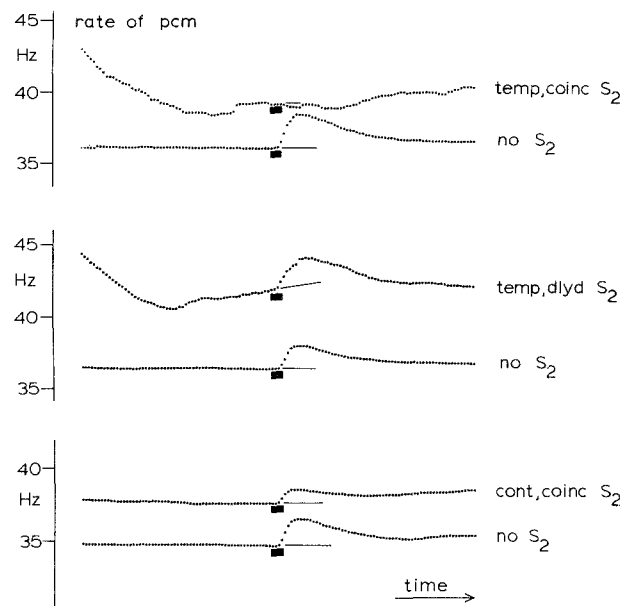


Fig. 3. Detection of novelty under 3 different jamming regimes: temporary, coincident S_2 pulses (top), temporary, delayed S_2 pulses (center, delay is 10 ms) and continually presented, coincident S_2 pulses (bottom). In each case, control performances (no jamming by S_2 pulses) were obtained in alternation with performances under jamming. Records are averages (see Methods, Fig. 1) of 22 to 26 experiments in each case. Thick black bar: 4 EODs which were short circuited; thin lines: EOD rate predicted from last 10 prestimulatory EODs. In all three instances, EOD rates are higher during jamming than in its absence. All data from same individual. S_2 intensity was 10 mV/cm in all cases

c) Jamming Pulses Presented at Random Latencies Are More Detrimental Than Pulses Presented at Fixed Latencies

S_2 pulses of 20 mV/cm intensity were presented in a longitudinal stimulus field (see Fig. 1) with 3 different latency regimes: either at a fixed latency of 10 ms with respect to the last EOD, or at a latency of one half of the previous EOD interval ($L/2$) or at a latency which was random and evenly distributed between 1 and 20 ms following the last EOD. Since the animal's EOD is approximately 1 ms in duration the earliest possible S_2 pulses (1 ms delay) could not coincide with the last EOD; and since experiments were conducted at EOD rates not higher than 40 Hz, i.e. with EOD intervals never shorter than 25 ms, even the S_2 pulses with longest latencies (20 ms) could never be closer than 5 ms to the subsequent EOD. This was of particular importance since previous experiments on the related species, *Hypopygus*, had demonstrated that electrolocation performance is particularly vulnerable to foreign pulses which precede the animal's EOD by a few ms (Heiligenberg, 1974). Preliminary experiments had demonstrated that S_2 pulses

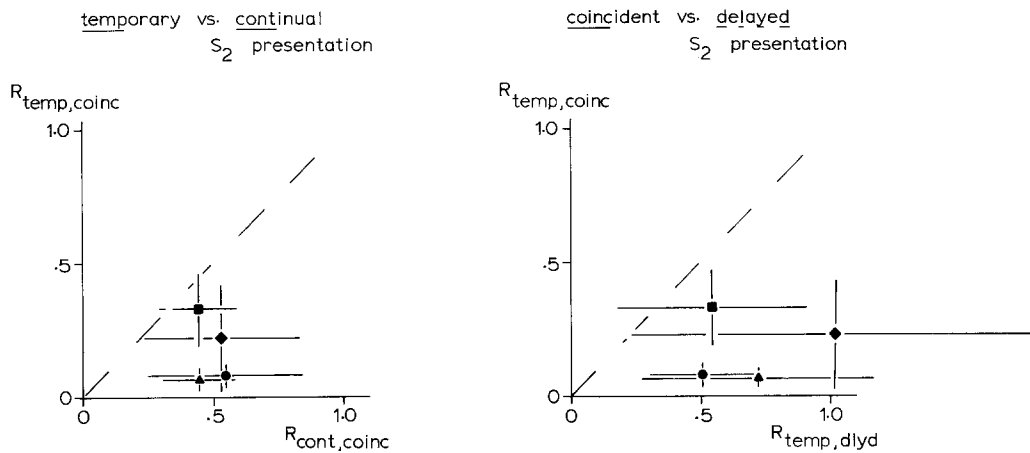


Fig. 4. Left diagram: Responses to novelty deteriorate more during temporary, coincident jamming ($R_{temp,coinc}$) than during continual, coincident jamming ($R_{cont,coinc}$). Right diagram: Responses to novelty deteriorate more during temporary, coincident jamming ($R_{temp,coinc}$) than during temporary, delayed jamming ($R_{temp,dlyd}$, S_2 pulses delayed by 10 ms with respect to EODs). S_2 intensity is 10 mV/cm in all instances. Symbols and bars: mean and standard deviation respectively of relative response, R , for 4 different animals. Dashed line: equality of performance under both jamming regimes. $R=1$ means unimpaired performance

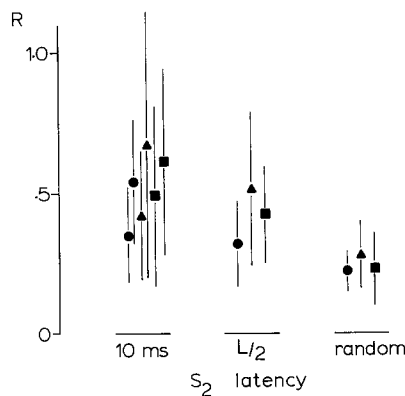


Fig. 5. Novelty detection under 3 different temporary jamming regimes, with S_2 pulses presented either at fixed latency of 10 ms, at latencies one half of previous EOD interval ($L/2$), or at randomly chosen latency with respect to last EOD. Mean R -values and their standard deviations are given for 3 different individuals (3 symbols). Two series of experiments were run for each animal under the 10 ms latency regime. R -values in random regime differ significantly ($P < 0.005$, non-parametric rank test) from combined set of R values in other two regimes. S_2 intensity was 20.0 mV/cm

presented at any fixed latency between 1 and 20 ms had similar effects, i.e. that there was no particular latency in this range to which the animal was overly vulnerable. All S_2 stimulation started at the beginning of the experiment and thus was a case of “temporary” jamming as described in 2b.

Data for 3 individuals (Fig. 5) demonstrate that random latencies are most detrimental. $L/2$ -latencies are not constant latencies because the animal’s EOD rate fluctuates. However, such fluctuations are so small that S_2 pulses triggered at $L/2$ latencies show little jitter with respect to the timing of the last EOD.

Performance under this regime may be slightly poorer than in the case of fixed latencies but the difference is not significant.

Under the assumption that novelty detection requires a steady pattern of electroreceptive “background” afferences, this result is to be expected on the basis of electroreceptor dynamics. The local intensity of the electric field is encoded by the number of spikes which special electroreceptors (“burst duration coders”, BDCs, Bullock, 1968) fire in response to each EOD. By virtue of this graded response, BDCs thus encode the electric images of objects, which are small distortions in the animal’s electric field. As will be demonstrated in connection with Fig. 8, the response of a BDC to any given stimulus intensity depends upon its previous history of stimulation, and, as a consequence, their coding of intensity becomes ambiguous if they are stimulated in an irregular manner.

3. Novelty Detection in Curarized Animals

Animals, measuring 10 to 14 cm in length, were injected intramuscularly with minimal amounts of the curare-like drug Alloferin (0.02 to 0.05 ml of 25 μ g/ml solution in saline) to silence their EODs. With sufficient injections no changes in pacemaker rate could be elicited any longer by scanning the pacemaker signal by a train of electric stimulus pulses, a most sensitive test to demonstrate the loss of the EOD (Heiligenberg et al., 1978a). An EOD substitute, S_1 , of 20 to 30 mV/cm was provided through electrodes placed in the stomach and near the tail respectively to mimic

the natural EOD field geometry (see Fig. 1 and Methods). S_1 pulses were provided continually, and experiments were conducted by starting at a given pulse, labeled # 1, and short circuiting pulses # 61 to 64. At the time of each S_1 of a given experiment, the pacemaker rate was recorded as the inverse of the most recent interval.

a) The Role of S_1 Intensity, Geometry and Pacemaker Reference

Animals respond to short circuits of a series of S_1 pulses in the same manner as in the case of natural EODs, provided that the intensity of the S_1 pulses is at least 10 to 20 mV/cm. This value is close to the animal's own near field intensity but 50% lower than the threshold value for tuberous electroreceptors which are normally driven by the animal's EODs (Baker, 1980). The relatively high threshold values in Baker's study are possibly due to stressful conditions of neurophysiological experiments.

The geometry of the S_1 stimulus field was found not to be crucial for the detection of short circuits. For example, a longitudinal S_1 field, provided in the manner of the S_2 field (see Fig. 1), resulted in good responses, i.e. there was no need to mimic the animal's natural field geometry. Furthermore, it was not necessary to phase lock the S_1 pulses to the animal's pacemaker signal which normally drives the EOD: A freely running S_1 pulse train yielded equally good responses to short circuits. The animal thus evaluates novelties in electroreceptive afferences without reference to its own pacemaker, and such novelties can be detected on any spatial pattern of background afferences from electroreceptors, even if this pattern largely differs from the particular pattern associated with the animal's normal EOD.

b) Detection of Novelty is Enhanced at Higher S_1 Rates

Responses to novelty were tested under different, constant S_1 repetition rates, such as 10, 20 and 40 Hz. A given rate was applied for at least 2 to 5 min prior to the presentation of the short circuit. Repetition rates of 10 and 40 Hz were tested with alternate presentation of the 20 Hz rate, the response to which was taken as a reference. The detection of novelty is poor at a rate of 10 Hz and improves dramatically with higher repetition rates (Fig. 6). The detection of sudden changes in electroreceptive afferences is apparently enhanced if pulses follow each other sufficiently closely, and animals appear to raise their EOD

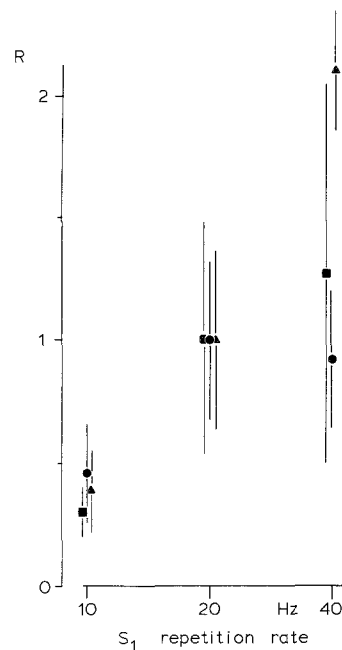


Fig. 6. Responses to novelty as a function of the repetition rate of the EOD-substitute, S_1 . Responses at 20 Hz, taken as controls, were compared with those at 10 and 40 Hz respectively to yield relative responses, R . As a consequence of this procedure, the mean R at 20 Hz is one. Mean values and standard deviations are given for 3 individuals

rate in novel situations for this very reason. Schlegel (1975) demonstrated in the related species *Gymnotus* that rhombencephalic electroreceptive units improve their responses to moving objects at higher S_1 rates.

c) Steadiness of S_1 Repetition Rate Enhances Detection Performance

In a preliminary series of experiments two different temporal patterns of S_1 pulses were tested: Pulses were either triggered at a constant rate of 20 Hz, to approximate the regular discharge pattern of a resting *Hypopomus*, or pulses were triggered by the irregularly occurring EODs of a resting mormyrid (an unrelated African electric fish) which discharged at a mean rate of approximately 20 Hz. Although the animal received the same mean number of pulses per unit time its detection of novelty was much poorer under the mormyrid's regime. This suggested that gymnotoid pulse species, such as *Hypopomus*, require the regular EOD repetition rate, which characterizes this group, for optimal electrolocation, and cannot "afford" to fire their EODs as irregularly as do mormyrids.

To compare the effect of regular and irregular S_1 repetition rates more rigorously, constant rates

of 20 Hz and random rates were tested in alternation. Random rates were generated by feeding amplified noise from a P15 GRASS preamplifier into the voltage controlled frequency input of an EXACT 504 function generator whose output in turn triggered S_1 pulses. The input of the P15 was shorted by a 1 MOhm resistance and was shielded against ambient noise by a grounded Faraday cage. By independently adjusting the mean frequency level of the function generator and the amplification and bandwidth of the P15 respectively, the mean inter- S_1 interval and its standard deviation could be controlled independently. A mean of 50 ms and a standard deviation of 20 ms were chosen. Successive intervals had a correlation coefficient of less than 0.05. The mean inter- S_1 interval of the constant rate regime (20 Hz) and that of the random regime were identical. Both regimes were offered in alternation, and the animal was given at least 2 to 5 min to adapt to either regime before the short circuit was presented. Mean response areas, A_{fxd} and A_{rnd} , were calculated from averages of 5 to 10 experiments under fixed and random rates respectively (see Methods and Fig. 1 for area definition). All three animals tested performed better under the fixed rate regime (Fig. 7).

As mentioned in 2c the response of an electroreceptor of the "burst duration coder" type to a given S_1 pulse depends upon the intensity of the stimulus as well as upon the previous history of stimulation, in particular upon the length of the interval since the last stimulus. The number of spikes in the burst, which is fired in response to a single S_1 pulse, decreases with the interval between S_1 pulses (Fig. 8). This also has been reported in other gymnotoid pulse species (Hagiwara et al., 1962; Hagiwara and Morita, 1963; Suga, 1967; Schlegel, 1975; Baker, 1980). As a consequence of this feature, receptor responses to a given stimulus intensity will vary if successive S_1 pulses arrive at irregular intervals. A local short circuit, much as the appearance of an object, alters the S_1 stimulus intensity in a certain neighborhood of electroreceptors, and it appears that the animal has difficulties in detecting this local novelty if afferences from the rest of the body surface are not constant over successive S_1 pulses. For the same reason, S_2 pulses presented at random positions between successive EODs are more detrimental to novelty detection than are S_2 pulses presented at fixed positions (see data in 2c and Fig. 5).

d) Novelty Detection Under the S_1 Regime is Vulnerable to S_2 Jamming

S_1 pulses were presented at a constant rate, in the range of 20 to 30 Hz and at an intensity of 20 to

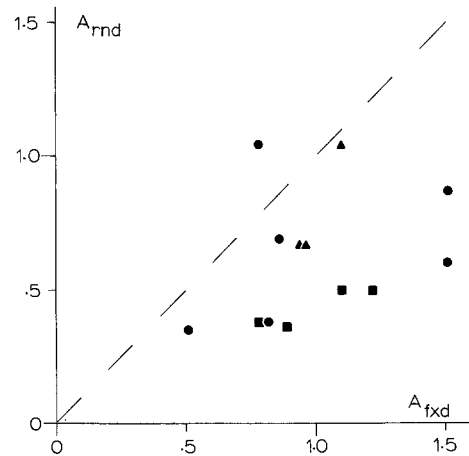


Fig. 7. Responses to novelty are stronger under a fixed rate S_1 regime, A_{fxd} , than under a random rate S_1 regime, A_{rnd} . Several mean response areas, A (see Fig. 1 and Methods for definition), obtained from alternate presentations of the two regimes, are plotted by different symbols for three individuals. For each individual, A -values were normalized to make the average abscissa value equal to one

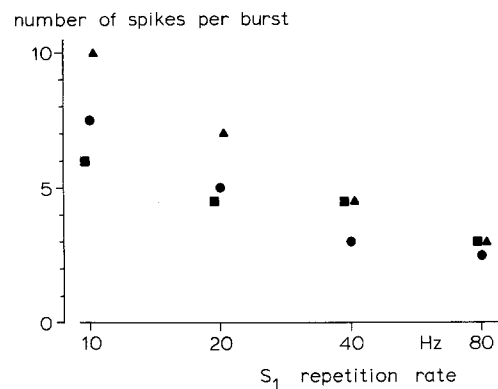


Fig. 8. The response of burst duration coders (ordinate) to each S_1 -pulse depends upon the repetition rate at which such pulses are offered (abscissa). Values for 3 units are given. A noninteger number of spikes, $n + 1/2$, is obtained if bursts with n and $n + 1$ spikes respectively are elicited by alternate S_1 -pulses. S_1 intensity was 40 mV/cm. The stimulus was presented between stomach and tail electrodes in a curarized preparation of *Hypopomus occidentalis*. Data courtesy of C. Baker

30 mV/cm, between stomach and tail electrodes. S_2 pulses of 10 mV/cm were applied in a longitudinal stimulus field (Fig. 1). The same jamming regimes as those discussed in Fig. 4 were tested by timing S_2 pulses with reference to the EOD substitute, S_1 , rather than with reference to the pacemaker signal. Jamming of the S_1 regime has the same effect on novelty detection as has jamming of the natural EOD (Fig. 9). The only difference observed was that novelty detection was slightly less vulnerable under the S_1 regime. One individual, whose data were too sparse

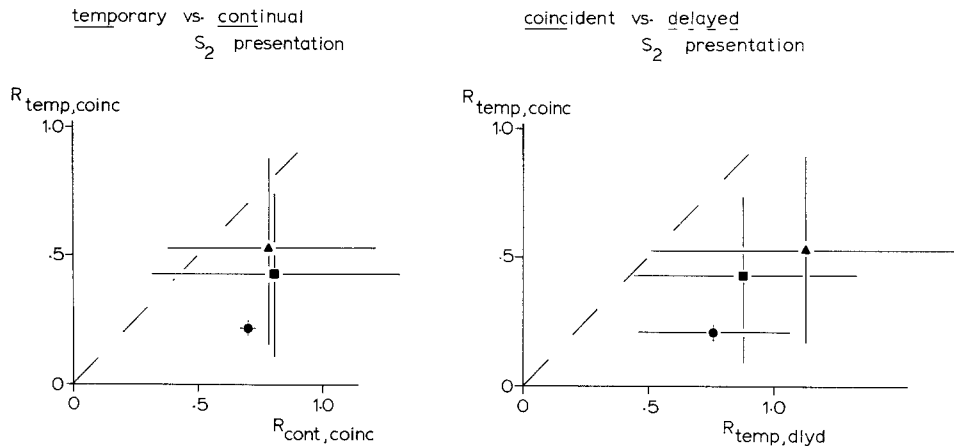


Fig. 9. The effect of different jamming regimes on novelty detection in curarized animals. Same presentation as in Fig. 4. Instead of the EOD, which was silenced, its substitute, S_1 , a freely running train of pulses, was jammed by different S_2 regimes. Data of 3 individuals

to be included in the Figure, showed almost no impairment under any jamming regime. This quantitative difference in vulnerability is to be expected if one considers that the EOD substitute, S_1 , was presented at a fixed rate, regardless of its jamming by S_2 , whereas the animal's own EOD changes its rate dramatically in response to sudden jamming. Since electroreceptor responses change with the rate of stimulation electroreceptive afferences are altered more drastically in the case of the natural EOD.

e) The Jamming Avoidance Response Stabilizes Electroreceptive Feedback

Two fish with similar EOD rates shift the timing of their pulses whenever coincidences are imminent. As a consequence of this JAR, the probability of successive coincidences, which are most harmful to electrolocation performance, is greatly reduced. However, it appears that electrolocation is not only impaired for the moment that coincidences occur but also for a short period of time following a series of coincidences. This is to be expected if one assumes that the animal requires a series of stable feedback messages from successive EODs in order to establish a central template on the background of which novelties can be detected more readily. To test this assumption the following experiment was performed.

A curarized animal was given an EOD substitute, S_1 , and a jamming stimulus, S_2 , as shown in Fig. 1. S_1 and S_2 were presented at constant rates of 30.5 and 30 pulses/s respectively. Since S_1 thus ran at a rate of 0.5 Hz faster than S_2 its phase with respect to S_2 progressively shortened (see upper left of Fig. 10), and coincidences occurred every 2 s, the peri-

od of the beat cycle. With S_1 and S_2 pulse rates of 30.5 and 30 Hz respectively, S_1 advanced in phase by $(30.5 - 30)/(30 \times 30.5) = 0.5$ ms per S_1 cycle (Heiligenberg et al., 1978a), and since both pulses were single period sinusoids of 1.0 ms in duration 3 to 4 successive S_1 pulses therefore overlapped with S_2 pulses whenever they scanned each other. Short circuits were presented, as in previous experiments, during the S_1 pulses # 61 to # 64, and this event was made to occur at specific phases of the beat cycle. As shown in the averaged records in Fig. 10 (left, a to c), each series of S_1 , S_2 -coincidences suddenly accelerated the pacemaker, and a short circuit presented shortly after a series of coincidences with S_2 pulses of sufficient intensity caused a smaller additional acceleration (record a) than a short circuit presented at a later phase of the beat cycle (record b). Record c, in which an S_2 intensity 10 dB lower than in all other records was employed, demonstrates that the coincidence related acceleration itself does not impair the response to the short circuit. This smaller S_2 intensity apparently does not upset the animal's template as badly as does the higher S_2 intensity in record a.

The experiment was then modified by introducing artificial jamming avoidance behavior into the timing of the S_1 pulse train (upper right of Fig. 10). Whenever the S_1 pulse had approached the S_2 pulse as closely as 4 ms the subsequent S_1 interval was shortened to make the following S_1 pulse appear 2 ms earlier than the following S_2 pulse. From there on, the S_1 pulse train ran at its original rate again. This "behavior" is an idealized form of the JAR that the fish with S_1 as its EOD would show, with the exception that the fish would shorten a few EOD intervals rather than only one. The fish with the lower EOD rate, which

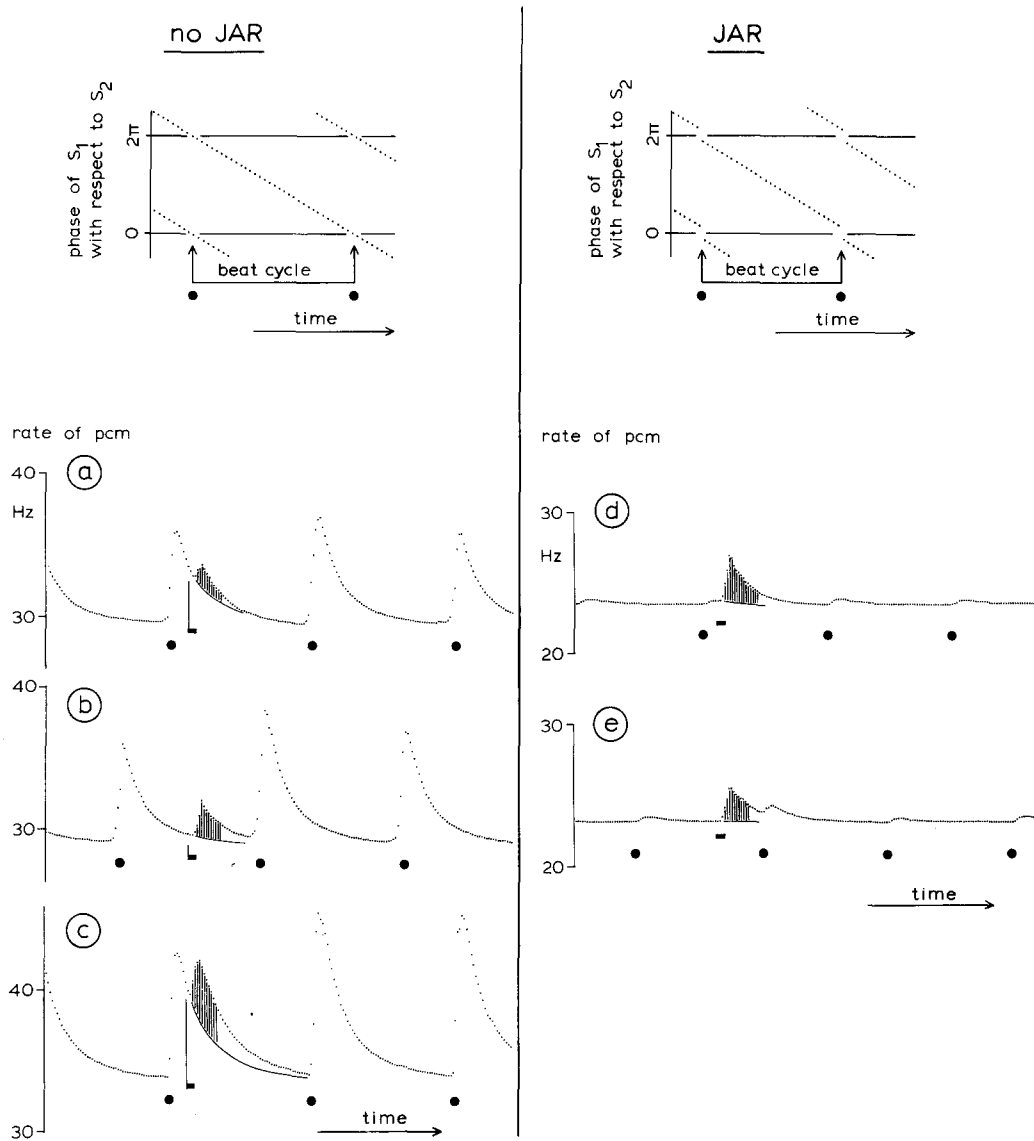


Fig. 10. An artificial JAR protects novelty detection against jamming. Upper graphs: schematic representation of S_2 stimulus regimes which interfere with an EOD substitute, S_1 . Left: S_1 and S_2 pulse trains run at constant rates of 30.5 and 30.0 Hz respectively so that S_1 gradually advances in phase with respect to S_2 (S_1 occurrences indicated by dots). Series of coincidences occur whenever S_1 scans S_2 , i.e. passes through phase zero (arrows), and this event occurs at the beat frequency, $30.5 - 30.0 = 0.5$ Hz. Right: Same as left with the exception that S_1 shortens its next interval before coincidences can occur and thereby "jumps" across S_2 . Lower graphs: Averaged data records (8 to 10 experiments in each case, for explanation see lower part of Fig. 1) obtained under two experimental conditions shown above. Small discs indicate moment of S_1 passing S_2 , and the resulting coincidences in the cases on the left cause sudden accelerations of the pacemaker. Black squares mark occurrences of S_1 pulses # 61 to #64 which experience short circuit, with the vertical line in the cases on the left pointing to the associated S_1 event, # 61. Records cover 200 successive S_1 pulses and thus a time of $200/30.5 = 6.5$ s. Shaded areas indicate beginning of response to short circuit. The time course of the data record expected in the absence of the short circuit presentation is indicated by a thin line. In the cases on the left this time course was obtained from the following peak. S_1 intensity was 30 mV/cm, S_2 intensity was 10 mV/cm in a, b, d, e and 3 mV/cm in c. Note full response to short circuit in c

would be S_2 in this instance, would hardly change the timing of its pulses at all (Heiligenberg, 1977; Heiligenberg et al., 1978 a).

Under the regime of this artificial JAR, short circuits were presented as in the previous case, at different phases of the beat cycle. The mutual scanning of the two pulse trains (see circles under records d

and e of Fig. 10) has hardly any effect upon the pacemaker frequency and short circuits cause sizable responses regardless of the phase in the beat cycle. Even short circuits presented right at the moment when the pulse trains scan each other yield full responses. This result supports the initial assumption that by avoiding coincidences by means of its JAR the animal

can detect specific novelties in electroreceptive feedback at any moment because its central template is never greatly upset.

Discussion

To study the evaluation of electroreceptive feedback it was necessary to control electroreceptive afferences experimentally, in particular, to dissociate them from the pacemaker which, by generating the EOD, ultimately drives the electroreceptive input. This could readily be achieved by curarizing animals and by replacing their silenced EOD by an artificial electric signal, S_1 . No evidence was found that *Hypopomus* employs a pacemaker related signal to identify feedback from its own EODs. Very different results are expected for mormyrids, an unrelated family of electric fish with pulse-type EODs, which gate electroreceptive input by a corollary discharge of their pacemaker (Bennett and Steinbach, 1969; Zipser and Bennett, 1976b; Russell and Bell, 1978). Presumably due to this mechanism, electrolocation in mormyrids is far less vulnerable to interfering pulses than in gymnotoids (Heiligenberg, 1976, 1977).

The appearance of an object which differs electrically from water locally alters the electric field generated by the animal's EOD. A similar effect is obtained if two points out in the water and near the animal's body surface are short circuited while the fish discharges its electric organ. The brief acceleration of the pacemaker elicited by this novelty in electroreceptive afferences yields a convenient measure of the animal's ability to detect such novelties. The pacemaker acceleration is a graded response in a twofold manner: First, it increases with the extent to which the animal's electric field is affected, i.e. with the distance of the short circuited electrodes from each other and with the potential difference they straddle. Second, it increases with the number of successive EODs (or S_1 pulses) affected, from one to a few tens. Maintenance of the distortion for a much larger number of EODs does not enlarge the response further, and the rapid return of the pacemaker frequency to its prestimulatory level indicates that the animal adapts to the new state. A similar novelty response is elicited if a maintained distortion is suddenly removed for a sufficient number of EOD cycles. A full response to local field alterations thus requires that at least a small number of successive EODs report a change from the previous state. This suggests integration of messages from successive EODs.

Experiments in this study have shown that the animal detects local distortions in its electric field more readily if the pattern of afferences is stable over

many successive EOD cycles and that any form of stimulation which alters feedback across successive EODs impairs the detection of local field distortions. Such forms of stimulation are the sudden coincidence of foreign pulses, S_2 , with the animal's own EODs (or its substitute, S_1), or the presentation of non-coincident pulses of an intensity high enough to excite electroreceptors, or the presentation of an EOD substitute, S_1 , with an irregular repetition rate. The regular discharge rate in gymnotoid pulse-species, therefore, is adaptive for the detection of novelties, and it is the function of the JAR to avoid sudden and strong alterations in electroreceptive feedback which would result if the animal allowed several successive EODs to coincide with foreign pulses.

Whereas transient alterations in electroreceptive afferences impair the detection of local field distortions, an alteration which is maintained over many EOD cycles becomes harmless as the fish adapts to the new state (cf. Fig. 3a and c). This finding explains that coincident pulses, which impair electrolocation in the related species, *Hypopygus lepturus* (Heiligenberg, 1974), lose their effect if they are presented continually, and with constant orientation to the animal's own EOD field, over tens of minutes (unpublished observation). Under natural conditions, sustained alterations of electroreceptive feedback will result if the animal loses part of its tail (which carries a large section of the electric organ) due to predation or if it decides to hover near an object or in a crevice rather than in open water. The data in this paper indicate that the animal requires only a number of seconds to adapt to a new steady state of electroreceptive afferences. The exact time course of this process could, in principle, be measured by behavioral experiments. The response to novelty in electroreceptive afferences is a typical example of the "orienting reflex" as described by Sokolov (1960). The simplicity of this particular response may facilitate the discovery of neuronal processes which underlie this very common form of behavior. Of particular interest is the nature of the central template which characterizes a steady state of a spatial and temporal pattern of sensory afferences and the way in which sudden deviations from this pattern are detected.

Two types of tuberous electroreceptors are found in gymnotoid pulse-species. The first type marks the occurrence of each EOD by firing a single spike (type I unit according to Szabo and Fessard, 1974, "pulse marker" according to Bastian, 1976). The second type encodes local EOD intensity by varying the number of spikes it fires in a burst with each EOD (type II unit according to Szabo and Fessard, 1974, "burst duration coder" (BDC) according to Bullock, 1968; Bastian 1976). Burst duration coders thus give

graded responses to distortions of the animal's field and therefore are crucial for the detection of moving objects (Schlegel, 1975) as well as for the detection of local short circuits as employed in this study. According to Baker's (1980) studies on tuberous electroreceptors in *Hypopomus occidentalis*, BDCs have thresholds between 30 and 60 mV/cm whereas pulse markers have thresholds between 8 and 50 mV/cm, in water of 5 kOhm·cm. Since the animal's own near field intensity, at this resistivity, is 20 to 30 mV/cm, EODs of neighbors should not be able to drive its BDCs unless they are very close. Pulse markers with lower thresholds, on the other hand, should respond to EODs of distant neighbors and therefore serve in social communication.

BDCs alter their responses if pulses coincide with or briefly precede the animal's EOD, even if these pulses are too weak to recruit BDCs when presented alone (Baker, 1980). In addition, responses of BDCs vary with the time interval at which they are recruited (Fig. 8). The assumption that the animal detects novelty in environmental impedance on the background of a central template, derived from BDC responses, is supported by the fact that all stimulus regimes which most drastically alter the responses of BDCs also most severely affect electrolocation performance. This was found in the present study as well as in a previous study on the related species, *Hypopygus lepturus* (Heiligenberg, 1974, 1977).

Earlier studies on other species of *Hypopomus* (Bastian, 1976) suggested that gymnotoid pulse-species identify feedback from their EODs on the basis of synchronous responses of pulse markers with thresholds so high that they could only be fired by the animal's own EODs (see Fig. 47 in Heiligenberg, 1977). Under this assumption, the animal would update its central template only by BDC messages labelled by these synchronous pulse marker responses and thereby discard BDC messages caused by other fish. However, the results of this paper suggest that the animal, in order to detect novelties in environmental impedance, has no need to identify BDC-feedback from its own EODs as long as it succeeds in stabilizing a central template based upon all BDC afferences. The stability of this template is indeed maintained by timing EODs in a manner that minimizes the probability of coincidences with foreign pulses which otherwise would drastically alter electroreceptive feedback.

A very similar situation appears to exist in gymnotoid wave-species. These fish discharge their electric organ in a continual, near sinusoidal manner rather than in single, discrete pulses. The period of their EOD cycles is so short that an ordinary burst duration coder could not fire more than one spike per EOD,

and EOD intensity is instead encoded in the probability of specific receptors, P-units (Scheich et al., 1973), firing a spike in a given EOD cycle. Again, no evidence could be found that these animals evaluate electroreceptive afferences in reference to their own pacemaker (Heiligenberg et al., 1978b). Electrolocation in wave-species is most severely impaired if the animal's EODs beat against a sinusoidal signal of similar frequency (Heiligenberg, 1977). This interference causes rhythmic surges of P-unit activity which follow the beat envelope and mask P-unit responses to moving objects (Scheich, 1977). However, electrolocation improves to the extent that afferences from P-units can be stabilized. Two different strategies are known: First, the animal succeeds, by means of its JAR (Bullock et al., 1972), in shifting its EOD frequency away from the foreign frequency until the beat frequency is so high that the activity of P-units and their higher order representatives ceases to follow the intensity modulation of the beating stimulus so that the image of objects again emerges (Scheich, 1977; Behrend, 1977). Second, the animal succeeds in abolishing the difference in EOD frequencies by phase locking its EOD to that of its neighbor (Langner and Scheich, 1978). If the orientation of the EOD fields is maintained in this case P-unit activity is stabilized and electrolocation performance improves (Matsubara and Heiligenberg, 1978). In order to detect electric images of objects, the animal does not need to distinguish feedback from its own EOD from sensations caused by foreign EODs. All that is required is a stable background of P-unit activity, regardless of its ultimate source. Much as in pulse-species, the JAR of wave-species serves to stabilize the pattern of intensity-coding afferences.

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