Disproportionate Distribution of Field Potentials Across the Toad's Tectal Visual Map in Response to Diffuse Light ON and OFF Stimulations

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In toads *Bufo marinus* and *Bufo bufo spinosus*, field potentials (FPs) were recorded from the surface of the optic tectum at different sites of the visual map in response to a sudden diffuse darkening (OFF) and lightening (ON) of the visual field of the contralateral eye. The OFF and ON responses were differently pronounced or even failed to occur. The latency of the former was significantly less than the one of the latter. FP amplitudes of the OFF and ON responses were strongest in the representation of a horizonto-superior anterio-lateral portion of the visual field and weakest toward the posterior field of vision. This phenomenon suggests various interpretations for subsequent experiments.

Optic tectum   Visual map   ON/OFF stimulation   Field potentials   Disproportionate representations
Bufo bufo spinosus   *Bufo marinus*

INTRODUCTION

The non-foveated retina in amphibians provides the brain with visual information preprocessed under various aspects and transmitted via special channels along the axons of ganglion cells. Lettvin, Maturana, McCulloch and Pitts (1959) recorded from the superficial layer of the frog's optic tectum responses of four types of retinal ganglion cell fibres distinguished by: the sizes of the excitatory receptive fields (ERF), the degree of sensitivity to moving objects, the presence of a sustained response when a moving object was suddenly stopped in the ERF, the erasability of such sustained response after a sudden darkening (OFF) and diffuse lightening (ON) of the visual field, the response property to brisk diffuse light OFF and ON stimulations, and the adaptation to repetitive ERF traverses by a stimulus object. Quantitative studies have further specified these classes 1–4 (Grüsser & Grüsser-Cornehls, 1976; Ewert, 1976), later termed R1–R4 (Ewert, 1984), whereby in toads the R1-type seems to be rare or even missing (Ewert & Hock, 1972). Information provided by the different classes is present from any locus of the visual field in accordance with the retinotectal map.

Since it is known that the anatomic retinotectal projection in amphibians (e.g. see Glaze, 1958) deviates from linearity much less than the one in mammals (e.g. Sprague, Berlucchi & Rizzolatti 1973), in the present paper we ask how retinotectal activity is distributed across the retinotectal map. Toward a first global approach in toads, we recorded the field potential (FP) from different sites of the tectal surface to alternating onset and offset of diffuse light. FPs express the postsynaptic activities of tectal neurons at their dendritic trees, reaching the superficial laminae, in response to visual input.

MATERIALS AND METHODS

Experimental animals

Twenty-three European common toads *Bufo bufo spinosus* and South American cane toads *Bufo marinus* were kept in vivaria under species relevant conditions. Since European amphibians are now protected in Germany by federal laws, our experiments, initially started with *B. b. spinosus* were continued with the South American *B. marinus* which is not protected regarding its broad distribution and massive propagation. A comparison of the data obtained from both species in the present investigation revealed no remarkable differences.

Preparation

Toads were anaesthetized with 100 mg/kg Ketavet[R]. After exposing the dorsal brain surface in the region

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of the mesencephalon, the first two meninges (dura mater and arachnoidea) were locally cut and carefully retracted. The experimental animal was then placed in a chamber equipped with head/body holders and a special cooling and ventilation procedure. (For details see Schwippert, Beneke & Ewert, 1995.)

Visual stimulation

Retinal stimulation was carried out by switching roomlights on and off. The light intensity was 98 lx at ON and 2 lx at OFF. Change of illumination was registrated with a photoelement. Repetitive OFF and ON stimuli lasted 20 sec each, or 3 sec. White cardboard surrounded the experimental set-up.

Recording

Field potentials (FPs) were recorded successively from different sites of the surface of the optic tectum (Fig. 1) by means of glass microelectrodes of a tip diameter of 10–12 μm, produced with a Sutter P-87 puller, and filled with a solution comparable to Frog–Ringer serving as electrolytic conductor. The step-motor driven recording electrode, fixed in the micromanipulator, was oriented perpendicular to the dorsal tectal surface and positioned

onto the pia mater at slight pressure. The FPs, preamplified and filtered at 0.3–1000.0 Hz (in the case of multi-unit recording at 300–1000 Hz), were fed to an oscilloscope, digitalized by a CED 1401-plus interface, stored on hard-disc of a 486 PC, and processed by means of the CED-internal and free-programmable signal analysing software "Spike 2".

RESULTS

General considerations

Field potentials, FPs (Fig. 2, see outlet), express the sum activity of neuronal populations in the neighbourhood of the recording electrode. After the FP theory of laminated structures (Vanegas, Williams & Essayag, 1984), synaptic excitation (EPSP) is due to a decrease and synaptic inhibition (IPSP) to an increase of extracellular positive charges. Since the laminated optic tectum (OT) contains the dendritic trees mainly in the superficial layer and the corresponding somata in deeper layers, synaptic input leads to different electric dipoles arranged perpendicularly to the tectal surface. Negative waves, N, of FP recorded from the tectal surface, therefore, indicate postsynaptic excitatory processes and positive waves, P, inhibitory processes (e.g. Jassik-Gerschenfeld & Hardy, 1984; Leung, 1990).

In cane toads B. marinus and common toads B. b. spinosus, FPs were recorded from the surface of OT in response to diffuse light ON and OFF stimulations of the contralateral retina, while the ipsilateral eye was covered with a tiny opaque hemisphere. According to a previous study, in which the optic nerve was stimulated electrically (Schwippert et al., 1995), nine equidistant tectal recording sites (A–I) served as a standard grid for FP mapping [Fig. 1(C)]. At the beginning of the experiments, animals were adapted to light (98 lx). Altogether 27 FP maps were established in response to OFF and ON stimulations, $n = 18$ maps from $i = 13$ B. b. spinosus and $n = 9$ maps from $i = 9$ B. marinus.

FP components

Figure 2 (see outlet) shows FP records to diffuse light ON and OFF stimulations in B. marinus. OFF and ON responses started with a small positive initial component P1* followed by two main negative waves N1 and N2, interrupted by a positive wave P2 and terminated by P3. The FP wave pattern was observed in both toad species. From this basic pattern more complex ones (see Fig. 2) can be derived, regarding additional deflections (N2 and/or P3 waves) and oscillations (starting during the P3 wave of the OFF response). This complexity, most obvious in the OFF responses, was surprisingly constant at a given recording site as the superimposed traces of subsequent records at 20 sec intervals show. The initial P1* component did not clearly emerge in all FP records.

With respect to the different degrees of complexity of the FP pattern, our latency measurements concerned in particular the N1 wave from recording site E. Switching room light, it started to OFF stimulation after
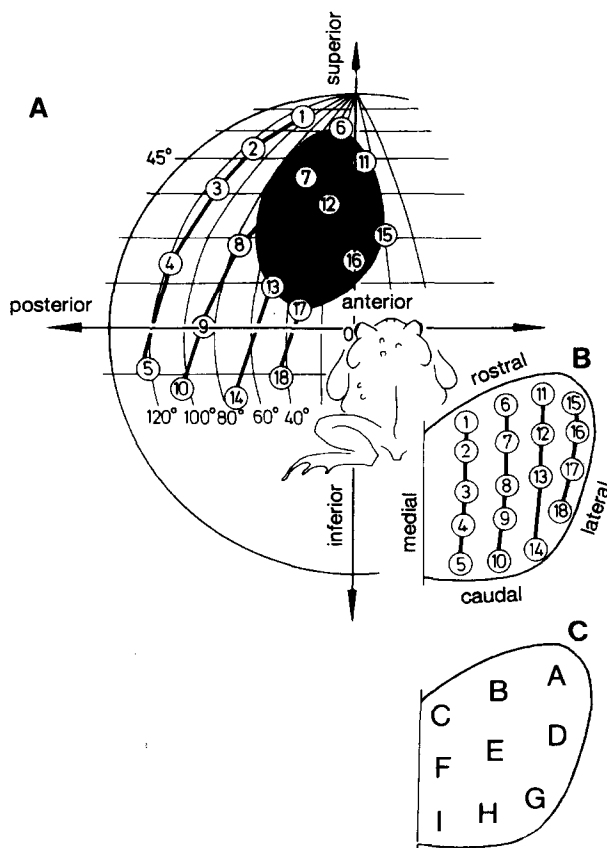

FIGURE 1. Projection of the visual field of the left eye (A) onto the dorsal surface of the common toad's right optic tectum (B) (after Ewert & Borchers, 1971). The standard grid of sites A–I, from which tectal FPs were recorded in this paper, are shown below (C). The sites displaying strongest FP responses correspond approximately to the black indicated portion in the visual field.
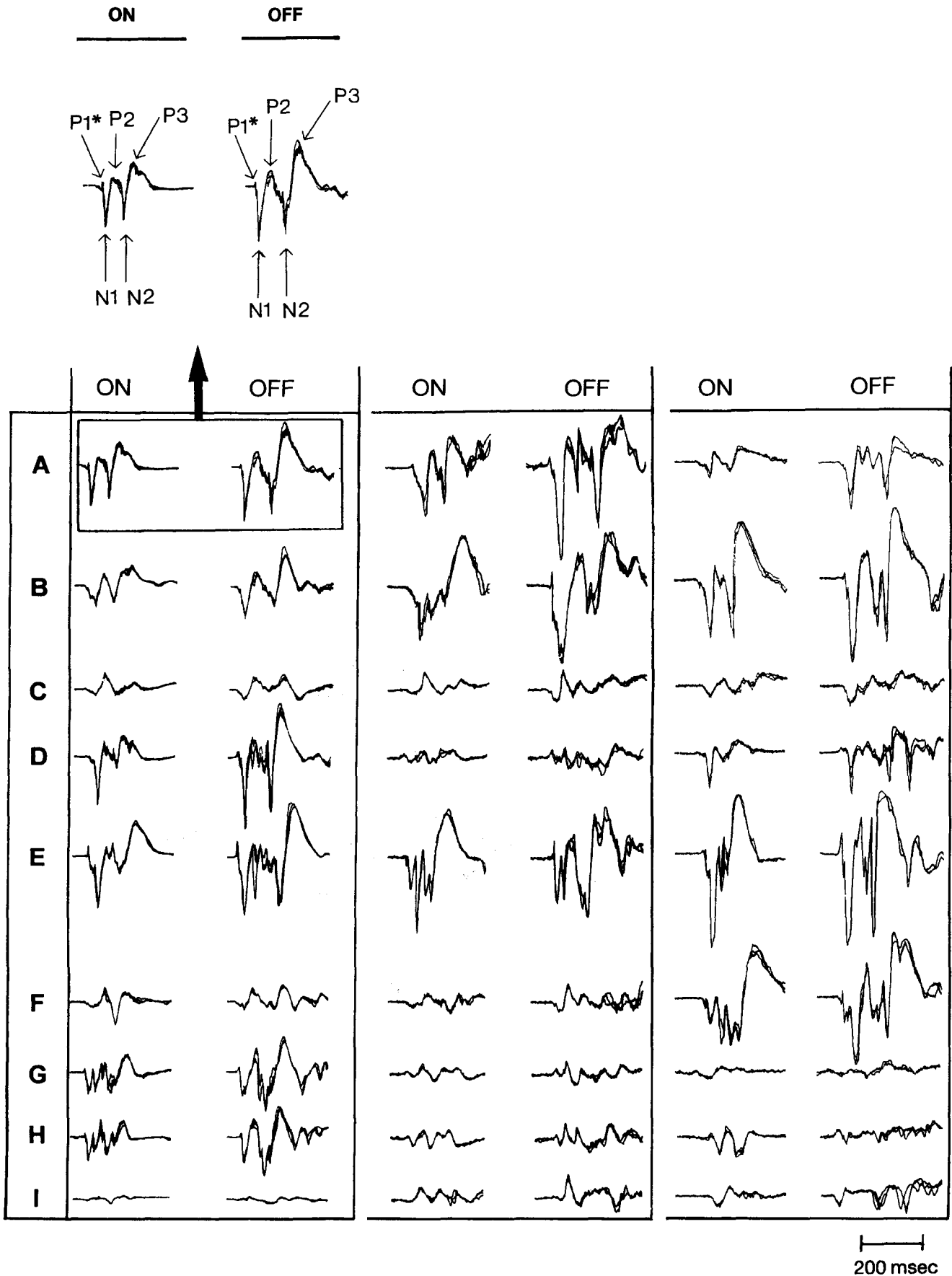
FIGURE 2. Distribution of tectal FPs in response to diffuse light ON and OFF stimulations across the recording grid A–I as depicted in Fig. 1(C). Repetitive stimuli lasted 20 sec; superimposed traces for the initial three respective stimuli are shown. Examples of three cane toads. Outlet: main components of tectal FPs to ON and OFF stimulation: P1*, N1, P2, N2, and N3. For explanations see text.

56.2 + 3.6 msec (*n* = 59, *i* = 9) and to ON after 154.7 + 2.9 msec (*n* = 87, *i* = 10).

Records across the tectal visual map

The FPs recorded across the tectal surface revealed disproportionalities regarding the amplitudes and the pattern of the wave components. Depending on the recording site, the N1 wave amplitudes in response to ON and OFF stimulation were almost equally strong (e.g. site E) or OFF dominated (e.g. site A) or both extremely weak (e.g. site I). At most sites the entire FP response was stronger to OFF stimulation. Figure 2 exemplifies this for FP maps of three cane toads. Within a map, the different wave patterns were remarkably constant as the superimposed traces at each recording site for subsequent ON/OFF stimulations in 20 sec intervals demonstrate. A comparison of the maps from the three individuals shows certain consistencies: responses from the site E were very strong, from sites I and C very weak. The fact that FPs of the remaining sites displayed differently strong responses can be explained by methodological reasons, since it was not possible to hold the recording grid in all individuals exactly congru-

ent. Site E which generally displayed maximal ON/OFF responses belongs to a response area spreading towards A, B, and D. The closer or farther the recording sites deviate from this tectal region in different preparations, FP responses may emerge more or less stronger (for example, cf. responses from sites D and F). The main FP response area in the tectum represents a portion of the frontolateral visual field of the contralateral eye, as Fig. 1(A) shows.

In the experiments described so far, the repetitive ON and OFF stimuli lasted 20 sec each. For stimulations >20 sec, the FP pattern showed no obvious change. However, if the ON and OFF periods were reduced to 3 sec, the response latencies of the FPs increased and the wave pattern became simpler (subcomponents were attenuated). Figure 3 shows superimposed traces of responses to the 4th, 5th, and 6th ON and OFF stimulations, respectively; the comparison between *B. b. bufo* and *B. marinus* reveals no obvious species differences.

Control experiments

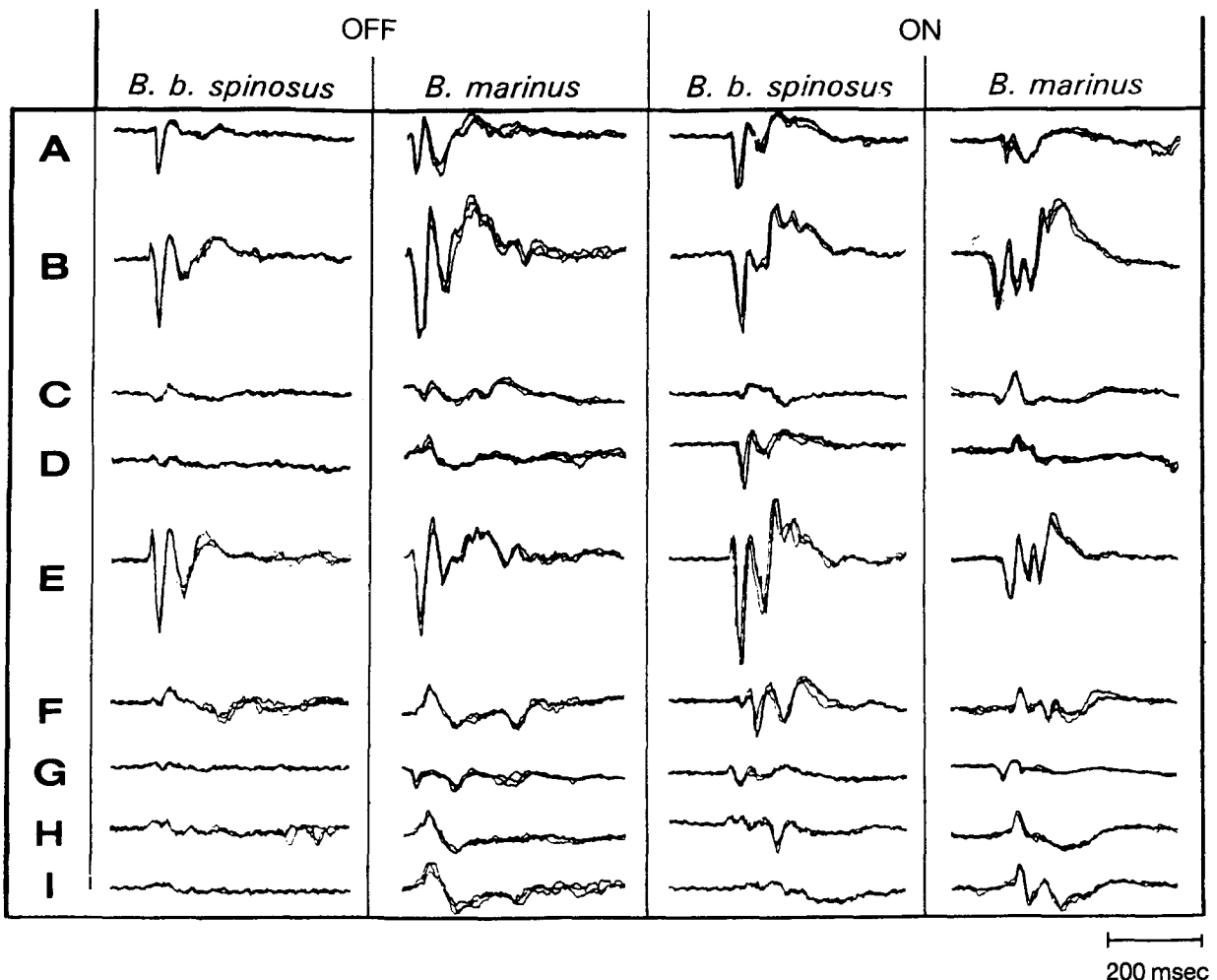A reason for the different FP activities across the

FIGURE 3. Rapid change of ON and OFF stimulations each one lasting 3 sec, and distribution of tectal FPs across the recording grid A–I in a common toad *B.b. spinosus* and a cane toad *B. marinus*. Superimposed traces for the 4th, 5th, and 6th respective stimulus.

tectal surface may be locally different resistances between the tip of the electrode and the pia mater. This possibility could be excluded by appropriate impedance measurements, yielding $8 \pm 1 \, M\Omega$ for all recording sites.

The disproportionate distribution of FP activities to the ON/OFF stimuli could be an artifact caused by light intensity gradients due to silhouettes of micromanipulators, electrodes, and other pieces of the equipment within the toad's visual field. To test this argument, the distribution of tectal FPs was recorded in three different set-ups. (1) The toad's contralateral eye was exposed to a bulb that actually produced a diffuse gradient. (2) A light conducting system was placed onto the cornea to assure a silhouette-free illumination. (3) A miniature perimeter consisting of a white diffuse transparent hemisphere, surrounding the toad except a small hole for recording and reference electrodes, was illuminated diffusely from outside; light intensity measurements at the inside of this arrangement showed a gradient-free illumination of the retina. In all cases (1)–(3), the differences of the FP activities across OT were maintained as exemplified in Figs 2 and 3.

Multi-unit recordings

Different classes of retinotectal inputs terminate in different depths of the OT. After penetration of the tectal surface, to ON and OFF stimulation short bursts of spikes were recorded at a depth of $200 \, \mu m$ when the bandpass filter was in the range of 300–1000 Hz. The OFF response was slightly pronounced indicating multi-units from R3 terminals. By the same electrode, FPs were recorded from this position when the filter was in the range of 0.3–1000 Hz. Regarding the course and the components, these FPs corresponded to those recorded from the tectal surface [Fig. 4(a, b)]. According to their latencies, the multi-unit and the FP responses showed that R3 inputs contribute at least to the excitatory postsynaptic Nl components. R3 multi- units can be recorded from every site of the tectal surface, mainly the region including E or B and less from C, G, or I. A comparison between records from site I [Fig. 4(a)] and site E [Fig. 4(b)] shows that R3 input in the former case is much less than in the latter and that in both cases the strength of R3 input corresponds to the amplitude of the Nl wave [see arrows in Fig. 4(a, b)]. The question arose, whether also disproportionalities regarding the response to different ON/OFF-frequencies exist. In preliminary experiments, R3 multi-units were recorded from site E and site I in response to alternating ON- and OFF-stimuli whose frequency was adjusted by a rotating sector. As preliminary data in Fig. 4(c, d) for representative examples shows, the R3 responses followed at the site E to higher ON/OFF-frequencies than at the site I.

DISCUSSION

The FPs recorded from toad's tectal surface in response to diffuse light ON and OFF stimulations show the main sequential components comparable to the ones obtained in response to quantitative electrical stimulation of the contralateral optic nerve (Schwippert *et al.*, 1995): a more or less pronounced initial positive deflection P1*, expressing presynaptic axonal inputs, and subsequent alternating negative and positive waves, expressing postsynaptic excitatory (N1, N2) and inhibitory processes (P2, P3). FPs were always finished by a strong positive wave P3 often displaying small oscillations, probably resembling reverberatory excitatory and inhibitory events (see also Debski & Constantin-Paton, 1990).

Regarding retinotectal inputs to diffuse light ON and OFF stimulations, previous studies reported that retinal ganglion cells of class R2 show mostly no or a weak ON response, R3 neurons display phasic ON and OFF responses, whereas R4 neurons discharge phasic-tonic OFF responses. Hence, R2 and R3 (terminating at a depth of 100–300 μm) contribute to FP's ON response, whereas R3 and R4 are responsible for the OFF response [cf. also Fig. 4(a)] (Chung, Bliss & Keating, 1974; Grüsser & Grüsser-Cornehls, 1976; Ewert, 1984).

Since the difference in FP's OFF and ON response latencies is also observed in the ON/OFF response displaying R3 neurons (Barlow, 1953; Tomita, Murakami, Hashimoto & Sasaki, 1961), it must be attributed to intraretinal processing (Aho, Donner, Helenius, OlesenLarsen & Reuter, 1993). Latencies also depend on the color of the diffuse light (Donner & Reuter, 1976), its intensity, the previous light or dark adaptation (Varju & Pickering, 1969), and the room temperature (Aho *et al.*, 1993).

Not only contralateral retinal input but also ipsilateral pretectal and isthmic visual inputs contribute to optically evoked FPs (Wang & Matsumoto 1990). We demonstrated that the Nl wave of the tectal FP in response to electrical stimulation of the contralateral optic nerve is attenuated by preceding electrostimulation of the ipsilateral pretectal Lpd/P area (Schwippert *et al.*, 1995). Evidence of ipsilaterally pretectotectal projecting visual widefield neurons was provided by neurophysiological (Buxbaum-Conradi & Ewert, 1995; Schwippert & Ewert, 1995) and histochemical investigations (Kozicz & Lázár, 1994) suggesting pretectal presynaptic inhibitory influences on contralateral retinal input in superficial tectal laminae mediated by the neuropeptide-Y. The declining oscillations of the large inhibitory P3 wave to OFF stimulation indicate either inputs of repetitive bursting R4 neurons or alternating postsynaptic excitatory and inhibitory loop-operations of tectal extrinsic (e.g. pretectal) and intrinsic origin. The latter is consistent with the hypothesis that tectal excitatory reverberatory processes in response to visual input are under inhibitory control (Ewert, 1976, 1989, Székely & Lázár, 1976).

Returning to the introductory question of this paper, we can confidently say that disproportionalities of FPs to ON and OFF stimuli exist across the tectum. This disproportionality is not congruent with the one seen in the visuotectal projection of anuran amphibians (e.g. Levine, 1984): there, a horizontal nasal/temporal strip in the visual field—corresponding to the retinal area
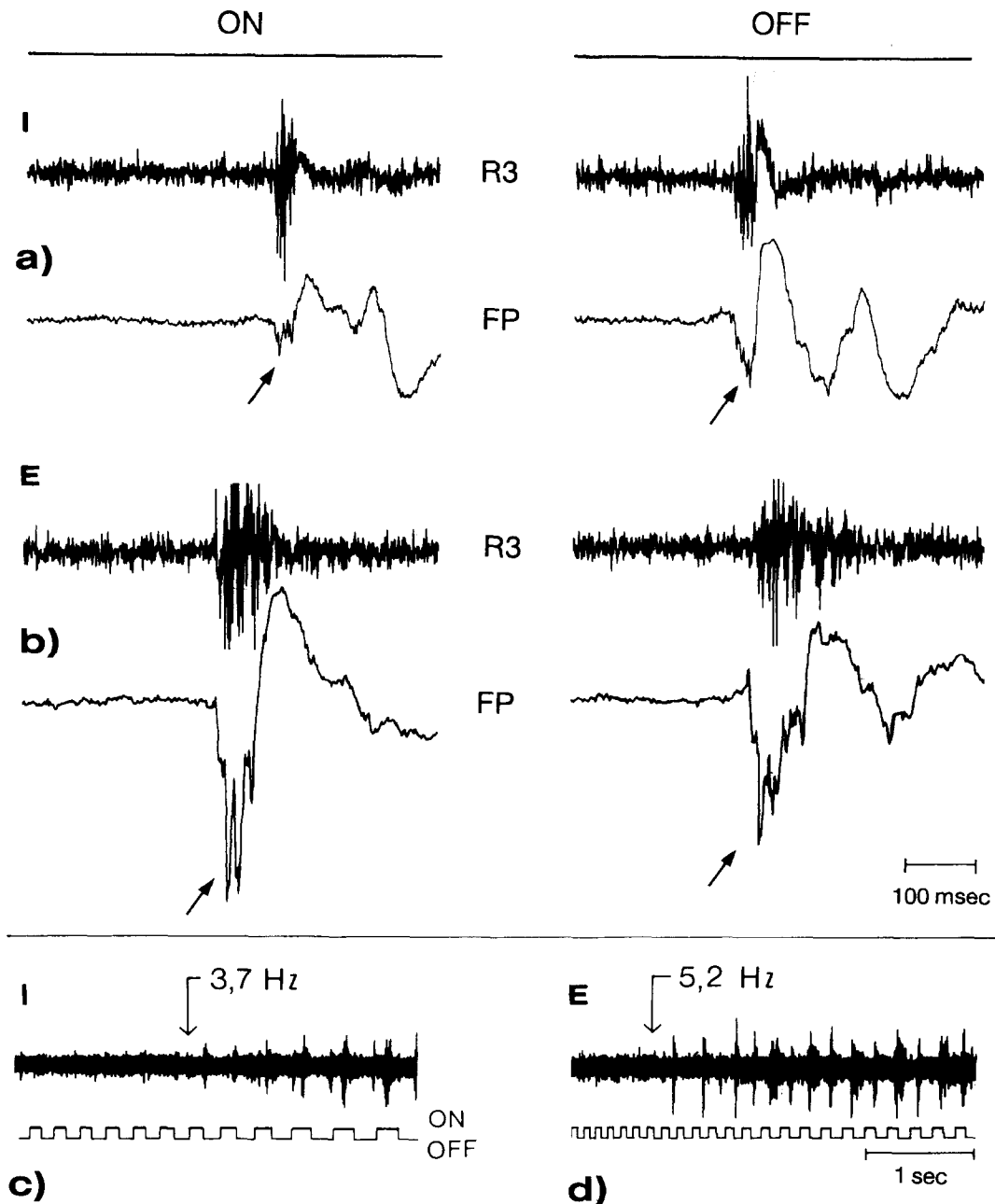
FIGURE 4. (a) Multi-unit activities of retinal R3 fibre endings and tectal FPs in response to ON and OFF stimulations, recorded with the same electrode 200 μm below the tectal surface at site I, and filtered at 300–1000 and 0.3–1000 Hz, respectively; the duration of the repetitive ON and OFF stimuli was 3 sec for each; FP represents the averages of 3 records; arrow points to the N1 wave. (b) Same experiment as in (a) for the tectal recording site E. (c, d) Following ability of R3 multi-unit responses to alternating ON and OFF stimuli at different frequencies, recorded from sites I (c) and E (d), respectively. Representative examples.

striata—is represented in a larger region of the tectum than a portion of an appropriate size from the horizontal/superior visual field. The results of the present study allow us to present the following four hypotheses for future investigations.

First, it is reasonable to suggest that retinotectal projecting R2, R3, and R4 neurons display different response properties to diffuse light ON and OFF stimulations with reference to the tectal visual map. Since retinal ganglion cells with intermediate properties (e.g.

Backström & Reuter, 1975) and subclasses (Ewert & Siefert, 1974; Tsai & Ewert, 1987) appear to exist, the question of functional continua is discussed (Gaillard & Garcia, 1991). For example, among R3 neurons— phasically discharging to onset and offset of diffuse light—either the OFF response dominates the ON response, or the latter is absent or both fail to occur. Teeters, Arbib, Corbacho and Lee (1993) presented a model of the anuran retina which simulates experimental data relating to toad's and frog's R2, R3, and R4

neurons, for example, with respect to ON and OFF responses. In Teeter's model, R3 neurons displaying OFF > ON, OFF > ON, and OFF = ON responses can be simulated by adjusting the relative weight of the depolarizing transient amacrine cell (ON) channels and the hyperpolarizing transient amacrine cell (OFF) channel. Such weights could display differences in retinotectal information transfer with reference to the visual field (Gaillard, 1982; Dowling, 1990). But ON = OFF = zero could not be simulated except by suppressing the OFF-channel input in the model.

Second, alternatively, we infer that different ON and OFF response displaying R-type neurons—according to Teeter's model with different weights of the ON- and OFF-channels—are equally distributed across the tectal visual map. The disproportionality of the FPs might result from a disproportionality of interactions between excitatory and inhibitory processes (Freeman & Norden, 1984). For example, comparing the records from sites I and E [Fig. 4(a, b)], the small spike amplitudes of R3 terminals and the corresponding weak N1 amplitude in I might result from presynaptic inhibition of retinotectal input (e.g. see Schwippert & Ewert, 1995), and the relatively large P1 and P3 amplitudes may be due to strong inhibitory postsynaptic input to OT.

Third, a comparison between R3 multi-unit spike activities and FPs recorded from tectal sites I and E [Fig. 4(a, b)] might suggest that the difference in FP amplitudes (regarding N1 wave) results from a different density of retinotectal projecting R3 fibres. Differences in thickness of the tectal structure, however, do not probably account for the observed FP disproportionalities, since such differences fail to occur in response to electrical stimulation of the optic nerve (Schwippert *et al.*, 1995).

Fourth, it should be considered that FP amplitudes might depend on the orientation of the terminal arborizations of retinal afferents (George & Marks, 1974), on the synaptic structure of the tectal dendrites, and on the way afferents contact the tectal dendrites (Grant & Lettvin, 1991).

This leaves open the question of the biological relevance of such disproportionate properties. Disproportionate representation of stimulus parameters is an important feature of sensory maps (Scheich, 1983). Biosonar frequency representation in mustached bat auditory cortex (Suga, 1990) and the over-representation of frequency bands in horseshoe bat's auditory system suitable for the detection of fluttering insects (Schnitzler & Oswald, 1983) are two illustrative examples. The fovea centralis of the mammalian retina is a classical example of a disproportionate representation of stimulus analysis. The retinally non-foveated amphibians show a variety of other disproportionate organizations, such as the densely packed distinct classes of tecto-bulbar/spinal descending neurons with reference to the frontal visual field (Ewert, 1989), or the black/white and white/black preferences regarding the dorsal vs ventral visual field (Ewert & Siefert, 1974), or a portion of the frontal visual

field presumably suitable for temporal resolution (as the present study, for example, suggests).

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