Question of Prey Feature Detectors in the Toad's *Bufo bufo* (L.) Visual System: A Correlation Analysis*

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Summary. 1. Toads *Bufo bufo* (L.) prefer as prey "worm-like" objects with long axis orientation parallel to the movement direction rather than the same objects oriented "antiworm-like" with their long axis perpendicular to the movement direction.

2. By means of statistical correlation methods with computer programs it was analyzed to what extent neurons from different regions of the visual pathway respond sensitively, selectively or specifically to moving configurational stimuli, such as worm-like and antiworm-like objects of equivalent sizes.

3. Neurons with *sensitivity* to particular moving configurational stimuli were found in the retina (classes R2, R3, R4) and the retinal projection fields in the thalamic pretectal region (class TH3) and the optic tectum (class T5(1)).

4. Neurons with *selective* responses to moving configurational stimulus objects, corresponding to the behavior, were found in a particular population of tectal neurons (class T5(2)).

5. No neurons were found with *specific* responses to a stimulus of a certain configuration.

Introduction

The common toad *Bufo bufo* (L.) prefers as prey worm-like objects with extension parallel to the direction of stimulus movement rather than antiworm-like ones extended perpendicular to the direction of movement (Ewert, 1968). The toad's ability to distinguish between a stripe moved as a worm and the same one moved as an antiworm is invariant for other stimulus parameters, such as (i) the direction in which the stimulus traverses the x, y coordinates of the visual

field (Ewert et al., 1978a), (ii) the direction of the stimulus background contrast (Ewert, 1968; Ewert and Burghagen, 1978a), (iii) the angular velocity within visible ranges (Ewert et al., 1978a and b), (iv) the mode of movement such as continuous or stepwise (Ewert et al., 1978b), (v) the object distance from the toad's eyes, within behaviorally relevant limits (Ewert and Burghagen, 1978a).

Using extracellular recording techniques, neurons were found in the visual pathway of the toad *Bufo bufo* (L.) with sensitivity to behaviorally relevant gestalt parameters mentioned above (for review see Ewert, 1976). The question has to be asked whether neuronal gestalt filters exist, which discriminate worm-like from antiworm-like objects corresponding to the toad's behavior. With the aid of statistical methods the present paper is designed to investigate possible correlations between prey-catching activity and neuronal activities of populations in the retina and the retinal projection fields in the TP-region and the optic tectum.

Stimuli

Toads *Bufo bufo* respond to particular *moving* objects with prey-catching behavior. Therefore it is reasonable to investigate those configurational stimulus parameters which are linked to the direction of movement.

Stimuli were two dimensional rectangular black stripes moved on a homogeneous white background (luminance 40 cd/m^2) by constant angular velocity at a constant distance from the toad's eyes in a horizontal direction (for procedures see Ewert, 1968, 1969; Ewert and Hock, 1972). *Worm-like objects:* From a configurational "indifferent" small square the side xl_1^+ parallel to the direction of movement

was elongated in steps with x=1, 2, 4, 8, and 10, whereas the side l_2^+ perpendicular to the movement direction was held constant. *Antiworm-like objects:* The side l_1^+ of the square parallel to the direction of movement was held constant and xl_2^+ perpendicular to the direction of movement, was varied in steps with x=1, 2, 4, 8, and 10.

Toads measure the absolute size of the stimulus during prey-catching behavior (Ingle, 1968; Ingle, 1976; Ewert and Gebauer, 1973; Ewert and Burghagen, 1978a and b). Therefore the values $xl_{1,2}^+$ have a metrical dimension. The neuronal activation in paralyzed toads, however, depends on the visual angular size of the stimulus. Thus in neurophysiological experiments the values $xl_{1,2}^+$ are measured in degrees of visual angle. During the behavioral experiments, stimuli were moved through the visual field at a distance of d=70 mm from the toad's eye. In this case the sides of the square were $l_{1,2}^+=2.5$ mm which is equivalent to a visual angular size of 2 degrees, and correspond to the lengths l_1^+ and l_2^+ used in the neurophysiological experiments. Since the relationships between $xl_{1,2}^+$ and the neuronal discharge frequency were not altered when the distance, d, of the stimulus from the toad's eye was varied within limits, we used d= 250 mm in these experiments for technical reasons (v. Wietersheim and Ewert, and Hock and Ewert, in preparation). It is assumed that the visual system of the toad is capable of transforming visual angular sizes into metrical dimensions (Richards, 1968; Eysel and Grüsser, 1971). The stimulus angular velocity was v=20 [degrees × s^{-1}] in the behavioral experiments and v=7.6 [degrees × s^{-1}] in the neurophysiological experiments. It was found that the behavioral and neurophysiological response relationships concerning the configuration of the moving stimulus were not generally altered within the investigated range of $5 \leqq v \leqq 20$ [degrees × s^{-1}] (Ewert et al., 1978a; v. Wietersheim and Ewert, 1978 in preparation).

Discriminative Values of Stimuli

The prey catching behavior of the toad *Bufo bufo* (L.) consists of a sequence of different motor patterns; (1) orienting movement towards prey; (2) following the prey; (3) fixating it and snapping; (4) gulping; (5) mouth cleaning. Toads respond to a moving prey object first with the orienting movement, which brings the stimulus into the binocular visual field. Should a moving stimulus have no prey features, the probability that the toad orients to it is low; providing no other components influence the toad's "normal" motivation, such as learning processes (Brzoska and

Schneider, 1978) and seasonal effects[1]. Thus, the decision "prey or not prey" precedes the orienting motor response. During laboratory experiments the relative effectiveness of prey dummies can be measured by the occurrence of orienting movements within a fixed time interval (orienting activity, R_b). For example, if the stimulus moves with a *constant* angular velocity at a constant distance around the toad and the animal follows the stimulus continuously, the product of the turning frequency R_b and the average turning angle $\bar{T}$ is constant (Ewert, 1969):

$$R_b \times \bar{T} = \text{[degrees} \times \text{min}^{-1}]$$

$$R_b = c/\bar{T} \text{ [orienting movements} \times \text{min}^{-1}]$$

where c is the angular velocity of the stimulus related to its center of rotation. c is held constant and R_b can be used as an index for the discriminative value of the stimulus and also for the probability that the stimulus fits the category prey. For a constant angular velocity the prey-catching activity R_b was measured for each toad in relation to both stimulus parameters xl_1^+ (worms) and xl_2^+ (antiworms) for x= 1, 2, 4, 8, and 10. Experiments were repeated with 20 different toads of the same species.

The activity of a single neuron in response to parameters xl_1^+ and xl_2^+ of stimuli traversing the receptive field center at a constant angular velocity was measured by calculating the average discharge frequency R_n [impulses × s^{-1}]. The responses of movement sensitive neurons belonging to different populations, called "classes" were investigated: Retinal ganglion cell classes R2, R3, R4 (with 10 single neurons in each class investigated), thalamic-pretectal neurons of class TH3 (21 neurons) and neurons of the optic tecum classes T5(1)[2] (20 neurons) and T5(2) (18 neurons).

The curves representing the stimulus response relationships for the prey-catching behavior activity and the neuronal activities are shown in Figure 1. The data on prey-catching behavior are from Ewert (1972), the neurophysiological data from Ewert and Hock (1972); v. Wietersheim and Ewert (1978); see also Ewert und v. Wietersheim (1974).

A quantitative measure of the discriminative value

[1] In spring time the female releases orienting responses from the male, which are components of courtship behavior; during this time prey-catching behavior fails to occur. Experiments with one-eyed toads showed that binocular prey fixation is not a precondition for prey recognition (for reviews see Ewert, 1976)

[2] We extend the nomenclature by Grüsser and Grüsser-Cornehls (1976). T5(1) and T5(2) neurons are different populations and they correspond to tectum-1 and -2 neurons described in *Bufo bufo* by Ewert (1974). The TP neurons (Ewert, 1974) correspond to thalamic type 3 neurons (Ewert, 1971) which are named class TH3 in the nomenclature by Grüsser and Grüsser-Cornehls (1976)
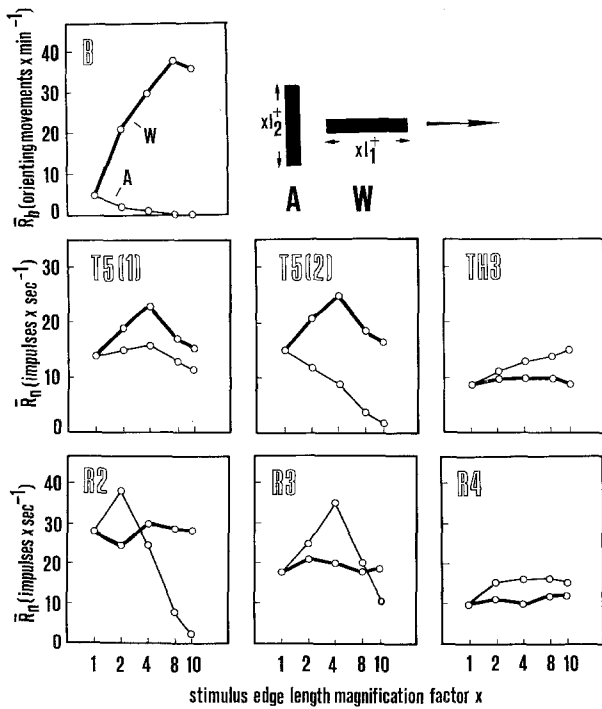
Fig. 1. Average prey-catching activity (*B*) and neuronal activity of retinal ganglion cell classes (*R2, R3,* and *R4*) and neuron classes of retinal projection fields (optic tectum: classes *T5 (1), T5 (2)*; thalamus-pretectum: class *TH3*) in response to worm-like (*W*) and antiworm-like (*A*) stripes of constant width $1_{1,2}^+$ (2.5 mm or 2°) and different length, xl_1^+ or xl_2^+ (for explanation see text). The black stimuli were moved on a white background at a constant visual angular velocity of 20°/s (B) or 7.6°/s (R2, R3, R4, T5(1), T5(2), TH3). Averages in B are from 20 individual toads *Bufo bufo*, in R2-4 from 10 different single neurons for each class, in T5(1) from 20, in T5(2) from 18 and in TH3 from 21 single neurons

Fig. 2. Discriminative value $D_{W,A}$ for selection between worms (*W*) and antiworms (*A*) of different length xl_1^+, xl_2^+ for the toad's prey-catching behavior (*B*) and for neurons of different classes in the visual system. *R2, R3, R4,* retinal ganglion cell classes; *T5(1), T5(2),* classes of cells in the optic tectum; *TH3,* class of neurons in the thalamic-pretectal region. (For explanation see text)

for selection between wormlike (*W*) and antiworm-like (*A*) objects of equivalent sizes is given by the "form-contrast" formula

$$D_{W,A} = \{\bar{R}_W - \bar{R}_A\} \{\bar{R}_W + \bar{R}_A\}^{-1}$$

where $\bar{R}_W$ is the average response to a worm-like object and $\bar{R}_A$ the average response to the same object presented as antiworm. $D_{W,A}$ is plotted against the stimulus parameters xl_1^+; xl_2^+ (see Fig. 2). The values of $D_{W,A}$ can be expected between $+1$ and -1. In the case of worm-like objects being preferable to the same ones presented as antiworm, $D_{W,A}$ is positive. When $D_{W,A} = +1$ or -1 both stimuli are distinguished by a clear "yes/no" decision.

Correlation Analysis

By means of a "Nicolet med 80" computer the Pearson waveform correlation of the stimulus response relationships from behavioral experiments (Fig. 1 B)
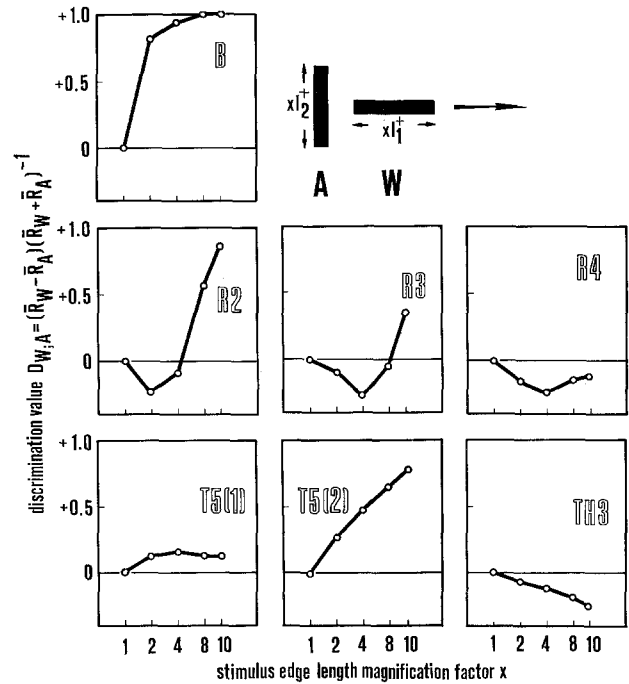
$$\bar{R}_b = f(xl_{1;2}^+) \text{ [orienting movements} \times \min^{-1}]$$

was compared with the corresponding neurophysiological stimulus response relationships (Fig. 1)

$$\bar{R}_n = g(xl_{1;2}^+) \text{ [impulses} \times s^{-1}]$$

where n = R2, R3, R4, TH3, T5(1), T5(2). The Pearson correlation coefficient routine allows the user to compare quantitatively the similarity of two waveforms. Continuity within each curve was approximated. The routine returns a number r between $+1$ and -1, where something close to $+1$ indicates a positive correlation, -1 a negative correlation, an $r=0$ a zero-correlation. r_W was calculated for the correlation of curves for worm-like (parameter xl_1^+) and r_A for antiworm-like objects (parameter xl_2^+). The question of correlation between behavioral and neuronal responses had to be analyzed for *both* parameters, xl_1^+ as well as xl_2^+. In the case of correlation a combination $\{r_A; r_W\} = \{1; 1\}$ should be expected. The results are shown in Table 1.

Table 1. Pearson correlation between prey-catching activity and neuronal activity of different neuronal classes in response to anti-worm-like (A) and worm-like (W) objects of different length xl_2^+; xl_1^+. (For explanation see text)

Neuronal class	$\{r_A$	; $r_W\}$
R2	0.8	; 0.9
R3	0.5	; 0.9
R4	0.3	; 0.9
T5(1)	0.5	; 0.9
T5(2)	0.9	; 0.9
TH3	0.2	; 0.9

Discussion

From the correlation table it becomes evident that the parameter xl_2^+ of a configurational stimulus plays a dominant role in the decision making neuronal processes.

Among retinal ganglion cell classes the R2 neurons show best but not optimal correlations with the behavioral results on prey-catching according to the discriminative responses to the configurational parameters xl_1^+ and xl_2^+ (c.f. Fig. 1 with Table 1 and also Fig. 2). No correlation was found in R3 and R4 neurons. Among neurons from central retinal projection fields no correlation was found for thalamic-pretectal class TH3 neurons and tectal class T5(1) neurons. The best correlation of all investigated neurons from the retina and the retinal projection fields was obtained for tectal T5(2) neurons (c.f. Fig. 1 with Table 1 and also Fig. 2).

We may assume that the first steps of information processing concerning evaluations of the stimulus configuration (worm/antiworm) are performed at the retinal level (R2 neurons) as Lettvin et al. (1959) already concluded from their early neurophysiological investigations. Configurational evaluation processes become *selective* at neuronal populations beyond the retinal level (c.f. Figs. 1 and 2). TH3 and T5(1) neurons show *sensitivity* to configurational area parameters, such as worms (T5(1)) and antiworms (TH3). Tectal T5(2) neurons [3] exhibit *selective* responsiveness to these parameters. But the T5(2) neurons have no "worm-*specificity*" and they may have additional properties which have not yet come under quantitative investigation individually. The activity of these neurons in response to moving configurational stimuli reflects to a good approximation the probability that the stimulus fits the category prey. They might be involved in a "master system" recognizing prey and commanding the orienting turn. A hypothesis which

[3] Statistical analyses showed that T5(1) and T5(2) neurons belong to two different neuronal populations (c.f. also v. Wietersheim and Ewert, 1978)

explains the selective sensitivity of T5(2) neurons in response to moving configurational stimuli was elaborated by Ewert (1974), Ewert and v. Seelen (1974) and recently further elaborated by Arbib et al. (1978 in preparation).

Conclusion

The correlation analysis of our quantitative experimental data concerning the question of neuronal prey-feature detector systems in the toad *Bufo bufo* (L.) confirms and increases the accuracy of our earlier conclusions (Ewert, 1974; Ewert and Hock, 1972; Ewert und v. Wietersheim, 1974; Ewert and v. Seelen, 1974). The statement of Grüsser and Grüsser-Cornehls (1976, p. 373) "If neither retinal nor tectal neurons perform the neuronal operations necessary for 'master units' to recognize prey or predator, one has to search for other possibilities to link neurophysiological and behavioral data" should be revised along our knowledge of the experimental data.

We emphasize that the entire prey recognition system of *Bufo bufo* might be more complex than our current results have been demonstrated. On the basis of different neuronal filter operations also variations of pattern recognition (prey selection) systems may be derived in the different amphibian species according to their special ecological and behavioral adaptations.

Remarks

Grüsser and Grüsser-Cornehls (1976) recently reviewed our results on configurational prey-selection incorrectly and they came to wrong conclusions. These authors write in their review on p. 373: "Ewert's main argument for the existence of a 'master unit' recognizing prey is the very close correlation between the neurophysiologically obtained area functions of tectum I (T5(1)) and tectum II (T5(2)) cells and the area function obtained for the prey-catching behavior of toads. In all of Ewert's publications in which this close correlation between neuronal responses and behavior is described, the behavioral area function for prey-catching has an 8° maximum for stimuli extending perpendicular to the movement direction." This review is incorrect in three respects:

1. Area Functions. One of our main arguments that T5(2) neurons are part of a master system recognizing prey is the close correlation of the responses to behaviorally meaningful moving *configurational* stimuli, such as stripes elongated *in* (xl_1^+) or *perpendicular* (xl_2^+) to the direction of movement (Ewert, 1974 and 1976; c.f. also B and T5(2) in Fig. 1; compare also the discriminative values $D_{W,A}$ in Fig. 2). Furthermore T5(2) neurons show, corresponding to the behavior, *intermediate* activity in response to squares of different sizes, when xl_1^+ and xl_2^+ were elongated by equal amounts (Ewert and v. Wietersheim, 1974).

2. Correlation with T5 (1) Neurons. No correlation was found between T5(1) neurons (tectum I) and prey-catching behavior activity

in response to moving configurational stimuli as claimed by Grüsser and Grüsser-Cornehls (1976) (see Ewert and v. Wietersheim, 1974; Ewert and v. Seelen, 1974; see also Table 1 in this paper).

3. Stimulus Extension Perpendicular to the Direction of Movement. For neither the prey-catching behavior of *Bufo bufo* nor their T5(2) neurons do the stimulus response functions show an 8° maximum for stimulus extension (xl_2^+) *perpendicular* to the direction of movement as stated by Grüsser and Grüsser-Cornehls (1976). The behavioral as well as the neurophysiological response relationships for these stimuli show a *continuous decrease* as described by Ewert, 1968; 1972; Ewert and v. Wietersheim, 1974; see also v. Wietersheim and Ewert, 1978 (c.f. B and T5(2) in Fig. 1).

No quantitative data are yet available to answer the question of *how* the toad's central visual system transforms visual angular sizes into absolute dimensions according to the results on "size constancy" investigated by Ingle (1968, 1976), Ewert and Gebauer (1973), Ewert and Burghagen (1978b). A hypothesis for mammals is reported by Richards (1968) and Eysel and Grüsser (1971). It should be emphasized that this function cannot be involved in the basic discrimination between stimuli having *equal size* but different configuration, as in the case of a worm and an antiworm.

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