

Configurational pattern discrimination responsible for dishabituation in common toads *Bufo bufo* (L.): Behavioral tests of the predictions of a neural model

DeLiang Wang^{1*}, and Jörg-Peter Ewert²

¹ Center for Neural Engineering, University of Southern California, Los Angeles, CA 90089–2520, USA

² Abteilung Neurobiologie, Fachbereich 19, Universität Kassel, W–3500 Kassel, FRG

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Summary. Recently, a neural model of visual pattern discrimination for stimulus-specific habituation was developed, based on previous behavioral studies which demonstrated that toads exhibit a dishabituation hierarchy for different worm-like stimuli. The model suggests that visual objects are represented by temporal coding and predicts that the dishabituation hierarchy changes when the stimulus/background contrast direction is reversed or the stimulus size is varied. The behavioral experiments reported in this paper were designed to test these predictions. (1) For a pair of stimuli from the contrast reversal prediction, the experimental results validated the theory. (2) For a pair of stimuli from the size reduction prediction, the experimental results failed to validate the theory. Further experiments concerning size effects suggest that configural visual pattern discrimination in toads exhibits size invariance. (3) Inspired by the Groves-Thompson account of habituation, we found that dishabituation by a second stimulus has a separate process from habituation to a first stimulus. This paper serves as an example of a fruitful dialogue between experimentation and modeling, crucial for understanding brain functions.

Key words: Habituation – Model testing – Visual pattern recognition – Non-associative learning – Toad

Introduction

In amphibians, as in other animals, stimulus responses habituate to repetitive presentation of the same stimulus,

Abbreviations: *a-h* worm-like stimulus patterns; *AT* anterior thalamus; *ERF* excitatory receptive field; *IRF* inhibitory receptive field; *RF* receptive field; *R2* to *R4* retinal ganglion cell types; *vMP* posterior ventromedial pallium

Present address (and to whom offprint requests should be sent): Department of Computer and Information Science, Ohio State University, Columbus, OH 43210–1277, USA

hence displaying non-associative learning. When presented repeatedly with the same visual prey dummy, toads or frogs orient less and less frequently to the stimulus. This habituation is locus specific: after habituation of the orienting response to a worm-like moving stimulus at a certain visual location, the animal orients again to the same stimulus presented elsewhere in the visual field (Eikmanns 1955). Habituation is thus specific to the location of a prey, i.e. toads and frogs (Ewert and Ingle 1971) rapidly habituate to the redundant movement of even a real prey within the same location, but are responsive again to the (same) prey moved to a new location. Furthermore, habituation in toads is partially stimulus specific (Birukow and Meng 1955), exhibiting hierarchical stimulus specificity (Ewert and Kehl 1978). In the dishabituation hierarchy shown in Fig. 1, all configural objects were black and moved at constant speed against a white background, and they had the same long extension of area parallel to the direction of movement and short extension perpendicular to it. In laboratory jargon we refer to these stimuli as worm-like (being aware that not only worms but also other small invertebrates moving in direction of their longer body axis, such as caterpillars, carabid beetles, woodlice and millipedes, fit this prey-schema). A stimulus pattern higher in the Fig. 1 hierarchy can dishabituate (i.e., release prey-catching despite habituation to) another stimulus pattern lower in the hierarchy, whereas a stimulus lower in the hierarchy cannot dishabituate a stimulus higher in the hierarchy. At the same level in the hierarchy, the left one can slightly dishabituate the right one, but not vice versa. Before any habituation, however, all the stimuli were about equally strong in releasing prey-catching response.

The biological significance of stimulus habituation may be to prevent the sensorimotor system from fruitlessly responding to repetitively occurring stimuli and keep it alert to novel stimuli (Birukow 1955; Schleidt 1962). For example, habituation may prevent repeated attempts of a toad from approaching prey-like non-prey, such as leaves moving in the wind or inert objects floating on water. The hierarchical stimulus specificity exhibited

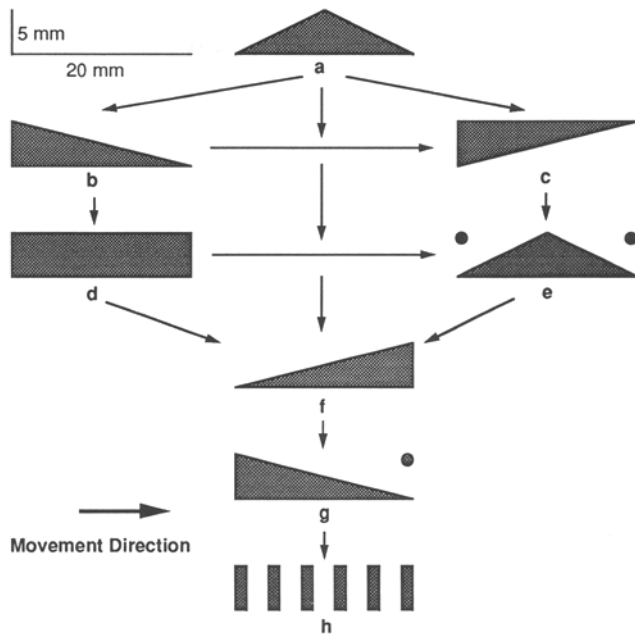


Fig. 1. Dishabituation hierarchy for the worm-like patterns used in stimulus-specific habituation of prey-catching orienting response in toads. Redrawn from Ewert and Kehl (1978). Between any pair of the 8 stimuli (*a-h*) in the hierarchy, one stimulus was presented first, and after full habituation of prey-catching to the stimulus, another stimulus was presented until it elicited no response. One stimulus can dishabituate all the stimuli below or to the right of it, but not vice versa. In these experiments, all objects were moved at the constant speed $v=20^\circ/s$, and their area extensions were 5 mm high (perpendicular to the horizontal direction of movement) and 20 mm long (parallel to the horizontal direction of movement) which correspond to 4° and 16° visual angles, respectively, from the animal viewing at a distance of 70 mm. Dots added to triangle objects were 1 mm in diameter which is about 1° . For further explanations see the method section

in toads suggests that it is the configural cues of the stimuli, not pure newness, which decide the animal's prey-catching behavior (Ewert and Kehl 1978). Because all the moving objects of Fig. 1 have the same height and length, the critical cues are (1) edge leading, (2) trailing edge, (3) isolated dot or (4) striped pattern. The dishabituation hierarchy clearly demonstrates that the toad visual system is capable of discriminating fairly fine differences in objects.

Dishabituation of the toad *Bufo bufo* is different from that obtained in lower invertebrates and mammals. In *Aplysia* for example, habituation seems to be independent of the specific patterning of the stimuli (Kandel 1976), whereas in mammals, habituation is stimulus-specific and dishabituation is mutual in the sense that if stimulus A can dishabituate stimulus B, then B can dishabituate A as well (Thompson and Spencer 1966; Sokolov 1975). In this context, the mammal and the primitive mollusc so-to-speak are extreme cases; the characteristic of hierarchical dishabituation in toads is an example of a kind of intermediate step toward stimulus specific habituation (for references on habituation and sensitization in vertebrates and invertebrates see Ewert 1967).

Wang and Arbib (1991) recently developed a neural model for simulating the dishabituation hierarchy. Drawing on known toad neurobiology, the model incorporates the neural structures of retina, optic tectum, and anterior thalamus, and the latter (AT) is assumed to be the structure where discrimination of the visual patterns is achieved with reference to the dishabituation hierarchy. The retina model produces the quantitative responses of 3 types of ganglion cells, R2, R3, and R4, which closely resemble physiological data (Ewert and Hock 1972). The AT model receives excitatory projections from tectal small pear cells, that relay the activities of retinal R2 cells, and direct inhibitory projections from retinal R3 cells. The output of the Wang and Arbib model clearly matches the ordered dishabituation hierarchy of Fig. 1. Not only do stimuli higher in the hierarchy generate larger AT responses in the model, but the stimulus pairs *b-c* and *d-e* which are on the same level in the hierarchy generate nearly equal responses. We emphasize that the proposed worm-discrimination system for stimulus specific habituation and dishabituation is distinct from the retino-pretectal/tectal system that determines the broad prey-schema (Ewert 1987).

Based on the model, the question was raised of whether the dishabituation hierarchy changes when the stimulus/background contrast is reversed or the stimulus size is varied. The former idea drew on previous behavioral experiments showing that common toads snap predominantly toward the leading edge of a black worm-like stripe moving against a white background, but mainly toward the trailing edge if the stripe is white and the background black (Burghagen and Ewert 1982), a phenomenon which can be traced back to the property of off-dominating retinal R3 ganglion cells (Tsai and Ewert 1987). On the basis of the simulated ordering of AT responsiveness, the model predicts a dishabituation hierarchy different from Fig. 1, as shown in Fig. 2A, if the direction of the stimulus/background contrast is reversed. In this situation, the response of R2 cells is about the same with respect to contrast reversal, since R2 responses are generated based on the equal contribution of depolarizing and hyperpolarizing amacrine cells; but now R3 cells show a trailing edge preference, since hyperpolarizing amacrine cells play a predominant role in generating R3 responses, thus leading to the different dishabituation hierarchy.

Turning to size effects, the model in general predicts that different hierarchies will be produced for different sizes of worm-like stimuli, because of an assumption that area effects for worm discrimination rely to a large extent on the interactions of the excitatory receptive field (ERF) and inhibitory surround (IRF) of retinal R2 ganglion cells, which have quite specific sizes. (Note that the retinal ganglion cells considered here have different ERF diameters: $4-6^\circ$ [R2] and $8-10^\circ$ [R3].) In particular, when the stimulus size is halved compared to Fig. 1 (10 mm corresponding to 8° visual angle), the previous IRF interaction is converted into an ERF interaction, resulting in the predicted hierarchy shown in Fig. 2B. A remarkable difference has been found in comparison with the original dishabituation hierarchy (Fig. 1). In particular,

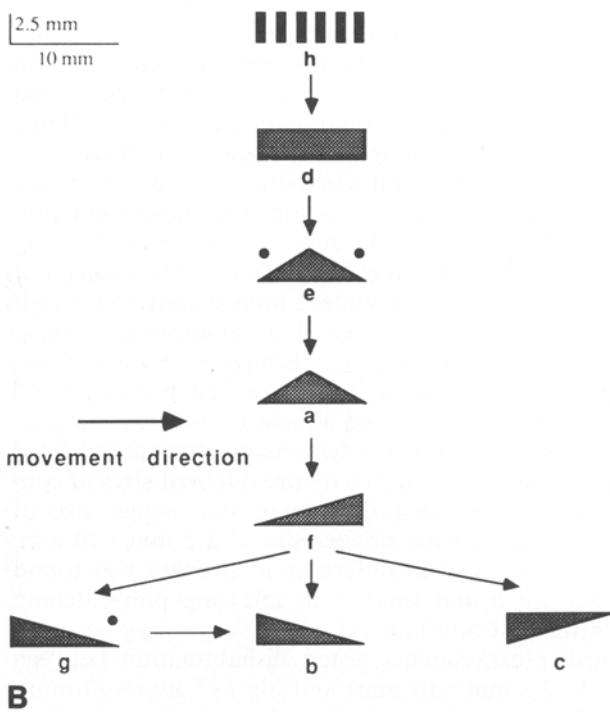
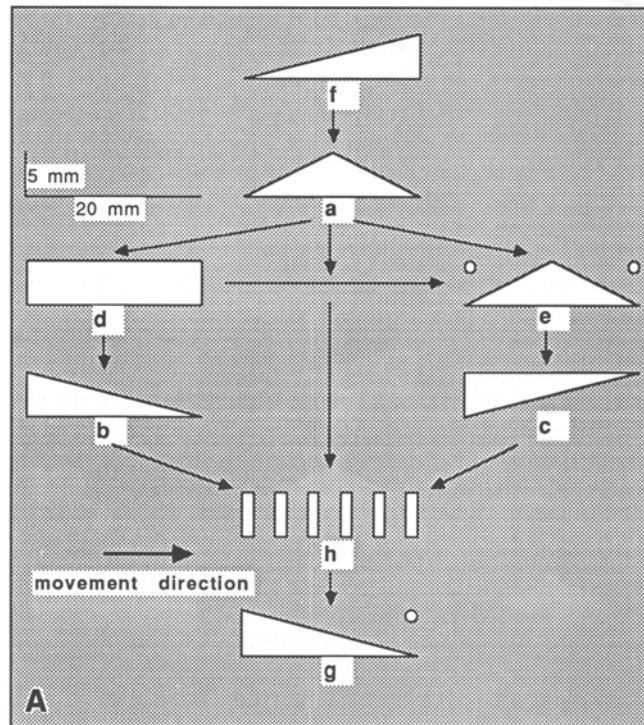


Fig. 2A, B. Predictions of the Wang and Arbib (1991) model. **A** Dishabituation hierarchy predicted by reversing stimulus background contrast. The same set of stimulus configurations (*a-h*) is used as in Fig. 1, but in contrast to Fig. 1 white stimuli were moved against a black background. **B** Dishabituation hierarchy predicted by reducing the stimulus size. The same set of stimulus configurations (*a-h*) is used as in Fig. 1, but all black stimuli are 2.5 mm high and 10 mm long, half of the previous linear size (from Wang and Arbib 1991)

stimulus *h* lies at the top of Fig. 2B, in contrast to the bottom position in Fig. 1, and the stimuli with dots appear higher in the hierarchy, reversing the original preference exhibited in Fig. 1. The reason for this prediction is that, since the stimulus size is halved compared to Fig. 1, the previous IRF interaction between the leading and trailing edges of a stimulus in the R2 receptive field is converted into an ERF interaction which strengthens overall responses. This ERF interaction is particularly manifested by *h*. The different R2 responses finally result in the different dishabituation hierarchy demonstrated by AT responsiveness via a tectal relay by small pear cells.

We have long been puzzled by the question of whether dishabituation counteracts previously learned effects of habituation, since different results would result in contrasting models for simulating habituation processes. In *Aplysia*, for example, it has been demonstrated that the synapses which were functionally inactivated due to profound habituation could be restored by a sensitizing stimulus (Carew et al. 1971). On the other hand, Groves and Thompson (1970) argued, mainly on the basis of the data from mammals, that sensitization, while releasing a new response, does not affect the trace of habituation. If in *Bufo* presentation of a dishabituating stimulus erases to some extent habituation traces of previous habituation, dishabituation processes may be underlain by presynaptic sensitization as demonstrated to be responsible for sensitization processes in *Aplysia*. If otherwise, dishabituation processes should have distinct neural processes.

The aim of the present behavioral study was to test the model's predictions as well as the relevance of the Groves and Thompson hypothesis to toad dishabituation.

Material and methods

a) Subjects. The behavioral experiments were performed with 200 common toads *Bufo bufo* (L.), which were kept in 30 aqua-terraria (60 × 30 × 30 cm³ each) at the constant room temperature of 20 °C and were fed regularly with mealworms.

b) Experimental set-up. A standard experimental set-up was used for measurements of the prey-catching turning activity of the toad (after Ewert and Kehl 1978). The animal sat in a cylindrical glass vessel within a homogeneous, white, and diffusely illuminated arena. Prey dummies were two-dimensional pieces of black cardboard with longer extension (20 mm or 10 mm) in the horizontal direction of movement and shorter extension (5 mm or 2.5 mm, respectively) perpendicular to it. A black (or white) stimulus was moved mechanically by means of an electric motor around the vessel at 20°/s against a 40 cd/m² white (or black) background at a distance of 70 mm from the vessel. All stimuli were moved from left to right from the viewpoint of toads, that is, clockwise from the observer looking downward. When the dummy fitted the prey category, the toad followed it by successive orienting turning movements. The orienting response habituated if the same prey dummy was continuously presented in the way described above, that is, the number of prey catching orienting turns per successive 1-min interval declined progressively. The criterion for habituation was reached when the animal responded less than 3 times to the dummy in a given 1-min interval. A habituation experiment usually lasted for 40 to 60 min. The total length of time for a stimulus series (till habituation occurred) could vary in different animals according to their different motivational levels. All experiments were performed

in early mornings or late afternoons, during which animals were most active.

c) Exchange of stimulus objects. After habituation of the prey-catching orienting response to a particular dummy, this stimulus could be automatically exchanged with another one, following the method of Ewert and Kehl (1978). Usually two different dummies were fixed in holders mounted opposite to each other on a disc which rotated around the center of the arrangement below the arena base. The holders beneath the arena were not visible to the toad. The position of dummy holders (within the slit beneath the base) could be shifted independently by means of electric motors which made one dummy disappear and another appear. More specifically, after habituation to a stimulus A – i. e. when the number of 1-min orienting turns to A reached the habituation criterion (< 3) – dummy A was switched underneath the arena base. At the same time, to test dishabituation, another dummy B was brought into the arena from underneath the arena base. The apparatus was designed such that the exchange of two dummies was done automatically outside of the toad visual field (for further details see Ewert and Kehl 1978).

d) Stimulus discrimination tests. Animals were used for the quantitative experiments if they showed 20–40 prey-catching orienting movements during the initial interval of 1 min in response to an optimal rectangular 2.5×30 mm² prey dummy. To determine whether toads are able to discriminate between two different prey dummies A and B, the prey-catching orienting activity was first habituated to stimulus A; then the response to B was tested and also habituated. Experiments were repeated with 10 different toads from the animal pool mentioned above. Another 10 animals were used in the reverse order: first habituated to stimulus B and then tested with A.

e) Definition of the term configuration. Configuration and shape are distinguished in this paper: *configuration* refers to the relation of features to each other, whereas *shape* describes the form of an object's contour. Depending on the way spatial and/or spatiotemporal features are related to each other, Tinbergen (1951) distinguishes static configurations [disregarding motion] and dynamic configurations [including motion]. Following this definition, for example, an area extension (or a contrast border) oriented in relation (perpendicular) to its direction of motion is a dynamic configurational cue.

Results

Contrast reversal

In order to test the prediction of the stimulus/background contrast effect on the dishabituation hierarchy, we selected a pair of stimuli b/f from Fig. 2A which showed a strong difference between the black experimental hierarchy (Fig. 1) and the predicted white hierarchy (Fig. 2A). The experimental results are presented in Fig. 3. In Fig. 3A, white f , which is the left-pointing triangle, was first presented to the animal; immediately after the habituation criterion was met, its mirror image, white b , was tested. All investigated toads failed to respond to b . In Fig. 3B, the presentation order was reversed: following habituation to white b , white f was presented. A statistically significant increase ($P < 0.01$, t-test) was shown in response to white f . Comparing the experimental results with the black b/f preference (Fig. 1), it can be concluded that the toad is able to distinguish between white b and white f of the same length and height, and that white f is preferred to

white b in dishabituation, opposite to the effect with the corresponding black stimuli. The experimental results are thus as predicted by the Wang and Arbib model.

Size effects

To test the prediction of size reduction (Fig. 2B), we selected a pair of stimuli b/d which yields an opposite preference of dishabituation to that in the original data (Fig. 1). Both were 2.5 mm high and 10 mm long, and thus called small b and small d hereafter. The model testing results are presented in Fig. 4. In Fig. 4A, small d was presented first, and immediately after the habituation criterion was reached, small b was tested. Remarkable dishabituation was exhibited in the toads ($P < 0.01$). However, if the order of presentation was reversed as in Fig. 4B where small b was presented first and small d was tested next, only slight dishabituation was observed. From these results, it can be concluded that the toad is able to distinguish small b and small d , and small b is preferred to small d in dishabituation. Although the stimulus size was halved, the same preference was established by the toads. At least for this particular pair of stimulus configurations, the model failed to be confirmed.

What went wrong with the model? The model predicts in general that the dishabituation hierarchy changes with stimulus size. One reasonable explanation would be that toads exhibit the same dishabituation hierarchy within a certain range of stimulus size. To test this conjecture of size invariance, we first compared two different size stimuli of the same configuration. We chose configuration b of both 2.5 mm \times 10 mm and 5 mm \times 20 mm, and the results are presented in Fig. 5. In Fig. 5A, small b was first presented and habituated; immediately afterwards presentation of big b elicited a remarkable increase ($P < 0.01$) of prey-catching behavior. However, as presented in Fig. 5B, if big b was first presented and habituated, small b elicited almost no prey-catching response. These experiments demonstrate that, as indicated by dishabituation, toads recognize different sizes of configuration b , and that they prefer the bigger size of 5 mm \times 20 mm to the smaller size of 2.5 mm \times 10 mm. Note that no obvious difference in strength was found between big b and small b in releasing prey-catching within the first min interval.

Further experiments tested dishabituation between small b (2.5 mm \times 10 mm) and big f (5 mm \times 20 mm). Two effects may take place for this particular pair. After a straightforward reasoning from Fig. 5, one would expect that big f should have a preference to small b . From the perspective of configurational cues, however, shape b has preference to shape f (Fig. 1). What actually happened is shown in Fig. 6. In Fig. 6A, if small b was presented and habituated first, and immediately afterwards big f was tested, no significant increase occurred in response to big f ; however, as shown in Fig. 6B, after habituation to big f , small b elicited strong prey-catching behavior ($P < 0.01$). These results clearly demonstrate that toads prefer small b to big f , as exhibited by the

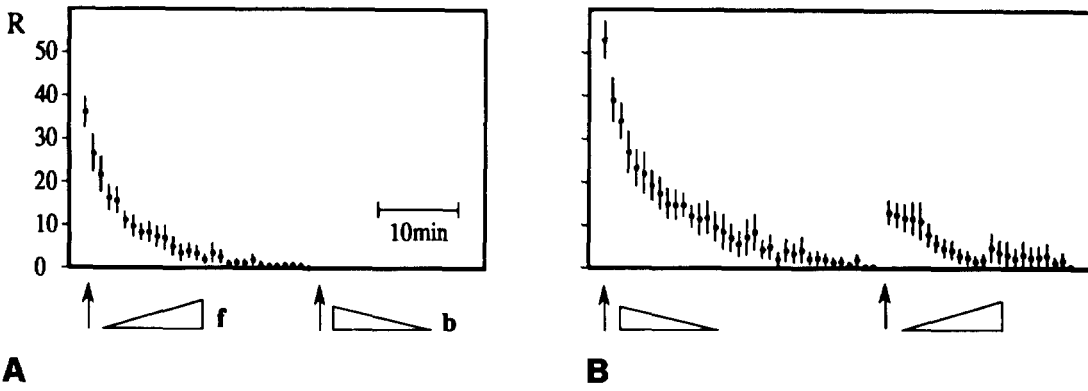


Fig. 3A, B. Experimental test of the contrast reversal prediction of the Wang and Arbib model. Dishabituation tests between a white right-pointing triangle of 5 mm × 20 mm extension (white *b*) and its mirror image (white *f*), as shown in the figure. **A** Habituation of toad's prey-catching orienting response first to the stimulus white *f* and immediately afterwards the test of the response (see vertical

arrow) to white *b*. **B** Reversed order of presentation. *Abcissa*: habituation time [min]. *Ordinate*: orienting activity, *R* [successive number of orienting turns per min]; each curve point represents an average value out of 10 individuals, and the vertical bar indicates the standard deviation

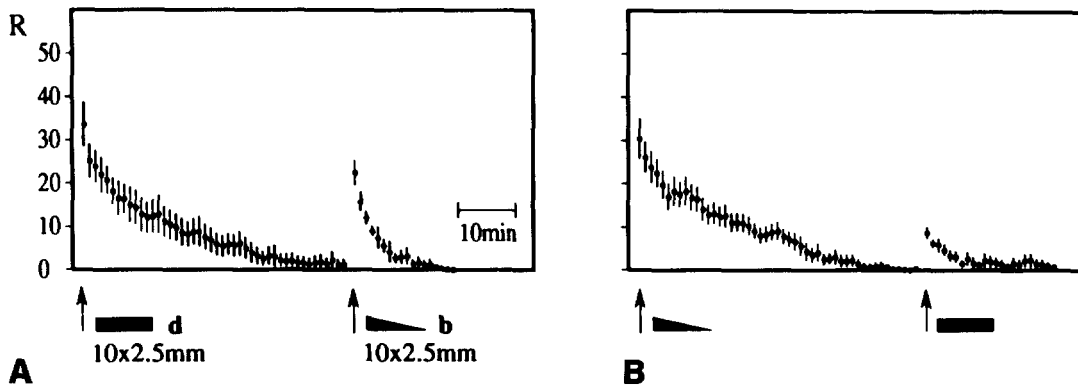


Fig. 4A, B. Experimental test of the model's size reduction prediction. Dishabituation test between black right-pointing triangle small *b* of 2.5 mm × 10 mm size and black rectangle small *d* of 2.5 mm × 10 mm size. **A** Habituation of toad's prey-catching orient-

ing response first to small *d*, and immediately afterwards a test of the response to small *b*. **B** Reversed order of presentation. For further explanations see legend of Fig. 3

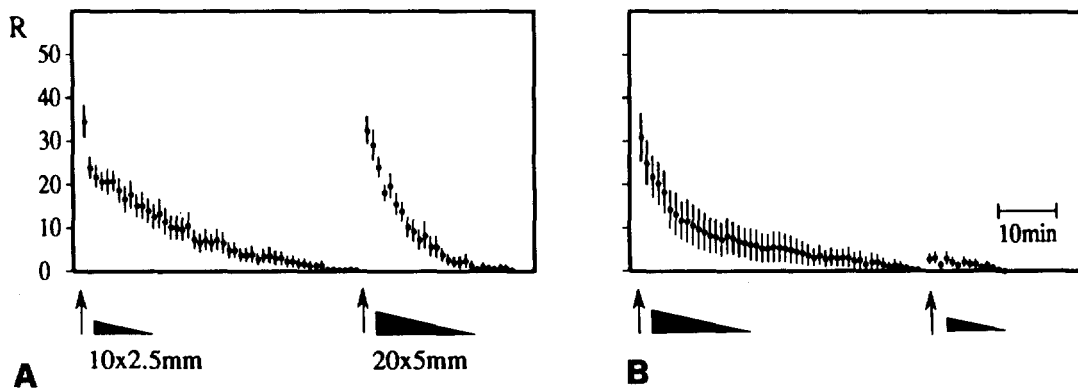


Fig. 5A, B. Test of size effect in dishabituation. Two black stimuli of different size and the same configuration, big *b* (5 mm × 20 mm) and small *b* (2.5 mm × 10 mm), were used. **A** Habituation of toad's

prey-catching orienting response first to small *b*, and immediately afterwards a test of the response to big *b*. **B** Reversed order of presentation. For further explanations see legend of Fig. 3

ordering of dishabituation, and configuration plays the predominant role in this situation. The only explanation we can offer based on the results presented from Fig. 4 to Fig. 6 is that visual object discrimination in toads is unaffected to some extent by object size.

Separate processes of dishabituation

Does dishabituation in the toad have a process separate from habituation, as suggested by the Groves and Thompson (1970) analysis of mammalian data? This

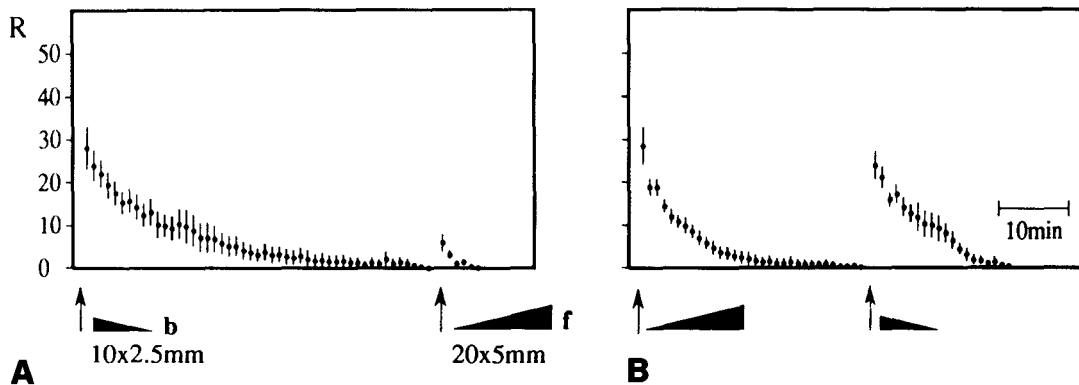


Fig. 6A, B. Test of size vs. configuration effects in dishabituation. **A** Habituation of toad's prey-catching orienting response first to black small *b* of 2.5 mm \times 10 mm, and immediately afterwards a test

of the response to black big *f* of 5 mm \times 20 mm. **B** Reversed order of presentation. For further explanations see legend of Fig. 3

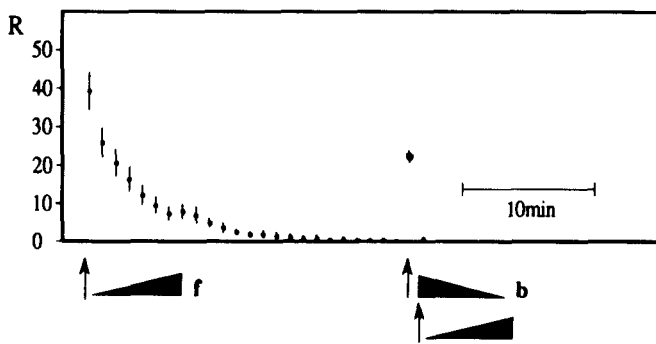


Fig. 7. Experimental test of the separate process question. Habituation of toad's prey-catching orienting response to black *f*, then immediately afterwards the test of the response to black *b* for 30 s, and then the test of the response to black *f* again. In the figure, the isolated empty circle and the vertical bar on it represent the average response activity and its standard deviation, for the period of 30 s. For further explanations see legend of Fig. 3

question could be best investigated by testing the toad's response to a habituated stimulus shortly (a number of seconds) after presentation of a dishabituating stimulus. Two black stimuli *b* and *f* from Fig. 1, and a white background were used for this investigation, and the results are presented in Fig. 7. As shown in Fig. 1, black *b* has preference over black *f* in dishabituation. In the experiments, *f* was first presented to the toad and immediately following full habituation, stimulus *b* was presented for 30 s. In response to *b*, the toad exhibited a remarkable increase ($P < 0.01$) in orienting activity. Note that the isolated circle in Fig. 7 represents the average number of orienting turns for a 0.5 min period while all other black dots represent the number for a 1 min period. Immediately afterwards, stimulus *b* was withdrawn and *f* was presented again. All tested toads showed a very sharp decrease in the orienting response, behaving as though still habituated to *f*. To further confirm our observation, we switched back again to stimulus *b* after the toad failed to release a response to the second presentation of stimulus *f*, and observed in all cases that the toads quickly recovered the response. Once again, when stimulus *f* was switched back, the toads stopped the

response. These results clearly demonstrate that dishabituation does not counteract the effect of previous habituation, but rather has a separate neuronal process. The same behavior was also observed from other pairs of stimuli, including white stimuli.

Discussion

Habituation property

Regarding the dishabituation hierarchy previously observed by Ewert and Kehl (1978, see Fig. 1), the present dishabituation study reveals that toad's pattern discrimination – within worm-like shapes – is even more sophisticated than originally expected. It should be noted that dishabituation is again unidirectional with the new group of stimuli used in this report. This is consistent with the basic hypothesis of the Wang and Arbib (1991) model, namely that toads and frogs use intensity (temporal) coding for representing different visual objects. The investigation so far suggests that pattern recognition in anurans takes advantage of visual cues like leading edge, trailing edge, dots, or striped patterns, rather than using literal images (eidetic templates). In this regard, some parallels could be drawn in visual perception between anurans and invertebrates like honeybees (Wehner 1981; van Hateren et al. 1990) and octopuses (for a review see Wells 1978), since it has been suggested that these invertebrates also use certain pattern parameters (like orientation and contour) in visual pattern recognition. The relevant data on these species of animals are mainly drawn from conditioned training, and very few investigations have been conducted with habituation, thus making a direct comparison difficult.

Background contrast dependence

The Wang and Arbib model (1991) predicts that the toad's dishabituation hierarchy depends on stimulus/background contrast. The predicted hierarchy of the contrast reversal (Fig. 2A) points out the preference be-

tween the 8 stimuli. This prediction is confirmed experimentally for the critical object pair *b* and *f*, the two mirror images of a right triangle. In terms of sensitivity to stimulus/background contrast these results are consistent with behavioral (Burghagen and Ewert 1982) and neurophysiological (Tsai and Ewert 1987) data on edge preference (leading vs. trailing edge) that switches with reversal of the stimulus/background contrast: the edge of a worm-like moving stripe producing an on-effect is less effective than the edge producing an off-effect, in prey-catching as well as in retinal R3 cells and prey-selective tectal neurons.

The results of leading/trailing edge preferences (Burghagen and Ewert 1982) are different from the data described by Ingle (1968; 1971) and Ingle and McKinley (1978) who suggest that head (leading edge) preference is invariant with contrast reversal. Our results are not – as Ingle (1978) criticizes – in conflict with the concept of object discrimination based on configural cues which refers to the visual analysis of the object in relation to its background (Ewert 1987). Since in common toads moving contrast borders are analyzed to a large extent (not exclusively) by off-dominating channels of the visual system, configural discrimination is sharpest for black objects moving against a white background and weakest for white objects moving against a black background. A reason for the latter effect is a kind of confusion elicited by the contrast border of the trailing edge, whereby part of the black background adjacent to (behind) the white object may be interpreted as belonging to the leading edge of a moving black object.

Size effects

The size variance prediction of the model failed to be validated, challenging development of the Wang and Arbib model to explain the new phenomenon of size invariance. Toads are able to recognize stimulus shapes by the dishabituation method, and their recognition is to some extent unaffected by stimulus size. Of course, toads will not respond with prey-catching if a stimulus is too big or too small. There is a biologically determined range of size for potential prey objects for toads; at the boundary of this range, object discrimination invariance – measured by means of the toad's prey-catching activity – breaks down, logically. The toad's ability to discriminate different configural objects is unaffected by stimulus size within limits yet to be determined. To our knowledge, these findings are the first to indicate that anurans, as lower vertebrates, exhibit size invariance in visual pattern discrimination. Pache (1932) investigating this phenomenon in training experiments in frogs pointed out that the data (he only collected from one animal) do not allow an interpretation in the sense that the shape of an object alone, independently of size, can be learnt (Pache 1932, p. 449). Comparing a small cross and a big circular disc, Pache put forward this conclusion although he was aware that the actually necessary experiment, namely testing a big cross against a small disc, was not possible

(because the only animal he investigated suddenly altered its previously tested shape preference). We hence conclude that Pache's data do not allow him to say anything about size invariance in shape discrimination.

Ingle (1971) reviewing object discrimination in fish refers to a study using circle vs. square discrimination: fish obviously fail to generalize with size changes in this training paradigm. Nevertheless it is interesting to note that fish, too, discriminate objects by noticing single features (edges, corners, etc.) rather than taking into account the entire shape of an object (Ingle 1978). It has been demonstrated that after training to discriminate two shapes, octopuses can transfer the discrimination to other shapes, including the same shape of different sizes, seeming to be able to generalize over size (Sutherland 1969; Wells 1978). However, no experiments show that octopuses can discriminate configurations of the same shape but different size.

When talking about size invariance or generalization, one must distinguish generalization from confusion. When an animal fails to discriminate two objects, it only confuses the objects. Generalization implies that the same response has to be elicited by perceptually distinguishable stimuli. (For a discussion about ambiguity of generalization tests see Ingle 1978.) From this perspective, we see no evidence suggesting that octopuses show size invariance in visual pattern discrimination. On the other hand, toads do distinguish size as shown in Fig. 5, and even when size effects favor an opposite preference, configuration still decisively triggers the animal's behavior (Fig. 6). Therefore, our suggestion of size invariance in toads is on firm ground.

It has been shown that pigeons can be trained to select a natural scene (like a human figure or an oak leaf) as a positive stimulus and their discrimination is not affected by a series of size variations (Herrnstein and Loveland 1964; Cerella 1975). In mammals, although it is not conclusive that rodents demonstrate size invariance in pattern recognition, evidences do exist that carnivores and primates exhibit visual pattern recognition based on abstract forms (Gellerman 1933; Smith 1934; Sutherland and Carr 1968; Ingle 1978). Since generalization over size is a crucial aspect for concept formation, the following questions rise naturally. Do toads form concepts in recognizing visual objects? Are anurans the phylogenetically lowest animals that have developed size invariance? Why do toads form this specific shape preference of Fig. 1 in recognizing visual objects by dishabituation? These interesting questions need to be further studied.

Learning capabilities

As demonstrated in Fig. 7, dishabituation of a habituated prey-catching response does not interfere (at least immediately) with previously acquired habituation. Presumably, toads are able to store different visual patterns in distinct neuronal substrates, and later recall them independently. (For a theoretical treatment of how multiple visual stimuli may be maintained in the habituation

memory see Wang 1991.) This characteristic essentially distinguishes the learning ability of *Bufo* from *Aplysia* where it does not seem that different patterns could be acquired through training (Carew et al. 1971; Kandel 1976). The strikingly clear result in Fig. 7 conforms with the dual process theory of habituation (Groves and Thompson 1970), making amphibians closer to mammals in terms of habituation. The neural mechanisms previously proposed for modeling *Aplysia's* habituation (e.g. Wang and Hsu 1990) thus have to be modified when modeling *Bufo's* habituation. The ability to separate different learning traces resulting from different stimulus patterns makes it possible to study directly the capacity of toad's visual pattern discrimination. This opens new ways for investigating visual pattern discrimination of individual toads, quantitatively studying the retention of each acquired pattern by the habituation method. Since Finkenstädt and Ewert (1988a) have shown that after lesions to the telencephalic posterior ventromedial pallium (vMP) – which is connected with AT – habituation of visual prey-catching is drastically retarded, the results should be particularly useful for modeling vMP of toads (the homologous structure to the hippocampus in mammals), the next step for modeling habituation processes.

Frogs and toads, or amphibians in general, have been sometimes considered difficult or poor learners (Pache 1932; Thorpe 1963; Boice et al. 1974; Thompson and Boice 1975). Pache using a training paradigm of positive and negative reinforcement for shape discrimination emphasizes the failures in positive training results in frogs (Pache 1932, p. 449); for example, only one tree frog (of 14 investigated animals) clearly discriminated a stationary triangle from a disc of the same size, whereas all 19 investigated grass and water frogs failed to show convincing data (Pache 1932, p. 430). Our current knowledge about toad's associative and non-associative learning in prey-catching behavior, however, is sufficient to discard the poor learner conception (Finkenstädt and Ewert 1988a, b; Finkenstädt 1989; Merkel-Harff and Ewert 1991; for review see Ewert 1984, 1992). Avoidance behaviors can also be trained in these animals (Schmajuk and Segura 1980; Karplus et al. 1981). Toads and frogs are also capable of discriminative learning and its reversals in a T-maze or a Y-maze (Schmajuk et al. 1980; Jones and Falkenberg 1980; Harvey et al. 1981). The study by Ewert and Kehl (1978) clearly demonstrates that toads can discriminate visual objects of same length and height by dishabituation, and the data of the present study suggest that toad's visual pattern discrimination is to an important extent size invariant. Note that, size invariance is one of the most important problems in engineering pattern recognition (e.g., see Fukushima 1988).

It can be safely concluded that amphibians in evolution have developed fairly advanced learning capabilities. Due to their relatively simple visual system compared to mammals and the relatively large amount of data available for various visual structures (Ewert 1984, 1987, 1992), toads provide an ideal example for investigating visual perception and pattern recognition.

Dialogue between experimentation and modeling

The interplay between experimentation and modeling is crucial for understanding brain functions (Arbib 1989). A neural model of brain functions must be able to explain experimental data. But this is not sufficient. A good model, whether it is physical, chemical, or biological, has to be predictive. Predictions not only help to realize the unknown, but also make the theory testable, and are important for setting up a dialogue between experimentalists and theoreticians. The study reported in this paper was triggered by the modeling paper of Wang and Arbib (1991), which was inspired by the experimental paper of Ewert and Kehl (1978). Therefore, this paper can be viewed as another step in a continuing dialogue between experimentation and modeling. It is also our hope that this paper can serve as an example for establishing such a dialogue. For the dialogue to be possible, theoreticians have to develop neural models constrained by experimental data and make their models predictive, while biologists, on the other hand, should relate their data to modeling and face challenges from modelers by testing their predictions. We believe that this kind of dialogue is both crucial and fruitful for understanding brain functions.

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