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Physiology & Behavior 68 (1999) 115–128

PHYSIOLOGY & BEHAVIOR

The "novelty response" in an electric fish: response properties and habituation

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Received 7 May 1999; accepted 30 July 1999

Abstract

The electromotor behavior evoked by novel sensory stimuli in the electrogenic teleost fish *Gnathonemus petersii* was examined. Novelty responses (NRs) consisted of a transient accelerations of the rate of electric organ discharges following a change in sensory input. NRs were basically similar in nontreated and in immobilized (treated with curare) fish. NRs could be evoked reliably by brief novel stimuli of all four sensory modalities (acoustic, visual, electrical, electrolocation) used in this study. Stimuli of a duration longer than 5 s caused an on- and off-response. A sudden change in the quality of an ongoing sensory stimulus also evoked novelty responses. NR properties depended on the stimulus modality, stimulus intensity, stimulus duration, and on the prior stimulus history. Habituation of several response parameters of the NR (latency, duration, maximal amplitude, response probability) occurred within a series of repetitive stimuli of a given sensory modality. Each modality appeared to habituate separately. Rate of habituation depended on stimulus intensity and on interstimulus interval. A strong disruptive stimulus of another modality lead to dishabituation. The novelty response evoked by stimuli of low or medium intensities resembled an "orienting response" as described by Sokolov.

Keywords: New stimuli; Orienting response; Defensive response; Weakly electric fish; Electric organ discharge; Arousal

1. Introduction

Animals may respond to novel sensory stimuli either by a defense reaction, a startle reaction, or an "orienting response" [1,2]. The relation between these responses is not clear [3,4]. They are all characterized by a vegetative component (e.g., transient changes in heart and respiration rates, skin conductance, and others) and an electroencephalographic (EEG) component, i.e., changes of certain brain potentials [3,5]. Often, they are also accompanied by a reaction of the skeletal muscles (see, e.g., [6,7]). Defense and startle responses tend to occur after a stimulus of high intensity, which may produce fright [8,9]. Orienting responses, on the other hand, are evoked by low or medium intensity stimuli, and could be a sign of evoking an animal's interest (arousal) in a changing environment [3,5,10].

Key features of the orienting response is the response to novelty and its habituation. According to Sokolov [2,5,10], orienting responses occur after a mismatch is detected between a stimulus and a hypothesized neuronal model of the stimulus (stimulus comparator theory). This mismatch is largest when a novel stimulus occurs, and becomes smaller and smaller with repeated presentation of this stimulus. Habituation of the response to a series of identical stimuli occurs through a permanent updating of the neuronal model by the sensory stimuli and the subsequent decreasing mismatch between the model and the actual stimuli. In general, the lower the stimulus intensity and the shorter the interstimulus interval (ISI), the faster habituation occurs [11,12].

When a strong stimulus is given after the response has habituated to a series of weaker stimuli, orienting will reoccur to the original stimulus, i.e., dishabituation takes place [13,14]. The dishabituating stimulus may reexcite the orienting responses, overriding the inhibition caused by the original habituation [15].

Most studies of orienting responses have been done with mammals, but fish also display behavioral and physiological responses to novel sensory stimuli that may be compared to the orienting responses of mammals. Movements of the pectoral and tail fins as well as erections of the dorsal and anal fins are regarded as orienting response-like arousal reactions in fish [16]. Following a novel stimulus, heart and ventilatory rates decrease and brain activity (EEG) increases [17,18]. In weakly electric fish, orienting responses to novel sensory stimuli are accompanied by a transient increase in the rate of production of electric signals, the so-called "novelty response" [19,20]. The novelty response of

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0031-9384/99/$–see front matter
PII: S0031-9384(99)00153-5

weakly electric fish occurs to mechanical [19,21], acoustical [22], electrical [23–27], and visual stimulation [28]. However, parametric studies of the novelty response in electric fish and analyses of its similarity to the orienting response of mammals have not been carried out.

Electric fish of the family mormyridae produce brief electric signals (electric organ discharges, EOD) with a specialized electric organ in their tail [29]. In the mormyrid *Gnathonemus petersii*, the subject of this study, each EOD is a short all-or-none electric pulse of about 400–500 μs duration. EOD rate depends on the behavioral context and varies from less than 1 Hz to more than 100 Hz [30,31]. During their active period at night, mormyrids orient in complete darkness through the use of active electrolocation [31,32]. In active electrolocation, the fish's own EODs are perceived through cutaneous electroreceptors. Objects close to the fish are detected and evaluated by the distortions they cause in the perceived electric signals. Because each EOD provides information about the environment, an increase in EOD rate increases the amount of information available to the fish. The transient increase in EOD rate during a novelty response thus can be regarded as an active orienting behavior towards a new sensory stimulus [33,34].

The novelty response is an excellent model system for examining the principles of arousal and orienting in fish [10,35–37], because it can be recorded even in a curarized animal that is fixed in an electrophysiological setup [34]. We report here behavioral results that form the foundation for future electrophysiological experiments aimed at finding the neurophysiological basis of the novelty response in this nonmammalian vertebrate. The purpose of the present study was to investigate which sensory modalities can evoke novelty responses, and look for modality- and intensity-specific differences. Furthermore, the dependence of the novelty response on the previous stimulus history was tested for different types of stimuli. Habituation and dishabituation were tested with repetitive stimuli that were sometimes interrupted by sudden disruptive stimuli. Finally, we tested in how far the novelty response fits into the framework of the Sokolovian concept of orienting and defensive responses.

2. Materials and methods

2.1. Subjects and housing

Elephant-nose fish (*Gnathonemus petersii*), of 10–15 cm in length, were obtained from a regular supplier and maintained in 0.5 × 1 × 0.5 m aquaria containing aerated, filtered water at a temperature of 25 ± 2°C and a conductivity of 100–150 μS/cm.

2.2. Experimental procedure

Most experiments were carried out in fish immobilized with curare. In these experiments, the fish was first anesthetized by brief immersion in 0.015% solution of tricaine methanesulfonate (MS-222) and then immobilized by injection of 8–12 μL of 1% Pancuroniumbromid (i.m.). The fish was placed in a water filled Plexiglas tank (16.5 × 40 × 30 cm) on a vibration-isolated table in an experimental chamber (2.25 × 3.25 × 3.3 m) with echo-reducing walls and Faraday isolation. Water conductivity was held constant at 100 μs/cm and temperature at 25°C. Experiments were done in complete darkness. Electric cables and water tubes for respiration were lead outside the chamber through small holes in the chamber's wall, and no electronic equipment remained inside the chamber. The fish was aerated by passing fresh aquarium water through its mouth and over the gills. Before starting an experiment, we waited at least 45 min to let the effect of the MS-222 fade away and calm the fish down after handling.

Curare blocks the generation of electric pulses by the electric organ. However, spinal cord motor commands, which elicit electric organ discharges in the noncurarized fish, are still produced at a regular rate, and can be recorded with a silver wire electrode bent around the fish's tail [38]. The rhythm of motor command production corresponds to the EOD rhythm in normal fish without curare [25]. In some experiments, prerecorded natural EOD signals were stored in an arbitrary waveform generator and substituted for the fish's own EODs (Wavetek Model 395). The substitute EODs were played to the fish through one chloride silver electrode inserted in its stomach and another electrode placed in the water behind its tail. Each of these EODs was triggered by the spinal motor command with a delay of 4.5 ms, a delay that corresponds to the natural delay between these two signals [38]. The geometry and amplitude of the substitute signal resembled that of the self-produced natural EODs [34].

Recorded motor commands of curarized fish were amplified, filtered between 600 and 1300 Hz, and transformed into trigger pulses. Trigger events were digitized by a "1401 plus" converter (CED, Cambridge) and fed into a computer. During each experiment, instantaneous discharge frequency was calculated (inverse of time period between two motor commands), and frequency–time plots were created, which could be observed on-line on the computer screen using "spike 2" software (CED, Cambridge). In these plots, novelty responses following a sensory stimulus consisted of a transient increase in command frequency lasting between 300 ms and several seconds.

Novelty responses were also investigated in some noncurarized fish. After brief anesthesia with MS-222, a fish was inserted into a custom-made loose-meshed plastic grid cage that was positioned in the center of the experimental tank. Fish could not move inside the cage, because its size was adjusted for each fish so that all four walls lightly touched its body. Because these fish did not receive any Pancuronium, they continued to produce EODs, which were recorded with two differentially amplified carbon electrodes positioned close to the head and the tail of the fish, respectively. Fish were stimulated in the same way as in curarized

fish, and recorded EODs were processed in the same way as spinal motor commands.

2.3. Sensory stimuli

Sensory stimuli of four different modalities were produced by the computer using the D/A-output channels of the CED 1401plus controlled by the Spike2 sequencer program. The computer triggered a frequency generator (Wavetek Model 395), which produced the acoustical or electrical stimuli. Acoustical stimuli were fed to a loud speaker suspended over the experimental tank at a distance of 40 cm. Sound stimuli (frequency: 500 Hz, duration: 100 ms, abrupt rise and fall times) were amplified by an 80-Watt audioamplifier. Several sound intensities were used, which were measured with a hydrophone (Bruel & Kjaer, Type 8103) in the water without a fish present at the same position where the fish was placed during experiments. All sound intensities are expressed in dB relative 1 dyne/cm^2. To present an electrical stimulus (electrocommunication), a single-period 3-KHz sinewave pulse was fed to two carbon rods (diameter 5 mm) separated by 3 cm and placed at a distance of 3 cm parallel to the fish in the water.

Visual stimuli were produced by a red photodiode placed at a distance of 2 cm in front of the fish's right eye. The diode was connected directly to one 1401plus output channel. Light flashes had a duration of 10 ms and variable intensities, which were measured with a Lux-meter (Panlux electronic 2, Grossen, Germany). Electrolocation stimuli were produced by changing the electrical properties of a so-called "dipole object" [39], which was placed at a distance of 3 cm from the fish's head. Dipole objects had the form of an inverted T. The horizontal part of the T was a Plexiglas tube with a diameter of 6 mm and a length of 2.5 cm, in which a carbon electrode with a cable connected to it was inserted at each end. Through the vertical part of the dipole object, the two cables from the carbon electrodes ran outside the water of the tank. The electrical resistance of the dipole objects could be changed by connecting these cables to resistors of certain values. Switching between different resistors was carried out by electrical relays, which were controlled by computer. The dipole object's electrical resistance thus could be varied between 10 MΩ and 3 Ω without moving the object. An electrolocation stimulus was produced by reducing the resistance of the object from its steady value of 10 MΩ to a value of 200 kΩ for a time period of 1 s.

2.4. Experiment I: Novelty responses in curarized and noncurarized fish

Experiments with acoustical stimuli were conducted to compare novelty responses of curarized ($n = 14$) and untreated ($n = 4$) fish. The experimental design was identical with the two groups of fish: a series of 10 brief sound pulses (duration: 100 ms, frequency: 500 Hz, intensity: 22 dB) was delivered to the fish. Interstimulus intervals (ISI) were either 60 or 5 s. During each session, which lasted about 8 h, approximately seven series of 10 stimuli each were delivered. Between two series there was a pause without any sensory stimuli of at least 10 min.

The EOD rhythm (nontreated fish) or the rhythm of spinal motor commands (curarized fish) were recorded during each stimulus series to investigate novelty response behavior. Each novelty response evoked by a stimulus was analyzed (see below) and response parameters of all fish of each group were averaged for each stimulus of the series.

2.5. Experiment II: Novelty response and stimulus intensity

The aim of this experiment was to examine the relationship between stimulus intensity and novelty response magnitude in curarized fish ($n = 6$). In addition, we tested whether the responses to two stimuli of different modalities presented simultaneously summarized ($n = 3$). Two different sensory modalities (visual and acoustic) were tested. Single visual (10 ms duration) and acoustical stimuli (100 ms) were given at the following intensities: light: 0.1, 3, 40, 120, 210, and 300 lx; sound: 14, 20, 26, 30, 32, 35, and 37 dB. Stimuli of different intensities were presented randomly with an interstimulus interval (ISI) of 10 min. Novelty response parameters were averaged for each intensity. The first 10 stimuli during each session were not included for averaging to bring the response magnitude to a constant habituation level (see below).

For pairing of two stimuli of different modalities, a light stimulus of 0.1 lx and a sound stimulus of 20 dB were presented simultaneously in such a way that the onset of the two stimuli occurred at the same time. For these tests, a number of three fish were used (the same fish that were also used for testing the effect of stimulus intensity), each presented with 21 pairs of stimuli.

2.6. Experiment III: Novelty responses to longer lasting sensory stimuli

Constant stimuli lasting longer than standard stimuli (see above) were used in order to test whether fish ($n = 9$) also responded with a novelty response to the end of a stimulus. Light or sound stimuli with durations of 2.5, 5, 10, 20, 30, 40, or 60 s were presented to the fish. The stimulus intensities were 0.1 lx (light) or 22 dB (sound), respectively.

2.7. Experiment IV: Novelty responses following a brief change in stimulus frequency

In this experiment we tested whether changes in stimulus quality evoke novelty responses ($n = 3$). A continuous acoustic stimulus with a frequency of 500 or 600 Hz and an amplitude of 22 dB was presented to a fish. After a time period of 60 s, the frequency of the stimulus changed from 500 to 600 Hz (or from 600 to 500 Hz), and then returned to 500 (600) Hz after 1 s. This brief frequency change was repeated 10 times with an ISI of 10 s. Stimulus amplitude was held constant throughout the experiment. Thirty seconds after the last frequency change, the acoustical stimulus was turned

off. We analyzed the fish's response to the brief changes in frequency. To detect novelty responses, the discharge frequencies of the fish were compared statistically 3 s before and 3 s after the presentation of the frequency change.

2.8. Experiment V: Habituation of the novelty response to a series of repeated stimuli

To test whether stimulus novelty was critical for novelty response elicitation, we presented series of 10 identical stimuli to a fish ($n = 10$). Four different stimulus modalities were employed: visual stimuli (intensity: 0.1 or 300 lx, duration: 10 ms), acoustical stimuli (intensity: 22dB or 37 dB, frequency: 500 Hz; duration: 100ms), electrolocation stimuli (change in resistance of dipole object from 10 MΩ to 200 MΩ, duration: 1 s), and electrocommunication stimuli (single sine wave at 3 kHz, amplitude: 4 mV/cm). Interstimulus intervals (ISI) of 120, 60, 30, 10, 5, and 3 s were used. In control experiments, no stimuli were presented and the spontaneous discharge behavior of the fish at fixed time intervals was recorded to determine the rate of occurrence of "spontaneous" discharge rate accelerations.

During one experiment, 7–10 series of 10 stimuli each were presented to a fish, with a 30-min pause after each series in which no stimulus was given. At least five individual fish were tested with each series. Responses of all fish to each stimulus of a given series were averaged.

2.9. Experiment VI: The effect of a change in stimulus modality on habituation of the novelty response

In this experiment we examined the effect of a change in stimulus modality within a stimulus series on novelty response habituation ($n = 4$). A total of 20 stimuli of two modalities (10 visual stimuli followed by 10 acoustical stimuli) were presented with an ISI of 10 s. Stimulus intensities of both modalities were weak (0.1 lx, 22 dB). The habituation of novelty response parameters within each series of 20 stimuli was monitored. Results were compared with those obtained with a series of 20 acoustical stimuli without any previous visual stimulation.

2.10. Experiment VII: Dishabituation of the novelty response

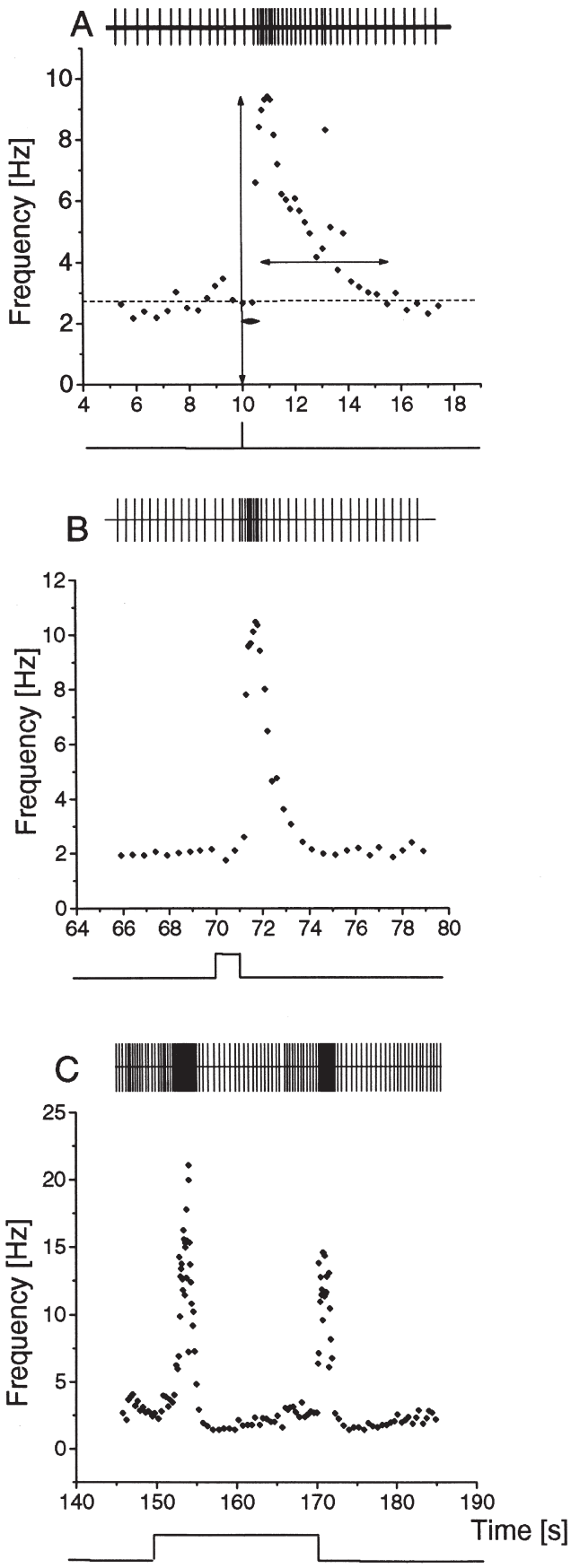
Habituation is characterized by the possibility of dishabituation, which means that a disrupting stimulus, for example, of another modality, leads to the reoccurrence of the habituated response [40]. In this experiment, we tested whether dishabituation of the novelty response occurs after a fish's responses has reached a constant habituated level during a series of identical sensory stimuli ($n = 15$). A series of 20 identical stimuli of one modality (acoustical, visual, electroreceptive) of weak intensity were given with an ISI of 15 s. Between the 10th and the 11th stimulus, a high amplitude stimulus of another modality was introduced. Novelty response parameters before and after the disrupting stimulus were compared. Different combinations of habituating and sensitizing stimuli were employed. In control experiments, the dishabituating stimulus was omitted.

2.11. Data analysis

In the absence of sensory stimuli, curarized fish usually generated spinal motor commands at a regular rate of 2–5 Hz in the experimental apparatus. The fish's mean instantaneous discharge frequency and its standard deviation was measured before each stimulus series (baseline rate). Fish sometimes showed spontaneous increases in discharge rate that resembled novelty response in shape and duration. Because of the spontaneous rate increases, a novelty response was only counted as such if it occurred within a time interval of 1.5 s after the stimulus. The beginning of a novelty response was defined as the time when the discharge frequency of the fish surpassed the baseline frequency plus one standard deviation. The end of a novelty response was defined as the time when the frequency fell below this value. The responses to stimuli that fell right into a time period containing a spontaneous discharge acceleration were not counted as novelty responses. These missed values in a sequence of stimuli were replaced by the average of the responses to the previous and to the following stimuli [41]. A missed response to the first stimulus of a series was replaced by the response value to the second stimulus. A missed last stimulus was replaced by the value previous to the last.

Several parameters of the novelty response were analyzed. We usually prepared frequency/time plots of the fish's discharge behavior and analyzed the duration, amplitude, and latency of the transient frequency increases that constituted a novelty response (see Fig. 1A). In most cases, the best quantitative response measure was novelty response duration (see Results). Therefore, duration of the response was used to quantify novelty responses in the habituation experiments. Relative habituation measures were obtained by normalizing the raw data to the maximum value within a series. To do so, the strongest novelty response (the one with the longest duration) measured within a series was set to 1. All other responses were expressed in numbers relative to this (between 0 and 1). Usually the responses of several fishes, each of which was given several identical series of stimuli, were averaged. For each stimulus number of a series we calculated the mean response magnitude and the standard error of the mean. Experimental designs with different interstimulus intervals were analyzed using normalized data to lower the effects of interindividual variation.

Habituation curves often show a negative exponential slope [42]. For this reason, habituation data points were fitted to a first-order exponential decay curve. The rate of habituation was expressed as the difference in response amplitude to the first and last stimulus determined from the fitted response curve. We tested for significance of habituation with a Wilcoxon signed-rank test comparing responses to the first and last stimulus of a series. All paired comparisons



of dependent data during Experiments II, IV, VI, and VII were done in the same way. Independent data sets (Experiments I, II) were compared statistically using a Mann–Whitney *U*-test. Comparisons of more than two data sets were done by using the Kruskall–Wallis ANOVA with multiple comparisons (Experiment V).

3. Results

3.1. Common novelty response characteristics

Curarized *Gnathonemus petersii* emit electric organ discharges at a rate of about 2–5 Hz. This baseline discharge frequency is relatively stable under constant conditions (Fig. 1). Novel sensory stimuli usually evoked novelty responses with the following basic properties (see Fig. 1): after latency of $\leqslant$1.5 s, the fish's discharge frequency increased up to 35 Hz. The first discharge interval, within which the stimulus occurred, is often shortened. After reaching a peak amplitude value, the discharge frequency quickly decreases and reaches baseline level after a variable response duration of between 400 ms and 8 s.

Fish usually responded with a novelty responses to the sudden occurrence of a sensory stimulus of every modality tested. Novelty responses were also evoked by the sudden offset of long lasting stimuli (see Experiment III; Table 1; Fig. 1C). In addition, novelty responses could be evoked by a change in quality of an on-going stimulus, for example, by a change in intensity or in frequency of an acoustical background stimulus (see Experiment IV; Fig. 1B). Finally, novelty responses were often evoked when a series of sensory stimuli with a short ($<\sim$2 s), constant interstimulus interval was suddenly interrupted, or the quality of individual stimuli within the series changed. In general, novelty responses were evoked when a sudden change in amplitude or quality of the on-going sensory input to a fish occurred. The probability of a novelty response to the sudden occurrence of a sensory stimulus was high; nevertheless, fish did not respond in 100% of the cases. As shown below, fish failed to respond when a spontaneous acceleration occurred just before the stimulus, and the probability of a novelty response decreased with repeated presentation of the same stimulus (see below).

Fig. 1. Examples of novelty responses to three different types of sensory stimuli in curarized fish. Each part of the figure shows the series of EOD commands of a single fish at the top with each EOD command represented by a vertical line. The middle diagram depicts frequency of EOD commands versus time. The third trace shows the occurrence of the stimulus. (A) The stimulus was a 10-ms light flash. The length of vertical double arrow corresponds to the maximal amplitude of the novelty response evoked by the stimulus. The small horizontal double arrow gives the latency, and the large horizontal double arrow depicts novelty response duration. (B) The stimulus consisted of a change in frequency from 500 to 600 Hz of an on-going constant amplitude acoustical stimulus. (C) The stimulus was a 20-s constant amplitude acoustical stimulus (constant frequency tone of 500 Hz). Note that the fish responded with a novelty response both to stimulus on and off.

Table 1
On and off responses to longer lasting, constant-amplitude acoustical (500-Hz) stimuli of different durations

Stimulus duration (s)	On and off responses (%)	Only on responses (%)	Only off responses (%)	*n*
40	80	20	—	5
30	70	30	—	10
20	77	23	—	13
10	60	30	10	10
5	44	56	—	9
2.5	30	70	—	10
2	—	100	—	5

In a few individuals, novelty responses to acoustical or visual stimuli were sometimes preceded by a discharge break, which occurred directly after stimulus onset. This means, that the first discharge interval following the stimulus lasted longer than the mean interval before the stimulus. Stimulus-evoked discharge breaks could last between 0.5 and 2 s. In most cases, the break was followed by a standard novelty response, i.e., by a discharge frequency acceleration. Sensory-evoked discharge breaks were not systematically analyzed in this study.

As noted above, most fish showed "spontaneous accelerations" of their discharge rate. The frequency of occurrence of these spontaneous accelerations varied between 2 and 12 accelerations/minute in different fish.

When a sensory stimulus occurred within or directly after (up to ~1.5 s) a spontaneous discharge acceleration, the fish did not respond with a novelty response to a weak or medium amplitude sensory stimulus. The length of this refractory period following discharge acceleration was inversely correlated with stimulus amplitude.

3.2. Experiment I: Comparison of novelty responses in curarized and noncurarized fish

Noncurarized fish had a basic EOD discharge rate between 5 and 10 Hz, which was higher than that of curarized fish. In addition, their rate of spontaneous accelerations was higher than that of curarized fish. It was between 10 and 30 accelerations/minute in individual fish. Curarized and noncurarized fish behaved basically similar in response to novel sensory stimuli (Fig. 2). They both responded to a sudden change in sensory input of any kind with a novelty response. However, absolute amplitudes and duration of novelty responses were usually larger in noncurarized fish than in curarized fish (Mann–Whitney *U*-test, $p < 0.0001$) (Fig. 2). In both groups of fish, novelty response amplitudes and duration decreased (habituated) in a similar way after repeated stimulation within a series of 10 identical stimuli. In both groups of fish, habituation was more pronounced when the interstimulus interval (ISI) was 5 s instead of 60 s (see below). The rate of habituation was similar in curarized and noncurarized fish, which became obvious when novelty response parameters were normalized. All normalized data sets were not significantly different (Mann–Whitney *U*-test), except for response duration with an ISI = 5 s (Mann–Whitney *U*-test, $p < 0.02$) (Fig. 2).

3.3. Experiment II: Novelty response and stimulus intensity

The amplitude of certain response parameters of the novelty response depended on stimulus amplitude. In general, high-amplitude stimuli evoked novelty responses that had a short latency, a high peak response amplitude, and a long duration (Fig. 3). We systematically studied the effect of acoustical and visual stimuli of different intensities on several novelty response parameters. When visual stimuli were used, novelty response latency was inversely correlated and response duration was directly correlated with stimulus amplitude (Fig. 3A and E). Novelty response amplitude remained almost constant, with increasing light intensities except for very high intensities (Fig. 3C). With acoustical stimuli, novelty response latency was again inversely correlated with stimulus intensity, while response amplitude was directly correlated with intensity (Fig. 3B and D). The rela-

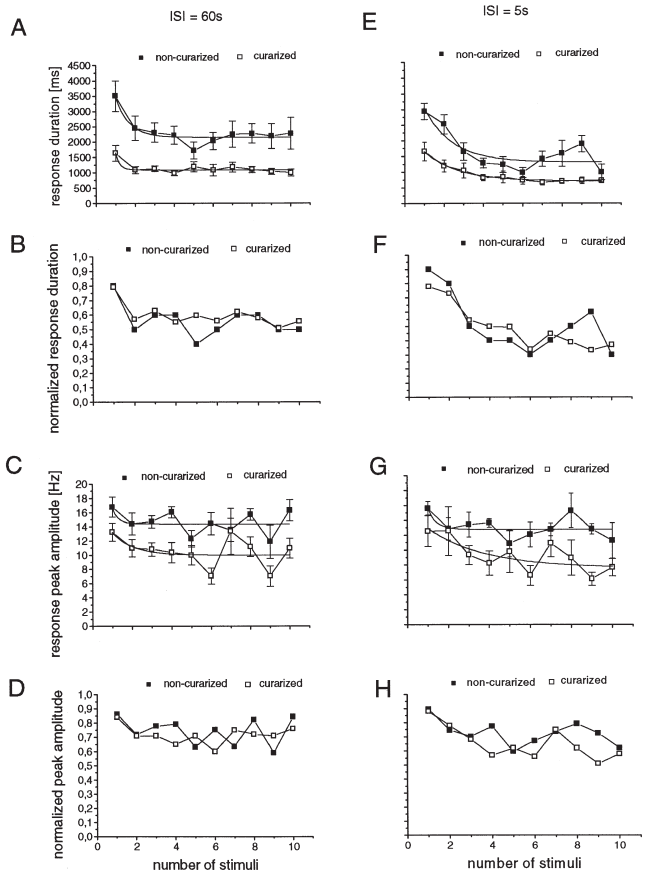


Fig. 2. Comparison of novelty response habituation in curarized (open squares, $n = 14$) and noncurarized fish (solid squares, $n = 4$). A series of 10 acoustical stimuli (100 ms, 500 Hz) were given with an interstimulus interval of 60 s (left column) and 5 s (right column). The novelty response parameters duration and amplitude were measured. In A, C, E, and G absolute mean response values (±SE) are shown together with an exponential function fitted to the data set. In B, D, F, and H the same data are presented as normalized response values (means). ISI 60 s: $n = 12$; ISI 5 s: $n = 12$.

tion between novelty response duration and sound intensity was more complicated: very low sound intensities evoked NR of relatively long durations, while medium and very high intensities caused response duration to be quite short. When acoustical stimuli of a very high intensity were presented, novelty response amplitude and duration decreased (Fig. 3D and F). With very weak sound stimuli, fish responded more unreliably, and the variation in responses latency and duration was larger (Fig. 3B and F).

When two low-amplitude visual and acoustical stimuli were presented simultaneously to a fish, the resulting novelty response was of a longer duration, and occurred at a shorter latency compared to that evoked by just one of the two stimuli presented alone (Fig. 4).

3.4. Experiment III: Novelty responses to longer lasting sensory stimuli

Longer-lasting sensory stimuli evoked two novelty responses: one at stimulus on, and one at stimulus off (Fig. 1C). The on-response was usually stronger and more reliable than the off-response (Table 1). Stimulus durations ⩽2 s evoked only an on-response. The probability of an off-response increased with increasing stimulus durations. However, even with very long lasting stimuli, fish failed to give an off-response in about 20% of the cases (Table 1).

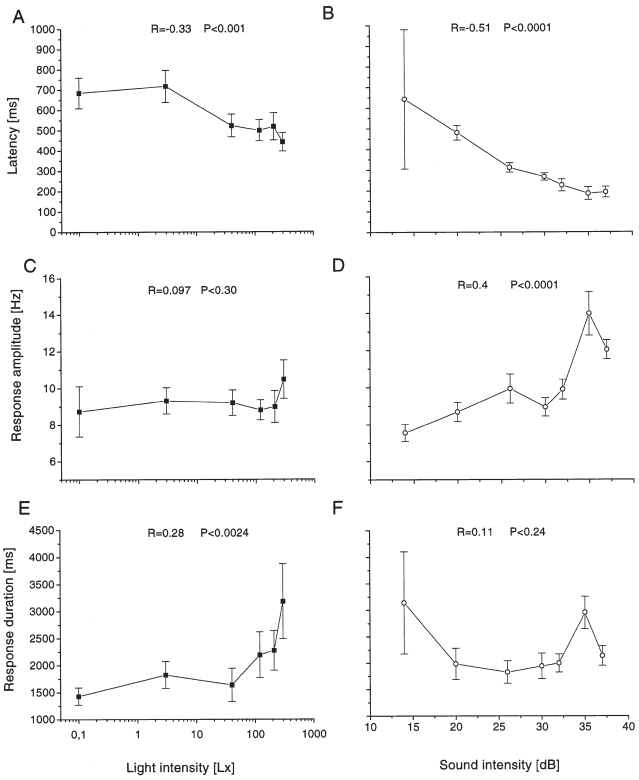


Fig. 3. Dependency of novelty response parameters on stimulus amplitude. Six 10-ms visual (A, C, E) or seven 100-ms (500 Hz) acoustical (B, D, F) stimuli of different intensities were presented to a curarized *G. petersii* in random order. Values are means plus standard errors. Three novelty response parameters were analyzed: response latency (A, B), response amplitude (C, D), and response duration (E, F). In each graph the correlation coefficients (*r*-values) and levels of significance are indicated ($n = 6$).

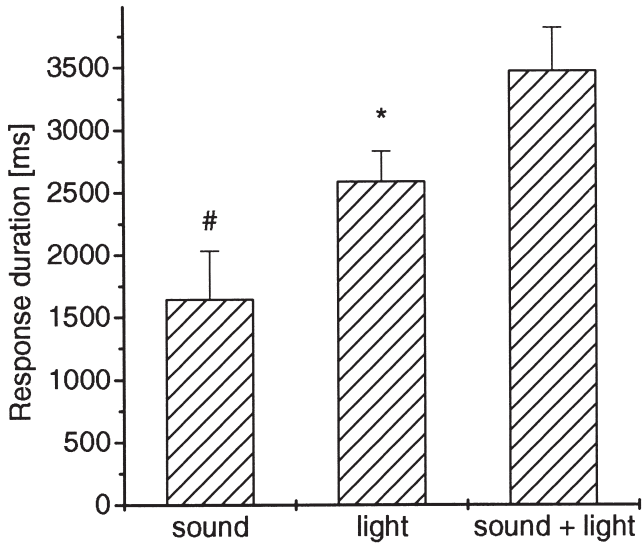


Fig. 4. Summations of the effect of two stimulus modalities presented simultaneously to a curarized fish. Mean (±SE) novelty response durations evoked by an acoustical stimulus (100 ms, 500 Hz, 22 dB) alone (left column), by a visual stimulus (10 ms, 0.1 lx) alone (middle column), or by the two stimuli presented simultaneously (right column) ($n = 12$). Columns with single modalities were compared with the column of two modalities on the right. $^{\#}p < 0.002$; $^{*}p < 0.04$.

3.5. Experiment IV: Novelty responses following a brief change in stimulus frequency

Gnathonemus petersii responded with a novelty response to a sudden change in frequency of a continuous constant-amplitude acoustical stimulus (Fig. 1B, Table 2). Both, a change to a higher (from 500 to 600 Hz) as well as to a lower frequency (from 600 to 500 Hz) evoked novelty responses with the same probability.

Table 2
Novelty responses after an increase or decrease in frequency of a constant-amplitude acoustical stimulus (mean interval duration 3 s before and 3 s after the change)

Frequency change	Number of experiment	Mean interval duration before change (ms)	Mean interval duration after change (ms)
500–600 Hz	1	493	228
	2	457	256
	3	360	224
	4	361	202
600–500 Hz	1	507	177
	2	486	200
	3	408	233

All changes in interval duration are significant, $p < 0.05$ (Wilcoxon signed-rank test).

3.6. Experiment V: Habituation of the novelty response to a series of repeated stimuli

When a series of 10 or 20 identical stimuli were presented to a fish, novelty responses to the later stimuli were usually weaker compared to those evoked by the first stimuli of the series, i.e., NRs habituated. However, individual responses in single series of stimuli could sometimes fluctuate considerably, and could even, in rare cases, show phases of increasing response amplitude after a number of stimuli, a phenomenon that has been found before in other species and other behaviors [42,43]. For this reason, response parameters were averaged across individuals and trials.

Several response parameters of the novelty response showed habituation: response amplitude was high to the first few stimuli of a series and then decreased to reach a constant habituation level after a certain number of identical stimuli (Fig. 5A). NR duration was long at the beginning of a stimulus series and then decreased (Fig. 5A). In contrast, response latency was short after the first few stimuli, and increased towards the end of a stimulus series (Fig. 5A). In addition, the probability of the occurrence of a novelty response, which was almost 100% to the first stimulus of a series, decreased quickly within a series to reach a level of 50–60% or less towards later stimuli (Fig. 5B). Novelty responses within a series of 10 stimuli habituated with every kind of sensory modality used in this study.

Even though all parameters mentioned above habituated within a series of stimuli, the degree of habituation and the amount of fluctuation of individual responses varied. Response latency turned out to be the most unreliable parameter. In individual trials, response latency was unpredictable and even after averaging over many series, response latency curves often stayed quite “noisy” (Fig. 5A). Response amplitude, i.e., peak discharge frequency values evoked by a stimulus, decreased within most stimulus series, but this decrease was clearly smaller than that for response duration, and there were always some experimental series with only a small changes in response amplitude after 10 stimuli (Fig. 5A). The probability of the occurrence of a novelty response varied rather strongly between individual fishes and was, therefore, not regarded as a reliable measure of for habituation (Fig. 5B). Therefore, the change in response duration was chosen as the most reliable measure for habituation. Response duration decreased reliably within a series of 10 stimuli, and its fluctuation between series and fish was less pronounced than that of the other NR parameters (Fig. 5).

3.6.1. Effects of stimulus intensity

In general, habituation of the novelty response was stronger in series with low stimulus intensities than in series with stimuli of high intensity (Fig. 6). No significant habituation of novelty response duration was found in most stimulus series when visual (300 lx) or acoustical (37 dB) stimuli of high intensities were used. However, because habituation also depended in an inverse manner on inter-stimulus interval (ISI, see below), there was some degree of habituation

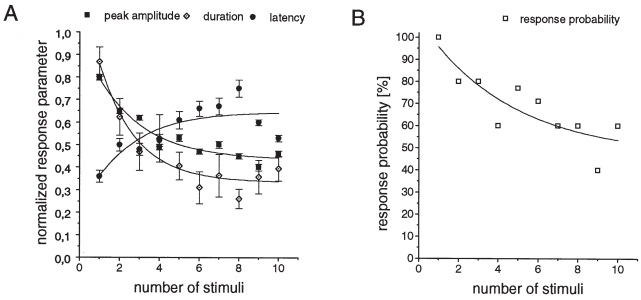


Fig. 5. Habituation of the novelty response in series of 10 identical visual stimuli (10 ms, 0.1 lx). Shown are mean values (±SE) for 20 curarized fish together with exponential functions fitted to each data set. (A) The normalized novelty response parameters peak amplitude, response duration, and response latency are shown. (B) The probability of the occurrence of a novelty response is shown ($n = 20$). In all four curves shown in A and B, the response to first stimulus was significantly different from the response to the 10th stimulus (Wicoxon signed-rank-test, p always < 0.01).

in stimulus series with high-intensity stimuli when the ISI was short (Fig. 6). In particular, there was no significant habituation in series with high-intensity sound stimuli except when the ISI was ≤5 s (Wilcoxon signed-rank test, $p < 0.05$). With high-intensity visual stimuli, habituation was only significant when the ISI was 30 or 5 s ($p < 0.05$). In contrast, with low-intensity stimuli, habituation was significant in most series. In particular, with visual or electrical low-intensity stimuli all series with ISIs smaller than 120 s showed significant habituation. With acoustical low-intensity stimuli, series with ISIs smaller than 60 s and with low-intensity electrolocation stimuli series with ISIs smaller than 30 s habituated significantly (Wilcoxon signed-rank test, $p < 0.05$).

3.6.2. Effects interstimulus interval duration

In general, shorter interstimulus intervals caused a more rapid habituation than longer ISIs. There was a gradual increase in the degree of habituation when ISIs were reduced (Figs. 7 and 8) for all modalities except for the acoustic modality used in this study. Response curves obtained with longer ISIs are significantly different from those obtained with shorter ISIs with all sensory modalities tested (see Fig. 8A, B, and D), except for acoustical stimuli (Fig. 8C) (Kruskall–Wallis ANOVA followed by multiple comparisons, visual stimuli $p < 0.0001$; electrical stimuli $p < 0.005$; electrolocation stimuli $p < 0.002$).

The four stimulation modalities used caused different rates of habituation when different interstimulus intervals were employed (Fig. 8). Rate of habituation was measured by subtracting the normalized novelty response duration to the first stimulus from that caused by the 10th stimulus of a series. Values were taken from the fitted exponential functions for each data set. In general, the amount of habituation decreased when the interstimulus interval increased. However, when acoustical stimuli were used, the rate of habituation was relatively small and almost constant for all ISIs,

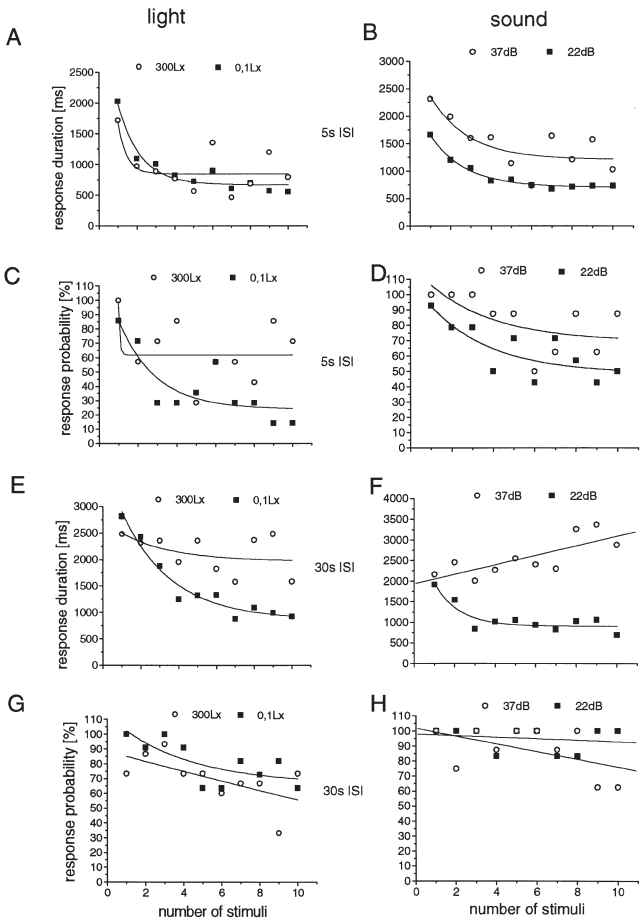


Fig. 6. Habituation of the novelty response at high and low stimulus intensities. Visual (left column) and acoustical stimuli (right column) of either high (solid squares) or low intensity (open circles) were used. A series of 10 identical stimuli was presented at an interstimulus interval of either 5 s (A–D) or 30 s (E–H). Novelty responses were quantified by measuring either response duration (A, B, E, F) or response probability (C, D, G, H). Shown are mean values obtained from 10 curarized fish together with exponential function fitted to each data set ($6 \leqslant n \leqslant 11$).

except for an ISI of 120 s. In the latter case, habituation was absent (Fig. 8C).

3.7. Experiment VI: The effect of a change in stimulus modality on habituation of the novelty response

The goal of this experiment was to test whether novelty responses evoked by sound and light stimuli habituate independently from one another. A series ($n = 11$) of 10 low intensity visual stimuli (0.1 lx) with an ISI of 10 s were presented to a curarized fish. Novelty response durations habituated in the usual way. Ten seconds after the 10th stimulus of the first series, a second series of ten low intensity (22 (dB) acoustical stimuli with the same ISI of 10 s was started. The change in stimulus modality between the 10th and 11th stimulus caused an increased novelty response at the beginning of the new series. With continued acoustical stimulation, novelty response quickly habituated

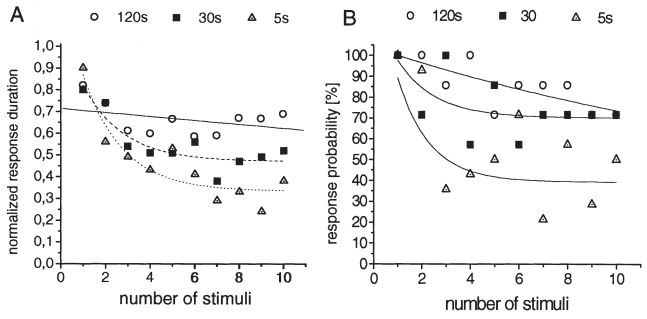


Fig. 7. Habituation of the novelty response at different interstimulus intervals. A series of 10 identical visual stimuli (0.1 lx) was presented to the fish at three different interstimulus intervals (120 s, 30 s, 5 s). NRs were quantified by measuring response duration (A; normalized data shown) and response probability (B). Given are mean values obtained from 10 curarized fish together with an exponential function fitted to each data set ($n = 9$).

again to a low level (Fig. 9). A Wilcoxon signed-rank test showed that the difference in response duration after the modality change was significant ($p < 0.01$). An acoustical control series ($n = 11$) with the same sound stimuli and the same ISI but without the previous visual stimulus series resulted in a similar habituation curve. However, there was a tendency for habituation to occur faster when a series of visual stimuli was presented before the acoustical stimulus series (Mann–Whitney *U*-test, $p < 0.02$).

3.8. Experiment VII: Dishabituation of the novelty response

The goal of this experiment was to prove the existence of dishabituation of the novelty response by a high amplitude stimulus of another modality. In a series of 20 test stimuli with a constant ISI of 15 s, a dishabituating stimulus was presented between the 10th and 11th stimulus. Figure 10 shows an example of dishabituation with a visual sensitizing stimulus (300 lx) within a series of 20 electrical test stimuli ($n = 20$). Within the first ten stimuli, the novelty response habituated in the usual way. The presentation of the high-amplitude visual stimulus between the 10th and the 11th stimulus, evoked a strong novelty response. In addition, stimulus #11 of the original series evoked a novelty response, which was of a significantly longer duration compared to the preceding 10th stimulus (Wilcoxon signed-rank test, $p < 0.008$). During the following test stimuli, the NR habituated again, and finally reached a level similar to the one before the sensitizing stimulus. When no sensitizing stimulus was given in the control series, habituation was unaffected and the novelty response duration remained on a low level after the 10th stimulus (Fig. 10).

Figure 11 shows the habituation plus dishabituation curves of different combinations of stimulus modalities for test and dishabituation stimuli. In four out of six combinations tested significant dishabituation occurred, and the resulting curves had a similar general shape (Wilcoxon signed-rank test, $p < 0.03$). Dishabituation was not signifi-

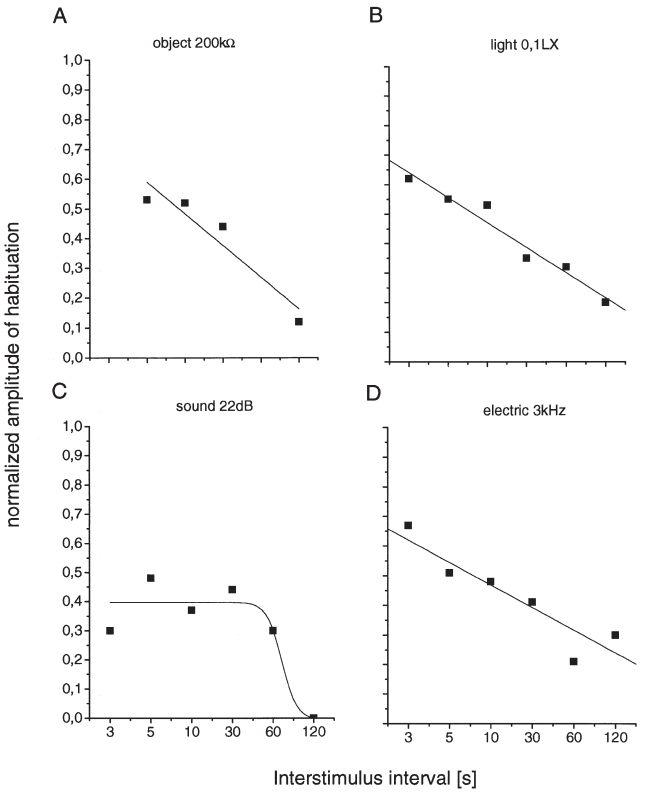


Fig. 8. Rate of NR habituation in curarized fish at different interstimulus intervals in four sensory modalities. Each diagram shows the rate of habituation, which was measured by subtracting the normalized novelty response duration to the first stimulus from that caused by the 10th stimulus of a series. Values were taken from the fitted exponential functions for each data set. Mean values are shown together with the function of best fit. (A) The stimulus was the sudden appearance of a resistive object of 200 kΩ ($N = 5$). (B) The stimulus was a low-intensity (0.1 lx) light flash of 10 ms duration ($N = 10$). (C) The stimulus was a 100-ms 22-dB tone of 500 Hz ($N = 10$). (D) Single-period sine wave electrical signals of 3 KHz were used as stimuli ($N = 10$).

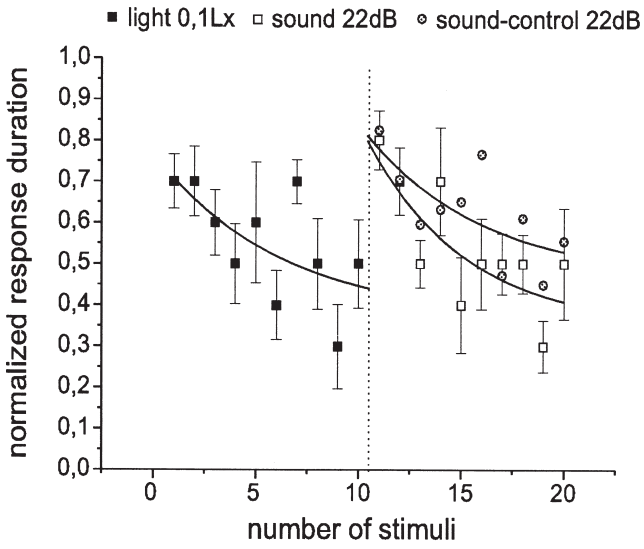


Fig. 9. Habituation to two subsequent series of 10 stimuli each of visual and acoustical stimuli. A series of 10 identical low-intensity (0.1 lx) visual stimuli (solid squares) was presented to the fish immediately followed by a series of 10 low-intensity (22 dB) acoustical stimuli (open squares). Gray circles give data of a control series, which consisted of 10 acoustical stimuli not preceded by visual stimuli. Mean values (±SE) obtained from four curarized fishes are shown together with an exponential function fitted to each data set ($n = 12$).

cant only when visual or electrical test stimuli were combined with an acoustical dishabituating stimulus ($p > 0.05$).

4. Discussion

Gnathonemus petersii responds to the unexpected occurrence of a sensory stimulus of every modality or to a change in quality of an on-going sensory input with a transient increase in discharge frequency of its electric organ (Fig. 1). This electromotor reaction has been called “novelty response” [20,34,44]. Similar “novelty responses” can be found in the two unrelated groups of weakly electric pulse fish from Africa and South America [23]. Because each electric organ discharge ultimately provides the fish with information about its environment (active electrolocation), an increase in the rate of EOD emission results in an increased flow of sensory information to the fish. One of the functions of the novelty response, therefore, might be to direct attention of the animal towards a novel sensory stimulus and to obtain more information about it.

Novelty responses occur both in untreated and in curarized animals. Even though there are differences in electromotor production when motor responses are blocked by curare, the basic features of the novelty response appear to be preserved. The rhythm of EOD production is slowed down with curare, and there are fewer spontaneous accelerations of the discharge rate. In addition, novelty response duration and amplitude is reduced (Fig. 2). However, with all interstimulus intervals tested, habituation of the novelty response still occurs. Moreover, normalization of the data revealed that the rate of habituation is similar in curarized and untreated fish (Fig. 2). The fact that novelty responses can still be recorded and their basic features remain intact in curarized fish opens up the opportunity to study the neural correlates of this behavior using electrophysiology.

In *G. petersii*, novelty response parameters such as duration, peak amplitude, and latency depended on stimulus intensity. In general, if stimulus intensity was high, the fish responded with a short latency, a high-response amplitude, and a long response duration. That is, high-stimulus amplitudes caused “stronger” novelty responses (Fig. 3). Response strengths to individual stimuli were quite variable, especially when stimuli of higher intensities were used. In addition, NR amplitude and duration decreased again for sound stimuli of the highest intensity used. Perhaps very high stimulus intensities induced fright leading to an inhibition of a larger response. Sound stimuli of very low inten-

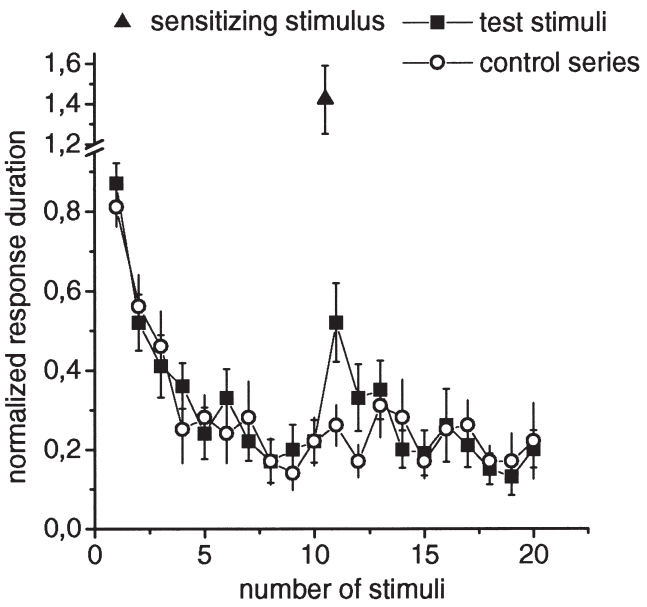


Fig. 10. Dishabituation of the novelty response. A series (solid squares) of 20 identical electrical stimuli (single period 3 kHz since wave, 4 mV/cm) with an ISI of 15 s was presented to a curarized fish. Between stimulus #10 and #11, a high-intensity visual stimulus (10 ms, 300 lx) was presented, which caused a strong novelty response (solid triangle). An uninterrupted control series of electrical stimuli is also shown (open circles). Values are means (±SE) ($N = 6$; $n = 20$).

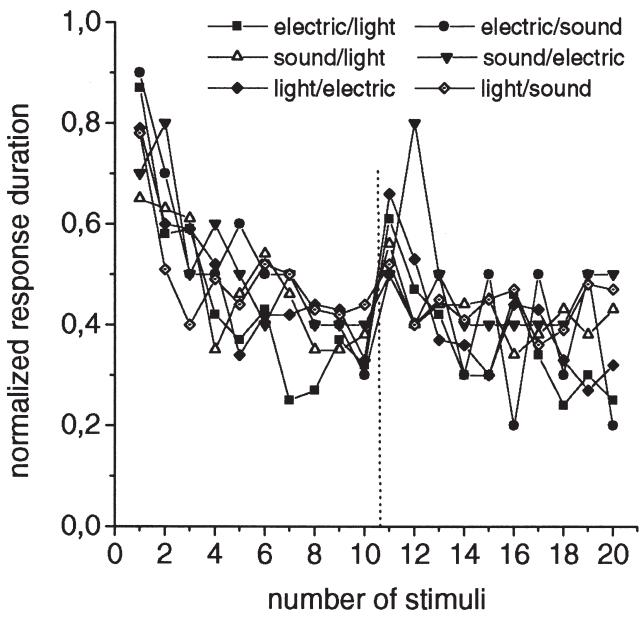


Fig. 11. Dishabituation with different sensory modalities in curarized fish. Six different combinations of series of test stimuli and dishabituation stimuli were tested. Similar as in Fig. 10, each curve shows the results for a series of 20 identical test stimuli that was interrupted by a high-intensity sensitizing stimulus of a different modality (not shown). The legend gives the combination of test stimuli/sensitizing stimulus ($N = 15$; $n = 20$).

sity, on the other hand, sometimes evoked NRs of long durations (Fig. 3F). All these effects together caused the correlation between stimulus intensity and certain NR parameters to be rather weak (Fig. 3). Linear relationships between stimulus intensity and response magnitude like those of Fig. 3 have been observed for orienting responses in humans [45–49]. In contrast, Sokolov [2] and Asafov [50] suggested that stimuli near threshold elicit larger orienting responses than those of moderate intensity, and that there exists a linear dependency of OR magnitude on stimulus intensity above this range.

When we presented two weak or medium stimuli of different modalities simultaneously, the resulting NR was stronger than when each of the stimuli was given alone (Fig. 4). This indicates that two modalities can interact and result in a nonlinear summation of the two effects.

The general characteristics of the novelty response as reported in this article are similar to those of the "orienting response" first described by Pavlov [1]. Pavlov hypothesized that "orienting responses" underlie perceptual processes, which extract important information from the environment. The concept of the orienting response was refined by Sokolov [2,10] and several other authors (e.g., by [5,51, 52]). Orienting responses consist of several autonomic reactions (e.g., changes in heart rate, blood flow, or skin conductance) and reaction of the skeletal muscles (e.g., head movements). Heart rate responses have often been used to quantify orienting responses and distinguish them from defensive and startle reactions, which also can be elicited by novel sensory stimuli. Behavioral changes during an orienting response are associated with orienting the sensor towards the eliciting stimulus, initializing investigative movements, and increasing information flow from the environment. Thus, the orienting responses serves to enhance the detection and analysis of novel stimuli and may signal that an event requires additional processing [53].

The electromotor novelty response of *Gnathonemus petersii* resembles orienting responses in mammals. It is a transient behavioral reaction that increases the information flow to the animal, and can be elicited by environmental novelty. In addition, it is associated with several autonomic reactions, such as transient change in heart and ventilatory rate [54, 55]. Orienting responses and arousal in other fishes were studied by measuring fin erection or changes in fin, eye, or opercular movement [16, 56].

An important characteristic of the orienting response in mammals is its habituation after repeated stimulation, especially to nonsignificant, innocuous stimuli [2,3,57]. Figure 5 shows that this also holds true for the novelty response in *Gnathonemus.* Habituation of the orienting response and of the novelty response in *Gnathonemus* both follow a negative exponential function of the number of stimulus presentations, and are more pronounced the more rapid the frequency of stimulation [40] (Figs. 7 and 8).

A series of weak acoustical stimuli was presented after a series of 10 weak visual stimuli leading to NR habituation. The acoustical stimuli evoked high amplitude novelty responses, which habituated similarly but a little faster than

those of the control series in which no previous visual stimulation was given (Fig. 9). These results suggest that novelty response habituation to each sensory modality is not completely autonomous. The interaction of the two modalities on habituation is rather weak, however, resulting in almost the same time course of habituation in the second modality no matter whether a previous stimulus series was given or not. An alternative explanation would be that the changes in sensory modality evoked dishabituation (see below). However, this appears to be rather unlikely because of the weak stimulus amplitudes used and the slow time course of the habituation to the second modality (compare Figs. 9 and 10).

Several authors (e.g., [1,15,40]) have stated that a strong new stimulus can dishabituate a previously habituated response to another stimulus quality. This also holds true for the orienting response. For example, Barry et al. [13] recorded habituation of electrodermal orienting response in humans. After a series of eight auditory stimuli that led to orienting response habituation, a single stimulus of changed frequency was introduced. Orienting responses to the following standard tones were of a higher magnitude suggesting dishabituation. Similarly, habituated novelty responses of *Gnathonemus* can be dishabituated by high-intensity stimuli of another modality (Figs. 10 and 11). Dishabituation is followed by a rapid second habituation process to the original modality. This result demonstrates dishabituation and, in addition, excludes a "fatigue" effect as a reason for the original habituation. Experiments with different combinations of sensory modalities show that there is no need to use a special combination of modalities (Fig. 11).

Sokolov [2] described another type of response to novel sensory stimuli besides the orienting response — the defense response, which can be elicited by intense and aversive stimuli. Sokolov described the orienting response as enhancing the sensitivity of the animal to future stimuli, but the defense response as reducing it [2, 4]. Traditionally, orienting and defense responses were distinguished by the direction of heart rate changes caused by a stimulus: orienting response are accompanied by a heart rate deceleration while defense or startle responses are accompanied by a heart rate acceleration. More recently these changes in heart rate during a defense response have been described in more detail, showing a series of heart rate accelerations and decelerations following an intense stimulus [4, 9]. The novelty response in *G. petersii* could be elicited by both high- and low-intensity stimuli (Fig. 6). Preliminary studies measuring heart rate changes in *G. petersii* showed that the heart rate always decelerated with both high- and low-intensity stimuli [55]. This means that heart rate cannot be used in electric fish to discriminate between orienting and defensive responses (Post and von der Emde, in preparation).

Graham [3] suggested four criteria for distinguishing between orienting and defensive responses: his first criterion is that the termination of an ongoing stimulus (the "offset") should not evoke a defense responses because a disappearing stimulus produces no pain and is, therefore, not efficient in producing fright. *G. petersii* responded to longer lasting stimuli with two novelty responses — one to stimulus on, and one to stimulus off (Table 1). Such a result would be expected if the novelty response is an orienting response, but not a defensive response. The onset of a stimulus should evoke an NR because the sensory input deviates from the input of the recent past. When the stimulus remains on for some time, the fish builds up a new sensory template including the stimulus. After some time, the fish should respond with a novelty response to the stimulus offset, because this is a deviation from the recently developed sensory template. The off-response should disappear with shortening stimulus duration, because of insufficient time to build up the template. Table 1 shows that this indeed is the case: the longer the stimulus duration, the more likely it is that an off-response occurs. However, even a stimulus duration of only 2.5 s evoked an off-response in 30% of the cases. It is surprising that a time period of such a short duration is sufficient to built up a sensory template.

Graham's second criterion for distinguishing between orienting and defense responses is that high stimulus intensities should produce defensive responses while low intensities should elicit orienting responses. His third criterion is that orienting and the defense responses should differ in their rate of habituation, with defense responses evoked by high-amplitude stimuli habituating very little or not at all [3]. The question of which part of the defense response habituates or not has been under debate [4, 9], but it appears that some components of the cardiac changes accompanying a defense response do habituate rapidly, while others do not [9].

The results obtained with different intensities of stimuli in *Gnathonemus* do not provide a coherent picture. We used visual and acoustical stimuli of high and low intensities presented at different interstimulus intervals. In general, it appears that high-intensity stimuli, especially sound stimuli, cause weaker habituation than low intensity stimuli. In some cases, as in Fig. 6D, habituation was absent with high-intensity acoustical stimuli. This supports the hypothesis that novelty responses to high intensity stimuli resemble defensive responses, while those to low intensity stimuli resemble orienting responses.

Graham's fourth criteria states that an orienting response but not a defensive response should recover with a stimulus change that does not increase intensity. For example, investigations in humans showed an orienting response recovery (skin conductance response) after a habituation series with visual stimuli if there was a intermodality change to vibratory stimuli [14, 58]. The novelty response of *Gnathonemus* recovers after an intramodality change in stimulus quality. A frequency change of a constant tone from 500 to 600 Hz (or from 600 to 500 Hz) evoked a novelty response (Table 2). Thus, the occurrence of stimulus recovery by a change in stimulus quality suggests that the novelty response to low-intensity stimuli resembles an orienting response.

Acknowledgments

This study was supported by grants from the Deutsche Forschungsgemeinschaft, DFG (Em 43/4-1, 2; Em 43/8-1). Dr. Horst Bleckmann made this study possible by providing laboratory space, equipment, and constant support.

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