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Probability and amplitude of novelty responses as a function of the change in contrast of the reafferent image in *G. carapo*

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Summary

Pulse electric fish evaluate successive electrosensory images generated by self-emitted electric discharges, creating a neural representation of the physical world. Intervals between discharges (system resolution) are controlled by a pacemaker nucleus under the influence of reafferent signals. Novel sensory stimuli cause transient accelerations of the pacemaker rate (novelty responses). This study describes quantitatively the effect of changes in contrast of reafferent electrosensory signals on the amplitude and probability of novelty responses. We found that: (i) alterations of a single image in an otherwise homogeneous series cause a novelty response; (ii) the amplitude of the elicited novelty response is a linear function of the logarithm of the change in image contrast; (iii) the parameters of this function, threshold and proportionality constant, allowed us to evaluate the transference function between change in stimulus amplitude and the amplitude of the novelty response; (iv) both parameters are independent of the baseline contrast; (v) the proportionality constant increases with the moving average of the contrast of hundreds of previous images. These findings suggest that the electrosensory system (i) calculates the difference between each reafferent electrosensory image and a neural representation of the past electrosensory input ('template'); (ii) creates the comparison template in which the relative contribution of every image decreases with the incorporation of successive images. We conclude that contrast discrimination in the electrosensory system of *G. carapo* obeys the general principle of appreciating any instantaneous input by the input's departure from a moving average of past images.

Key words: contrast discrimination, contrast adaptation, electric fish, *Gymnotus carapo*, fovea, short term memory, sensory representation.

Introduction

Pulse-discharging, weakly electric fish actively electrolocate by emitting electric organ discharges and sensing changes provided by objects on transepidermal self-generated electric fields. In this way they create a series of discrete electric images on a cutaneous electroreceptive mosaic (Lissmann, 1958; cf. Bullock, 1986, 1999; Bastian, 1986). In this study we examine how fish discriminate between electrosensory images of different contrast. This kind of analysis requires unambiguous definition and measurement of the stimulus (input) and of the related performance of a sensory system (output; Marr, 1982). Our recent knowledge of electric image generation mechanisms allowed us to control and measure the electrosensory image (Caputi and Budelli, 1995; Rasnow, 1996; Caputi et al., 1998; Stoddard et al., 1999; Nelson and MacIver, 1999; Budelli and Caputi, 2000; Sicardi et al., 2000; Caputi et al., 2003). Whereas the input is a clearly defined physical entity, the output of a sensory system can be considered as a broad spectrum of 'intangible facts'. Although sensation and perception may exist independently of any behavioural response, only behaviour can be measured objectively (Spector, 2000). So, we restricted our research to the analysis of an orienting behavior ('*a specific behavioural act directed towards the extraction of information from the environment*'; Sokolov, 1990) elicited by changes in stimulus contrast, aiming to infer electrosensory processing mechanisms.

Pulse gymnotids show a typical orienting behavior, the novelty response (Lissmann, 1958; Szabo and Fessard, 1965; Larimer and McDonald, 1968; Bullock, 1969; cf. Hopkins, 1983; Kramer, 1990; Moller, 1995). This behavior consists of a transient shortening of the inter-electric organ discharge (EOD) interval triggered by changes in nearby impedance. It has been frequently used to test a fish's electrolocation ability and to assess the effects of reafferent and exafferent input on pacemaker frequency (Bullock, 1969; Heiligenberg, 1980; Grau and Bastian, 1986; Hall et al., 1995; Zellick and von der Emde, 1995; Post and von der Emde, 1999).

After studying novelty responses evoked by a short-circuit in the presence of different amounts of noise, Heiligenberg (1980) inferred that *B. occidentalis* '*develop and maintain a 'template' or central register of past electroreceptive afferences against which novel afferent input is compared*'. Taking into account

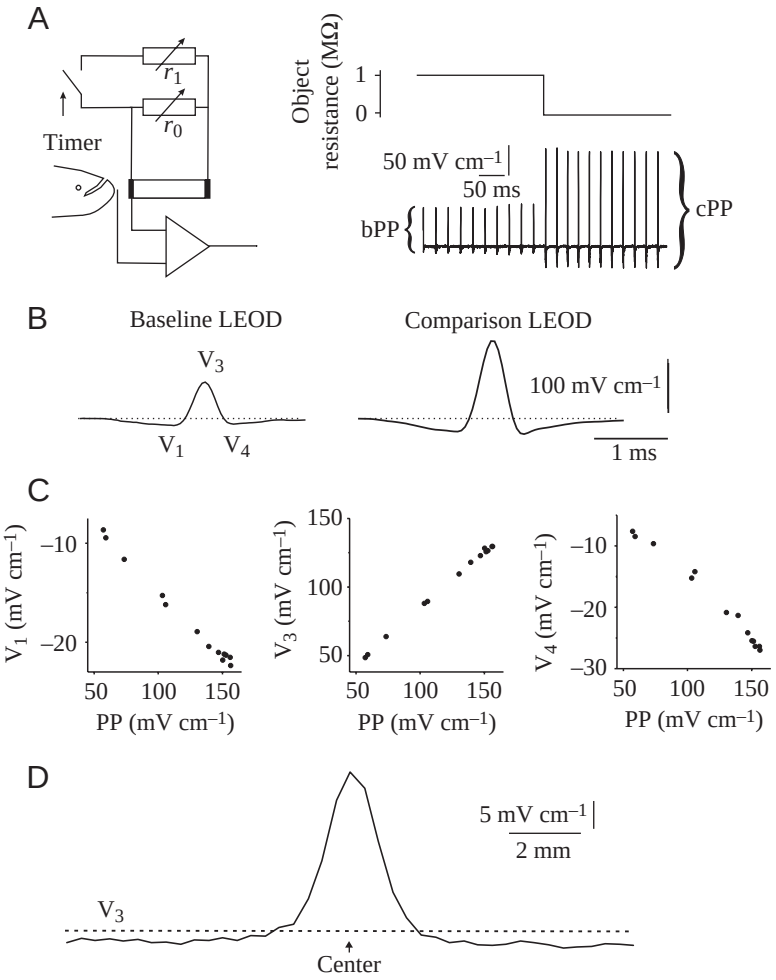

Fig. 1. Characterization of reafferent electrosensory image and its changes. (A) The diagram illustrates the methodology employed. Local electric organ discharge (LEOD) of *Gymnotus carapo* was recorded between an electrode adjacent to the skin, and the closest base of a cylindrical object placed 2 mm away from the skin. The electrode was a 100 µm bare-tip insulated wire; the object consisted of a 2 mm diameter, 10 mm long plastic tube with a carbon plug electrode in each opening. An external variable resistor r_0 was connected to the carbon plugs to set the baseline amplitude (bPP) of the local EOD. A second variable resistor r_1 was periodically connected in parallel, using a timed switch setting the comparison LEOD amplitude (cPP). Changes in object longitudinal resistance resulted in marked changes in image contrast. (B) LEOD recorded at the center of the image of a cylindrical object facing the electrosensory fovea. Left: baseline LEOD obtained without load (r=∞) and right: comparison LEOD obtained when the same object was loaded with a short circuit (r=0). Wave components are labeled as V_1, V_3 and V_4 (according to the nomenclature introduced by Trujillo-Cenóz et al., 1984; V_2 is not present at the foveal region). (C) The object resistance change mainly effects the contrast of the image. The amplitudes of each of these LEOD peaks are 'one-to-one' functions of the peak-to-peak LEOD (PP), indicating that changes in waveform are small and predictable from the change in PP. (D) The electric image of a metal cylinder consists of a Mexican-hat spatial profile. This is illustrated by the plot of the change in the peak of V_3 caused by the presence of the object as a function of distance from the projection of the center of the object. The dotted line indicates the amplitude of V_3 in the absence of the object (modified from Caputi et al., 2003).

this hypothesis we posed the following questions: what information is extracted from the input? What information is stored in the comparison 'template'? What are the rules relating changes in electrosensory image and electromotor output?

Our experiments showed that: (i) the system compares the contrast of every input image with a moving average of the contrast of past images, (ii) when contrast difference between the actual input and the moving average of past images overcomes a threshold, a novelty response is evoked, and (iii) the amplitude of the novelty response is graded with the contrast difference.

Materials and methods

Non-sexually differentiated *Gymnotus carapo* L., a South American pulse-emitting, weakly electric fish, 12–25 cm in length, were used in this study. Fish were gathered in the Laguna del Sauce, Uruguay, under the regulations of the Ministry of Ganadería y Agricultura. All experiments conformed with the rules of the Committee for Use of Experimental Animals of the Instituto de Investigaciones Biológicas Clemente Estable, and the guidelines of the Society for Neuroscience and the International Guiding Principles for Biomedical Research Involving Animals.

Experimental set up

Fish were held in a net in the middle of a tank (18 cm×25 cm×10 cm) containing 3 liters of water with a conductivity of 100±10 µS cm^{-1}. To create and change an electric 'stimulus-object' we used a method introduced by von der Emde (1990). A cylindrical stimulus-object (2 mm diameter, 1 cm length) was oriented with its long axis perpendicular to the skin of the electrosensory fovea (Castelló et al., 2000). The two ends of the cylinder were made of graphite carbon discs (1.5 mm in diameter) inserted into a non-conducting plastic tube. The carbon ends were connected to an optocoupled switch (Hamlin HE721 Eneka SA, Montevideo, Uruguay) *via* insulated copper wires (Cerba SA, Montevideo, Uruguay), which left the tube at its center. To avoid non-controlled stimuli due to the reaction of carbon impurities with water, the probe was maintained immersed in water of 100 µS cm^{-1} conductivity for a few days prior to beginning the experiments until completion. In addition, and for the same purpose, we followed the procedure described by von der Emde (1990) of connecting a large capacitor (2.2 µF) in series with the switch that did not alter the recorded local EOD (LEOD) waveform.

To quantify the local electric image contrast, the voltage drop between the bare tip of a 100 µm diameter insulated

copper wire placed against the skin and the base of the stimulus-object cylinder nearest to the fish was measured (Fig. 1A). These electrodes were 2 mm apart and thus the electric field in V cm^{-1} was five times the voltage drop between the electrodes. Signals were amplified (×100), and filtered (band pass 10–10000 Hz, AM Systems, Inc. Carlsborg WA, USA); a digital oscilloscope (Hewlett-Packard model 54601A, USA) was used for observation of individual LEOD waveforms that were also sampled (20 kHz, 12-bit resolution, Lab Master DMA A/D card, Scientific Solutions Solon, Ohio, USA) for off-line measurement of the inter-EOD interval (home made signal processing program).

Experimental design

The experimental design was inspired by the methodology introduced by Weber and formalized by Fechner (cited by Werner, 1980). Weber's procedure was based on what is now known as 'comparative unidimensional judgements', where a subject is asked to discriminate between two stimuli. A particular stimulus of a given type (baseline or standard stimulus) is applied alternately with one of a number of other stimuli (the comparison stimulus) that are of the same type but differ in a single physical parameter (Werner, 1980).

According to Caputi et al. (1998), Sicardi et al. (2000) and Budelli and Caputi (2000), the electrosensory image of a resistive cylindrical object has a 'Mexican-hat'-shaped profile, controllable by changing the load resistance, and confirmed by our results obtained in the present study. Thus a single parameter, the amplitude of the signal at the center of the 'Mexican-hat' profile, can be used to estimate the contrast of the electric image of the stimulus-object.

The experiments were performed at the perioral region, where density, variety and central representation of the sensory mosaic are maximal, and therefore this region has been defined as an electrosensory fovea. At this region, background stimulus in the absence of objects is spatially coherent (i.e. it shows the same triphasic waveform all over the foveal region; Aguilera et al., 2001). At the perioral region, resistive objects modulate the local field, generating a 'Mexican hat' spatial profile of the stimulus amplitude (Fig. 1). Despite this, modulation is associated with small waveform changes, which are predictable from the total energy of the local stimulus (Aguilera and Caputi, 2003; Fig. 1). Therefore, the amplitude pattern is sufficient to describe the image of resistive objects. Since the normalized spatial pattern is not modified when the distance of the object remains constant (Budelli and Caputi, 2000), the change in amplitude at the top of the 'Mexican hat profile' (i.e. the skin facing the object) describes the change of the image. Consequently, the contrast of the image generated by a resistive stimulus-object can be estimated by a single parameter: the peak-to-peak amplitude (PP) of the local electric field at the skin facing the object.

It should be noted that PP in the presence of the object may be larger or smaller than PP recorded in the absence of the object. When the object load was a resistor of 100 kΩ a flat profile equivalent to that observed in the absence of the object was recorded, and this image has null contrast. Resistors lower than 100 kΩ generated top-external 'Mexican hat' profiles (Fig. 2A, right) and resistors higher than 100 kΩ generated top-internal 'Mexican hat' profiles (Fig. 2A, left).

Four variables were controlled during the experiments: (i) baseline contrast estimated as PP before a change in the resistance of the object, (ii) baseline duration, (iii) comparison contrasts estimated as PP after a change in the resistance of the object, and (iv) comparison stimulus duration. The difference between baseline contrast and comparison contrast (ΔPP) is referred to as contrast change. As the electromotor activity is a series of brief and discrete events, the changes in duration of either the baseline or the comparison periods lead to changes in the number of images evaluated during these periods.

In order to control these four parameters, the longitudinal resistance of the stimulus-object was changed by means of the optocoupled switch timed with an S88 stimulator (Grass Instruments, Quincy, MA, USA). In each experiment, an external variable resistor r_0 was connected between the carbon discs to set the baseline contrast. A second, variable resistor r_1 was connected periodically in parallel to shunt r_0, and thus set the comparison contrast (Fig. 2).

Data analysis

Novelty responses are transient reductions of the interval after a change in image contrast. To detect novelty responses, we plotted the peristimulus inter-EOD interval (I) sequence. For each response the intervals were numbered starting at the first interval after the resistance change (I_1, I_2....I_n). The baseline inter-EOD interval (I_0) was defined as the mean of the 5 intervals preceding the change in stimulus-object resistance and its lower confidence limit as the mean minus 2 standard errors (S.E.M.). Two criteria were employed to define a novelty response: (1) a successive shortening of two intervals immediately after the change in impedance and (2) a second interval (I_2) significantly smaller than the baseline confidence limit ($I_2<I_0$–2 S.E.M.). The probability of the novelty response for a given experimental condition was estimated as the relative frequency of novelty responses in a set of trials. We defined the amplitude of the novelty response as the normalized maximum shortening of the inter-EOD interval (novelty response amplitude = 1 – minimum of I/I_0). The second interval was the briefest in most cases (I_3 was exceptionally the briefest).

Experimental paradigms

Stimulus-object resistance (determining PP) was controlled in a trial-to-trial manner, setting independently the number and amplitude of both baseline and comparison stimuli. Our experimental paradigms were designed to answer the following questions.

(1) How many images different from baseline have to occur to be detected? In order to elucidate whether the number of comparison stimuli determine the characteristics of the novelty response, we compared the effects of two stimulation patterns differing only in the duration of the comparison period. Single

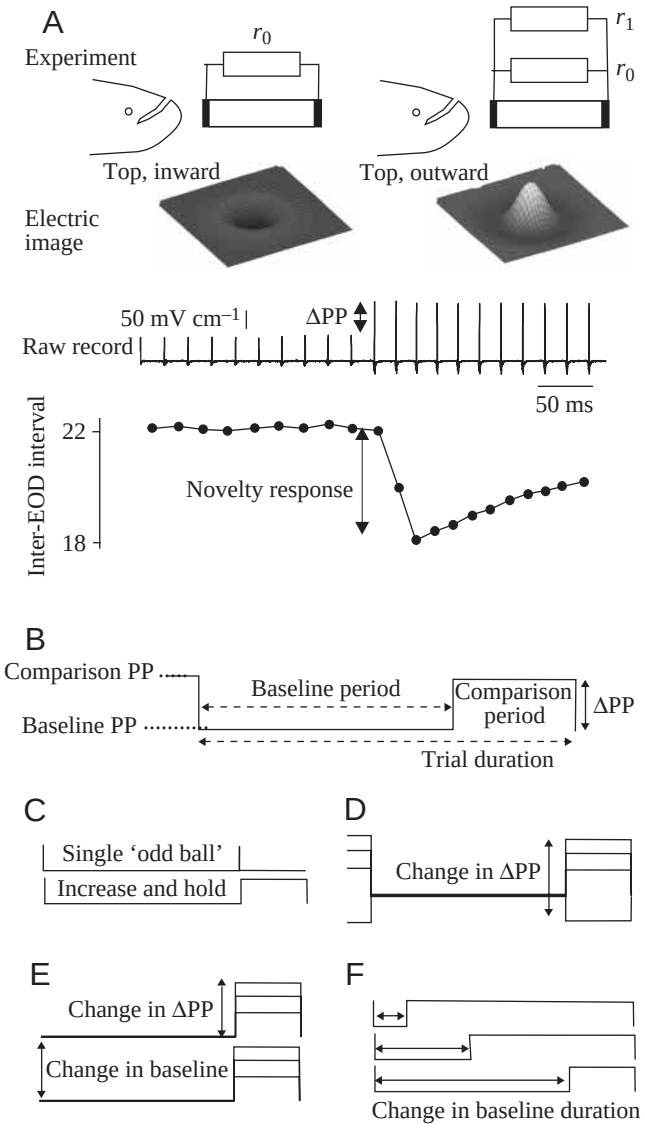

Fig. 2. Experimental paradigm. (A) The schematic diagrams illustrate the experimental procedures and the corresponding electric images when the change in contrast is maximum (r_0=∞ and r_1=0). Note the opposite orientation of the 'Mexican-hat' profile, referred in the text as 'top-inward' and 'top-outward', respectively. The raw record at the center of the 'Mexican hat' allowed us to measure the difference (ΔPP) between the baseline amplitude and comparison amplitude of the stimulus. The temporal course of the corresponding novelty response elicited by the change in object resistance is shown in the bottom plot. (B) Studies were performed using series of trials consisting of a baseline period followed by a comparison period. Four variables were controlled: the baseline amplitude (depending on r_0), the comparison amplitude (depending on r_1), the number of baseline images (depending on the duration of the baseline period), the number of comparison images (depending on the duration of the comparison period). (C–F) The experimental paradigms used to elucidate the following issues. The number of images different from the baseline that suffice for detection (C); the effect of the difference between baseline and comparison amplitudes (ΔPP) on the amplitude and the probability of the novelty response (D); the effects of the baseline on amplitude and probability of the novelty response (E); and the effect of stimulus history on the amplitude and probability of the novelty response (F).

odd events (in which the contrast of a single image was increased) were compared with increase-and-hold patterns (in which the contrast of approximately 100–120 successive images were increased during a 4 s period). For every change in contrast (ΔPP), two trials were done. In one case the sequence was baseline–increase and hold–baseline–single odd event, and in the other it was baseline–single odd event–baseline–increase and hold. Baseline contrast was constant (r_0=∞ open circuit) and baseline duration was 30 s. The results are shown in Fig. 4.

(2) How different should the comparison image be for detection? In most sensory systems, discrimination depends on baseline level (Weber and Fechner's and Stevens' laws; Werner, 1980). In order to study whether the baseline contrast level influence the amplitude of the novelty response, we explored the effects of similar changes in contrast (ΔPPs) starting at different baselines. Increase-and-hold patterns (baseline period, 29 s; comparison period, 1 s) were applied, starting at several different baseline PP values. Up to 30 ΔPP values were explored in each fish for every baseline PP (7 fish; the results are shown in Fig. 5A).

(3) Is the amplitude of the response graded with the change in image contrast? If so, what is the function that describes the relationship? To explore the effect of the previous electrosensory stimulation on the amplitude of the novelty response, we performed two sets of experiments. In the first set, the relative duration of the baseline and comparison periods were modified from trial to trial, without changing the total trial duration (the results are shown in Fig. 6). In five fish, trial duration was 30 s, and in the other two fish trial duration was 100 s. In all trials, the amplitudes of the baseline and comparison image contrasts were set by stimulus-object resistances of 470 kΩ and 15 Ω, respectively. In the second set of experiments, the duration of baseline period and ΔPP were both varied (three fish; the results are shown in Fig. 7A,B). Three baseline periods and four ΔPP were explored for each fish. In each case the comparison stimulus was set by one of four different r_1 values (100 kΩ, 47 kΩ, 22 kΩ or 15 Ω) connected in parallel with r_0 (470 kΩ), which also set the baseline contrast. Each trial began with a period in which the stimulus had the same amplitude as the comparison stimulus, followed by a baseline period of the desired duration (2, 10 or 29 s), and ending by a comparison period lasting 1 s. In all cases the trial lasted 30 s.

(4) Does the baseline level have influence on the amplitude or probability of the response? Similar experimental paradigms were used to explore the probability of eliciting novelty responses. The probability of novelty response as a function of ΔPP and baseline PP was studied in five fish. Discrimination experiments consisted of 10–20 cycles in which object resistance was alternated between two values, every 30 s. We never found novelty responses for decreases in the image

contrast even though we explored up to the largest possible ΔPP (stepping from short to open circuit, Fig. 3B). Thus, for the purpose of detailed analysis, the low amplitude period was considered as the baseline contrast. Probability distribution curves as a function of ΔPP were constructed for 4–6 baseline contrasts (results shown in Fig. 5B). Threshold$_{50}$ (T_{50}) was defined as the ΔPP eliciting novelty responses in 50% of the cases.

(5) Finally, does the stimulation history have an influence on the amplitude or probability of the response? In three other fish we applied asymmetric cycles to evaluate the influence of stimulation history on the T_{50}. Cycles consisted of 29, 10, 2 or 0.5 s baseline periods and 1, 20, 28 or 29.5 s comparison periods, respectively, and the results are shown in Fig. 7C,D.

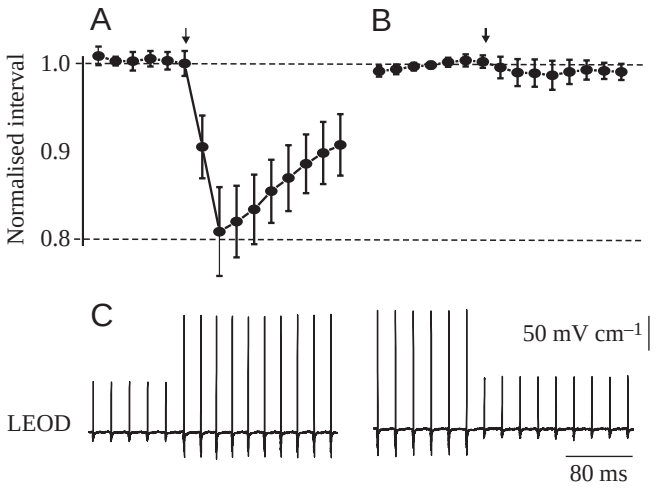

Fig. 3. Electromotor responses to changes in contrast of the electrosensory image of a cylindrical object. (A,B) Mean ± S.D. of the normalized intervals ($1–I/I_0$) plotted as a function of the interval order (N=10 trials). (A) The increase of electric image contrast elicits a typical novelty response characterized by a shortening of the first two intervals after the change in image contrast followed by a slow relaxation curve. Note the significant increase in the S.D. (ANOVA, P<0.01). (B) The same change in contrast but in opposite direction does not elicit a novelty response although there is a significant increase of variability (ANOVA, P<0.01). (C) Single trial recordings of the local electric organ discharge (LEOD) illustrating the experimental paradigm.

Results

The novelty response evoked by changes in electric image contrast as a tool to explore electrosensory discrimination

The effective stimulus for each electroreceptor is the local self-generated transepidermal field. This field, in turn, corresponds to the mean current density flowing locally through the skin facing the stimulus-object. It is proportional to the voltage drop between the recording electrodes (called in most previous literature 'local electric organ discharge', LEOD). It is important to note that *G. carapo* is a pulse fish that evaluates discrete electric images generated by its own EODs (reafferent electrosensory input) emitted every 20–50 ms. The EOD in fact generates a complex time waveform, whose four components have different origins and distributions along the fish body (V_1, V_2, V_3 and V_4, following the nomenclature of Trujillo-Cenóz et al., 1984). In each trial, object resistance was alternated between a baseline and a comparison value, producing marked changes of PP at the skin facing the object. At the snout of *G. carapo* the skin is densely covered with electroreceptors and has been likened to an electrosensory fovea (Castelló et al., 2000). In this region the field is a collimated and spatially coherent waveform composed of V_1, V_3 and V_4 components (Castelló et al., 2000; Aguilera et al., 2001) (Fig. 1A). For different resistive loads, the amplitude of each of these components is unambiguously related to PP (Fig. 1B). Electrosensory images generated by pure resistive cylindrical objects consist of a 'Mexican-hat' center-surround opposed pattern. Its general shape depends on the object distance and its center-surround difference is scaled monotonically with object conductivity (Caputi et al., 1998; Sicardi et al., 2000; Budelli and Caputi, 2000; see Fig. 1C, modified from Caputi et al., 2003). A large object close to the electric organ should provoke changes of the equivalent load impedance in the surrounding medium and, consequently, in the total current output. However, in our experiments the net change in total current caused by the presence of the probe (stimulus-object) can be considered negligible due to its small size and relative distance from the energy source. Therefore, the stimulus resulting from the presence of our stimulus-object can be considered as a local modulation of the transcutaneous current density pattern without changing the total output current. We altered the stimulation pattern by changing the longitudinal resistance of a cylindrical stimulus-object placed with its axis perpendicular to the skin of the foveal region. Thus, a change in the stimulus-object resistance caused what is operatively defined (by analogy with vision nomenclature) as a change in the contrast of the electric image at the electrosensory fovea. In addition, as mentioned above, the shape of the image of the stimulus-object remained similar whereas its amplitude changed in proportion to the value of PP at its center. Therefore, in our experimental conditions this single parameter, PP at the center of the 'Mexican-hat' profile, was used to estimate the contrast of the electric image of the object and will be considered in this study as the control stimulus.

A decrease of object impedance (that produced an increase in electrosensory stimulus contrast, Fig. 2B,C) evoked a typical novelty response consisting of an immediate shortening of the next two inter-EOD intervals (Figs 2C,D and 3, left). The third interval after the change in image contrast was usually similar or a little longer than the second. Over the subsequent discharges the inter-EOD intervals slowly returned to the initial baseline values. In addition, the variability of the EOD interval after the change in object resistance was larger than during the baseline period (Fig. 3A). This typical pattern was constant for novelty responses evoked by changes in self-generated electric images, allowing us to distinguish these novelty responses unequivocally from other acceleration-slow return patterns (cf. Moller, 1995).

Interestingly, we found that only the variability of inter-EOD intervals increased in response to a reduction in image contrast; novelty responses were absent (Fig. 3B). Although the observed change in interval variability could indicate image discrimination, its analysis was not included in this study.

Changes in image contrast induced by a change in object impedance were presented with a minimum interval of 30 s. This period included 600–1200 EODs, depending on the baseline pacemaker mean frequency. During successive trials, the amplitude of the novelty response elicited by the same pattern of stimulus varied randomly around a mean value, which indicates that under our experimental conditions the electrosensory-evoked novelty response did not show habituation. This finding is consistent with the observations of Grau and Bastian (1986), who showed the lack of habituation of novelty responses to novel stimuli presented at intervals larger than 20 s.

A single discrepancy in image contrast is sufficient to provoke the novelty response

Novelty responses, as other types of orienting responses, result from comparing a sensory input with some kind of expectation (Sokolov, 1990). To understand this kind of comparison we investigated firstly how many images constitute the sensory input that is compared with the expectation signals. In other gymnotid fish and under a different stimulation protocol, the amplitude of the novelty response has been reported to increase with the number of images modified by the novel stimuli (Heiligenberg, 1980). On the other hand, Bullock (1969) studied the novelty response in a variety of pulse gymnotids and concluded that '*… the electroreceptor input has a cycle by cycle access to the pacemaker*'. Similar results were obtained in pulse mormyrids by Meyer (1982), suggesting that fish evaluate single images against a stored representation.

Thus, the first set of experiments were designed to test the hypothesis that a sustained increase in contrast of various subsequent reafferent images is more efficient for provoking novelty responses than an increase in the contrast of a single reafferent image.

In three fish a series of 10 novelty responses resulting from a maximum increase in contrast of a single image (single odd event) were compared with a series of 10 novelty responses resulting from a maximum increase in contrast of several consecutive images (increase-and-hold pattern). For the same experimental conditions, the mean amplitude of the novelty response evoked by a single odd event was larger in some fish and smaller in others than the mean amplitude responses evoked by an increase-and-hold pattern. Statistical analysis performed for each of the fish showed no significant differences between the means (*t*-test, $P<0.01$). Fig. 4A shows an example from one fish comparing the effects of both stimulus patterns. The mean amplitude of the novelty responses to a single odd event was larger but not statistically significant (*t*-test, $P<0.01$, $N=10$) than the mean amplitude of the novelty responses to a increase-and-hold pattern. The

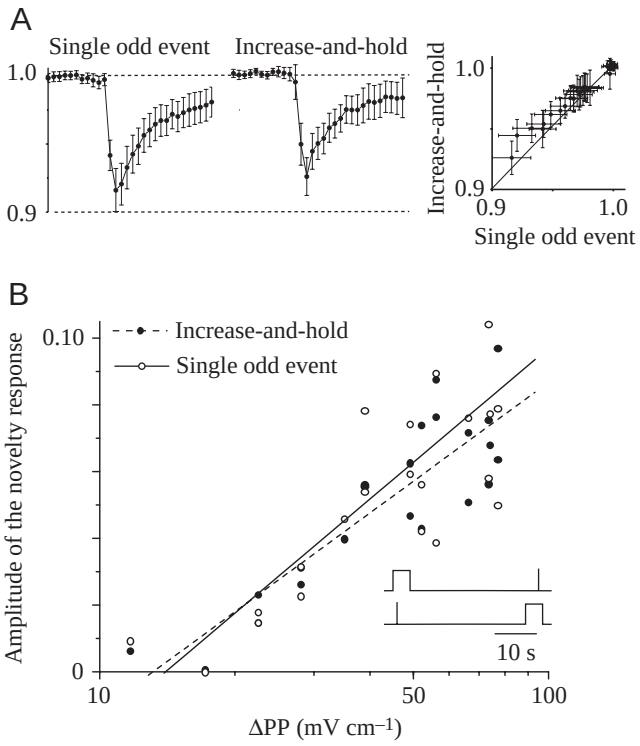

Fig. 4. Study of the effect of the number of comparison images on the amplitude of the novelty response. (A) The amplitude of the novelty responses elicited by a single odd event (left) and an increase-and-hold pattern (middle) are not significantly different (*t*-test, $P<0.05$, $N=20$). In the right plot, normalized intervals ($1–I/I_0$) obtained using both experimental paradigms are plotted one-to-one, according to their ordinal number. The linear relationship indicates a similar time course for both novelty responses. (B) Amplitude of the novelty response as a function of difference between baseline and comparison amplitudes (ΔPP) obtained applying a single-odd-event pattern (open symbols) and an increase-and-hold pattern (filled symbols). The experimental protocols are illustrated in the inset. Starting from a single baseline level (43 mV cm^{-1} in the example), each trial consisted of a pair of stimuli: a single odd event followed 30 s later by a 4 s held stimulus of identical ΔPP, or *vice versa*. In successive trials ΔPP was varied in a random fashion.

similarity in the relaxation time course of both novelty responses is illustrated by the linear relationship when one response is plotted against the other (Fig. 4A, right); the slope of the line depends on the occasional difference between mean amplitudes. From these experiments it can be seen that, irrespective of the subsequent duration of the comparison period, the initial increase in contrast of the image (ΔPP) not only triggers the novelty response but also determines its amplitude. Once the response is triggered, it follows a time course that is not controlled by the subsequent electrosensory input.

The amplitude of the novelty response was graded according to the evoked increment in the image contrast, following the same relationship independently of the number of comparison stimuli (Fig. 4B). Responses to the increase-and-hold pattern

were compared with those evoked by single odd event following the protocols illustrated in the inset. Starting from a single baseline level ($r_0=\infty$), each trial consisted of a pair of stimuli: a single odd event followed 30 s later by a 4 s held stimulus of identical ΔPP, or *vice versa*. In successive trials ΔPP was varied randomly. We observed that the amplitude of the novelty response increased similarly with ΔPP for both stimulation patterns. The amplitude of the novelty response was well fitted by a logarithmic function of ΔPP:

$$\text{Novelty response amplitude} = K \times \log_{10}(\Delta PP/\Delta PP_0), \quad (1)$$

in which ΔPP_0 is an incremental threshold and K is a scaling constant. These parameters, obtained by regression analysis, were not significantly different between results obtained with single odd events and increase-and-hold patterns (Fig. 4B; *t*-test, $P<0.01$). In addition, the mean of the differences between the amplitudes of the novelty responses evoked by the two stimulus patterns in each pair was zero (paired *t*-test, $P<0.001$, $N=22$ pairs, fish 1; $N=12$ pairs, fish 2).

Discrimination function and scaling of the response are independent of the contrast baseline

The general rule is that discrimination threshold increases with the baseline amplitude (following a function characteristic of the considered sensory system; Werner, 1980). This kind of rule would imply a dependence on the absolute value of the contrasts of the compared images. It has been also speculated that fish compare images pulse-to-pulse, against a fixed template (Moller, 1995), or have the '*ability to remember what the current flow through its skin would look like in the undisturbed condition and be able to compare at this site the field in the presence of shadows from objects*' (Hopkins, 1983).

In a second set of experiments we tested the hypothesis that the described function parameters are baseline dependent. As shown in Fig. 5, the relationship between ΔPP and the amplitude and probability of the novelty response was independent of the reafferent image baseline contrast. For data obtained starting from any given contrast baseline, the threshold (ΔPP_0) and scaling constant (K) were similar to values calculated from the pooled data of the same fish (ANOVA-test, $P>0.1$, Fig. 5A). For the overall population of the seven fish, means and standard deviations (S.D.) of these parameters obtained from pooled data for each fish were: $\Delta PP_0=18\pm12$ mV cm^{-1} and $K=0.13\pm0.07$.

We also measured the probability of evoking a novelty response as a function of ΔPP. Changes in object resistance induced ΔPP of different amplitudes, ranging from –120 mV to +120 mV. Each amplitude change was induced from different baseline contrasts (10–20 trials for each ΔPP and each baseline contrast). Novelty responses occurred only for ΔPP larger than 4–8 mV cm^{-1}. This ΔPP was comparable to the 'spontaneous' variation of the local signal due to respiration and other small movements. As illustrated in Fig. 5B, the probability of evoking a novelty response was a sigmoidal function of ΔPP. This function was the same for every baseline contrast. Thus, unlike other sensory systems, the critical factor for evoking a novelty response was the absolute increase above the baseline contrast rather than a function of the baseline contrast. The contrast increment that evoked novelty responses

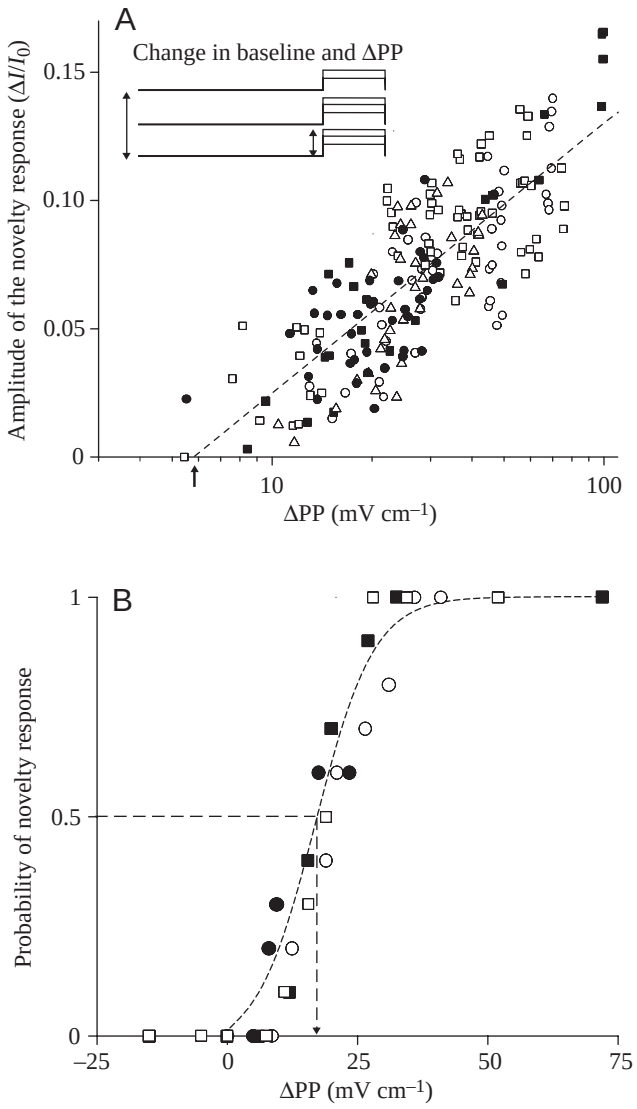

Fig. 5. Probability and amplitude of the novelty response as functions of the increase in image contrast (ΔPP). (A) Amplitude of the novelty response plotted as a function of ΔPP. Data obtained, starting at different baseline contrast, are represented by: 109.27 mV cm^{-1} (closed circles), 101.35 mV cm^{-1} (open triangles), 85.43 mV cm^{-1} (open circles), 58.15 mV cm^{-1} (open squares) and 51.05 mV cm^{-1} (closed squares). Parameters calculated fitting the data obtained, starting from every baseline contrast, were similar to those from pooled data. Curve-fitting of the pooled data: novelty response amplitude=$0.105\times\log_{10}(\Delta PP/5.77)$, $r=0.778$, $N=216$, $P<0.0001$. (B) Probabilities of evoking novelty responses are plotted as a function of ΔPP. Each point represents the probability of evoking a novelty response estimated by its relative frequency in 10 trials using a given pair of baseline contrast and ΔPP in the same fish. Baseline contrast: 58 mV cm^{-1} (closed squares), 77 mV cm^{-1} (open circles), 88 mV cm^{-1} (closed circles) and 108 mV cm^{-1} (open squares). The threshold$_{50}$ (ΔPP yielding novelty responses in 50% of the cases) is indicated by the arrow.

in 50% of the cases (T_{50}) was characteristic for each fish (ranging between 5 and 25 mV cm^{-1}). It is worth noting that ΔPP_0 and T_{50} yielded similar values, despite being estimated by different methods (Fig. 5A,B). It is also important to recall that ΔPP_0 was similar when explored with a single odd event pattern or with an increase-and-hold pattern in the same fish (Fig. 4B).

Threshold and scaling constant depend on the preceding temporal pattern of stimulation

The experiments illustrated in Figs 4 and 5 show that the difference in contrast between the baseline and the very first image that surpasses an incremental threshold value determines the amplitude of the orienting responses according to a logarithmic law. This relationship is baseline independent. It should be noted that the same change in contrast can be achieved by flattening a 'top-inward' 'Mexican-hat' profile or increasing a 'top-outward' 'Mexican-hat' profile. These results indicate that *G. carapo* is permanently evaluating the change of the stimulus pattern independently of the baseline contrast. This means that the fish does not compare incoming images with a fixed template. Moreover, this suggests that novelty responses result from the comparison of the neural response to the very first altered electric physical image with a central representation of the past sensory input. This leads to the question of how many images contribute to such representation. In the third type of experiments we tested the hypothesis that fish evaluate PP in a pulse-to-pulse manner, simply comparing the contrast of each image with that of the immediately preceding image. We found that this is not the case (Fig. 6). Novelty response amplitude is a function of the number of images of the same baseline contrast that precedes the change in contrast. In these experiments, we changed the duty cycle regulating the relative timing of baseline and comparison stimulus periods without altering the total trial duration (Fig. 6 inset). Object resistance was alternated between 470 kΩ and 15 Ω to produce large changes in contrast. This procedure allowed us to control the number of EODs included in the baseline and comparison periods of the trial. Novelty response amplitude increased with the number of baseline EODs from 50 to 900, with a maximum slope at approximately 120 EODs (representing 3–6 s, depending on pacemaker frequency). Similar results were obtained for different EOD pacemaker frequencies and for both trial duration studied (100 or 30 s), suggesting that the number of EODs, and thus the number of electrosensory images, is the relevant variable.

The increase in novelty response amplitude as a function of the number of images during the baseline period could result from changes in either the scaling constant, the threshold, or both. We addressed this issue in a fourth series of experiments (N=3 fish) in which the duration of the baseline period (r_0=∞, open circuit) was set at 2, 10 or 29 s, and trial duration was kept constant at 30 s. The results consistently showed that the scaling constant was an increasing function of the number of baseline EODs (Fig. 7A,B). The ΔPP_0 values calculated by curve-fitting were similar for 10 and 29 s in all fish; however,

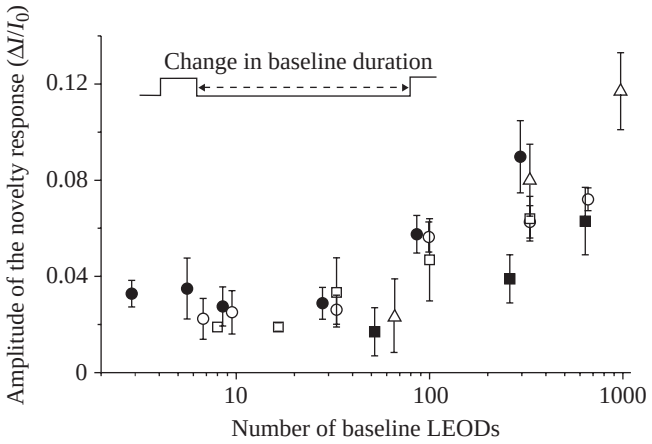

Fig. 6. Dynamics of the storage and update of the neural representation of the electric image. Amplitude of the novelty response is plotted as a function of the number of local electric organ discharges (LEODs) in the baseline period. Values are means ± S.D. of the novelty response amplitude (I/I_0) obtained in series of trials having baseline periods of the same duration. The inset illustrates the experimental paradigm. The duration of the baseline period of the increase-and-hold pattern was varied to change the number of baseline LEODs before the amplitude step. The number of baseline LEODs were counted (short baseline periods) or estimated by multiplying the period duration by the fish EOD rate. Trial duration was 100 s (two fish, filled symbols) or 30 s (three fish, open symbols). Each symbol shape represents a different fish.

curve-fitting was not a reliable method for calculating ΔPP_0. Note that all amplitudes of novelty responses obtained with a baseline period of 2 s were similarly small, which is consistent with the flat profile shown in Fig. 6 for less than 80 baseline EODs.

The dependence of novelty response threshold on recent past sensory history was further studied by comparing the probability distribution functions of novelty responses for baseline periods of 29, 10, 2 and 0.5 s (including approximately 900, 300, 60 and 15 EODs). For baseline periods lasting 2, 10 and 29 s, the probability distribution curves were similar (N=3 fish, Fig. 7C). Although a small increase in T_{50} was consistently observed for baseline periods lasting 2 s, the change in scaling constant was the most important factor to explain the decay of the amplitude of the novelty response with this stimulation pattern. Data obtained with a very short baseline period (0.5 s) were more dispersed and had a larger T_{50}. In these experiments there were an important number of failures even when the explored ΔPP was the maximum possible (r_0=∞, open circuit, r_1=0, short circuit, Fig. 7D).

Discussion

Our results provide behavioural evidence that pulse fish of the family Gymnotidae are able to discriminate the change in contrast of the stimulus pattern. This implies their ability to compare electrosensory information obtained from consecutive electrosensory images.

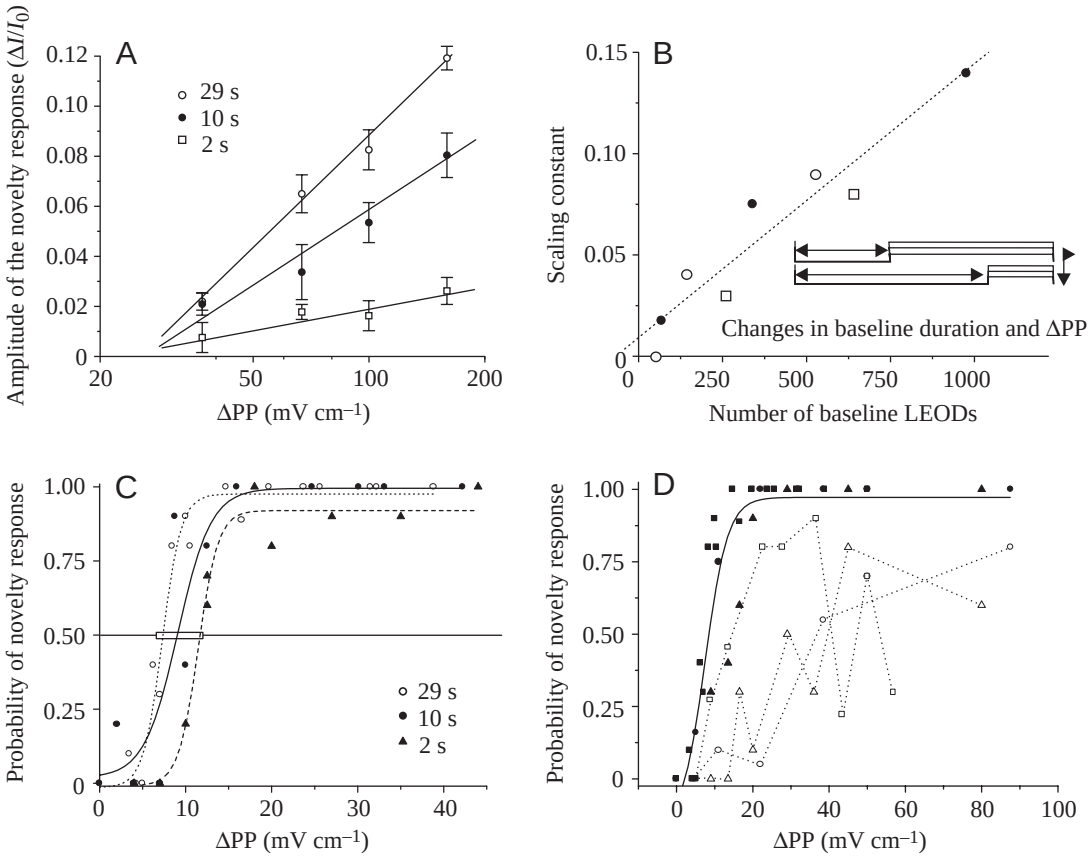

Fig. 7. Parameters of the function relating novelty response and the change in image contrast (ΔPP). (A) Results obtained in a single fish using different increase-and-hold patterns of stimulation, where the amplitude of the novelty response (I/I_0) is plotted as a function of ΔPP for three different baseline periods. Symbols indicate the duration of the baseline period: 2 s (open squares; 44 EODs), 10 s (closed circles; 210 EODs), 29 s (open circles; 600 EODs). Trial duration was the same in all experiments (30 s). Note that the scaling constant (the slope of the line fitting the data) increases as a function of the duration of the baseline period. (B) The scaling constants, obtained in the same way in three fish, are plotted as a function of the number of baseline local electric organ discharges (LEODs) (r^2=0.88, P<0.01, N=8). Each symbol corresponds to a different fish. (C,D) Threshold$_{50}$ was studied in three fish for different baseline periods. Probability of evoking novelty responses is plotted as a function of ΔPP. In (C) data obtained from a single fish using baselines of 2 s (closed triangles), 10 s (closed circles) and 29 s (open circles) are compared. In (D) the results were obtained using extreme baseline periods; 0.5 s (open symbols) and 29 s (filled symbols) are compared. Each symbol shape corresponds to a different fish (N=3).

We used the novelty response as an index of discrimination. This is an electromotor orienting behavior consisting of the transient reduction of the inter-EOD interval followed by a gradual return to baseline. The dependence of the amplitude of the novelty response on the change in stimulus indicates that occurrence of this orienting behavior is a reliable index that the stimulus has been sensed and evaluated. For this reason novelty responses have been extensively used as index of electrolocation (Bullock, 1969; Heiligenberg, 1980; Grau and Bastian, 1986; Hall et al., 1995; Zellick and von der Emde, 1995; Post and von der Emde, 1999). However, the failure of a sensory stimulus to evoke a novelty response does not mean that it has not been sensed. In fact, our experiments show that the interval variability can be modified by a change in image contrast even though it might not evoke novelty responses. Therefore, it is important to establish first what kind of information is obtained by analyzing the amplitude and probability of the novelty response as a function of the change in electric image contrast.

The function relating probability and change in image contrast is the same when starting the experiment from different baseline image contrasts. It is important to note that the compared images consist of spatial modulations of the self-generated electrosensory carrier, which provides a basal effective stimulus for electroreceptors. This indicates that the observed behavioural threshold is not set by the electroreceptor threshold. It also suggests that the response to the comparison stimulus should be contrasted with the response to the baseline stimulus by a sensory readout mechanism somewhere in the central nervous system. The observation that the effect of a single odd event is the same as the effect of an increase-and-hold temporal pattern indicates that only the response to the very first event of the comparison stimulus train (actual input) is contrasted with the response to the baseline input. By contrast, Heiligenberg (1980) found that a change of at least two or three images is necessary to elicit novelty responses in *B. occidentalis*. Differences between studied species and experimental designs might account for the discrepancies. While Heiligenberg's (1980) strategy was to add artificial background noise against which a single relatively broad and blurred image generated on the side of the fish was compared, our results were obtained by changing the contrast of smaller and sharper images on the electrosensory fovea.

Our finding of a function relating the amplitude of novelty

response to the change in image contrast indicates that the above-mentioned read-out mechanism provides the electromotor system with the relevant input for controlling the amplitude of the novelty response. Thus, the changes in the parameters of the described function were used to study the dynamic effects of stimulus presentation.

As occur with the probability function, the parameters of the amplitude function are the same for different baseline contrasts held constant for a long period. This is opposite to the common finding across most sensory systems where the discrimination threshold generally depends on the baseline stimulus (Weber and Fechner's and Stevens' laws; Werner, 1980). For baselines equal or larger than 2 s the amplitude of the novelty response was scaled with contrast increase, according to a baseline-duration-dependent rule (Fig. 7B). For the same change in contrast, the amplitude of the novelty response gradually decreased as the fraction of baseline period in the total cycle of stimulation was shortened (Fig. 6). This suggests that the amplitude of the novelty response is influenced by a long-lasting stimulation period including baseline images and also images belonging to the comparison period of the preceding trial. The most important reduction of the response was observed when the baseline period included less than 80–100 EODs (2–4 s), but some influence was detected up to 900 EODs (29 s), indicating that the relative importance of an electrosensory image on the transference function parameters fades out as the following images are integrated in a central expectation signal.

The threshold is significantly affected by past input only when the baseline period is shorter than 2 s (including up to 60 EODs). This period might correspond to the '*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*' as described by Heiligenberg (1980). However, our results suggest that threshold for eliciting novelty responses is not the best parameter for extracting information about sensory processing. Threshold is independent of previous history, except when the increase in image contrast is just preceded by a decrease in image contrast. The interaction of two successive, opposite and different lasting effects (the increase in image contrast eliciting otherwise a novelty response and the preceding decrease in image contrast generating a longer lasting effect indicated by the increase in interval variability) might explain this change in threshold. By contrast, the scaling constant appears to be a reflection of sensory processing features such as the generation of a central template. In fact, while the certainty of provoking a novelty response is only affected by the contrast of the few preceding images, the amplitude of the novelty response is affected by the contrast of images occurring up to half a minute before. The scaling constant is an increasing function of the number of baseline images for all the explored range of baseline duration, which suggests that the central expectation signal or 'template' is renewed with a much longer constant than previously calculated based on threshold analysis (60 EODs *versus* hundreds of EODs).

Our results support the hypothesis of a 'template' generation initially proposed by Heiligenberg (1980), but reject the hypothesis of a fixed template, or a pulse-to-pulse comparison of the incoming images. In addition, study of the transference function of the electrosensory–electromotor transformation indicates that the scaling constant of this function is the most sensitive parameter for evaluating the template dynamics. The growth of this parameter with the number of low contrast baseline images indicates that the relative load of a given image in creating the 'template' fades as consecutive EODs continue to occur.

The most likely structure suited for storage and comparison of sensory responses is the electrosensory lobe. The principal output cells of this cerebellum-like structure are driven by the integration of electrosensory inputs with the parallel fiber input coming from other sensory and motor structures, as well as serving feed-back from higher level electrosensory structures (Réthelyi and Szabo, 1973; Maler, 1973, 1979; Bell et al., 1997b; Berman and Maler, 1999). This type of circuit fulfils the requirements to act as the kind of comparator between input and internal sensory representations proposed by Sokolov (1990). Recordings from single cells in the electrosensory lateral line lobe of mormyrids (Bell, 1981; Bell et al., 1993, 1997a–c), wave type gymnotids (Bastian, 1995a,b, 1996a,b, 1998, 1999) and elasmobranch (Bodznick et al., 1992, 1999; Bodznick, 1993; Montgomery and Bodznick, 1995) have demonstrated that sensory expectations – mirror imaging the moving average of the past sensory input – cancel out expected inputs and boost novel inputs. It is important to note that this process does not rule out other synergistic mechanisms such as peripheral receptor adaptation (Xu et al., 1996) or further processing at higher levels of the electrosensory pathway. In fact, Grau and Bastian (1986) found that '*most units studied in the torus semicircularis showed very strong, increased responsiveness*' to novel stimuli.

Unlike gymnotid and mormyrid wave fish, exhibiting continuous sine-wave-like EODs (Bass, 1986), pulse fish electrosensory system must identify a change in the images generated by the fish's own EOD involving an additional associated task. Pulse mormyrids compare and update the reafferent information in a pulse-to-pulse manner by a plastic change of an electromotor command corollary discharge signal interacting with the reafferent electrosensory input (Bell, 1981, 1982; Bell et al., 1993, 1997a). However, in *G. carapo*, as well in other pulse gymnotids, there is no evidence of a pacemaker corollary discharge (Heiligenberg, 1980; Bastian, 1986; Castelló et al., 1998). The presence of a well-timed expectation signal independent of an electromotor corollary discharge is reflected in the occurrence of 'omitted stimulus potentials' when stopping repetitive electrosensory stimuli in elasmobranch (Bullock et al., 1990). This phenomenon, signaling the time during which the omitted sensory input should have occurred, is widespread in nature; it is observed in both vertebrates and invertebrates, from the very peripheral to the highest levels of sensory processing (Bullock et al., 1990, 1993; Karamürsel and Bullock, 1994, 2000; Ramon et

al., 2001), and it might underline the central expectation mechanism suggested by our data. However, invasive techniques will be required to elucidate whether and how pulse-discharging gymnotids simultaneously deal with detection, storage, comparison and discrimination of reafferent and exafferent signals.

The stereotyped time course of the novelty response is independent of the stimulus pattern, suggesting that this behaviour is probably not completely organized within electrosensory structures. Transient accelerations of the pacemaker frequency are elicited not only by reafferent electrosensory signals but also by exafferent signals of various sensory modalities, which indicates that the electromotor control of pacemaker is the final common path of an alert system triggered by novel sensory stimuli. Theoretical and experimental studies of pacemaker structures show that the interval between pulses is a logarithmic function of pacemaker input (Hansel et al., 1998). Thus, to fit the present results it should be considered that pacemaker cells, which set the timing of the EOD, might introduce the logarithmic rule.

In conclusion, we propose the following hypothesis to explain the sensory-motor integration of the novelty response: (1) the central nervous system of the fish computes the difference between the response to each incoming electric reafferent image and a 'central expectation signal' or 'template' that is repetitively updated with each EOD; (2) the novelty response is triggered by a threshold-based decision process; (3) once threshold is achieved, the amplitude of the novelty response is determined by the difference between the 'template' and the response to the reafferent input; (4) the relaxation curve following the initial shortening of the interval is determined by the electromotor side of the system. The creation of the 'template' and the comparison process are most probably carried out on the sensory side in electrosensory lateral line lobe. The triggering decision and the logarithmic scaling processes are probably carried out at the pre-pacemaker and pacemaker structures, respectively.

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