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Simulander: A neural network model for the orientation movement of salamanders

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Abstract Simulander is a feedforward neural network simulating the orientation movement of salamanders. The orientation movement is part of the prey capture behavior; it is performed with the head alone. Simulander is a network which consists of 300 neurons incorporating several cytoarchitectonic and electrophysiological features of the salamander brain. The network is trained by means of an evolution strategy. Although only 100 tectum neurons with fairly large receptive fields are used ("coarse coding"), Simulander is able to localize an irregularly moving prey precisely. It is demonstrated that large receptive field neurons are important for successful prey localization. The removal of a model tectum hemisphere leads to a network which accounts for investigations made in living monocular salamanders. The model also yields an understanding of electrical stimulation experiments in toads.

Key words Neural network · Evolution strategy Salamander · Optic tectum · Orienting

Introduction

During the last years, many investigations have been undertaken to uncover the relationship between neural activity and animal behavior. In experiments with amphibians, emphasis was laid on prey capture behavior and predator avoidance (Grüsser-Cornehls 1984; Ewert 1987; Roth 1987). In contrast, only few models exist which yield a quantitative description based on the available data (Arbib 1989; House 1989; Straub 1993). In the present paper, we introduce a neural network model which performs part of the prey capture behavior in salamanders using all relevant empirical data.

We want to stress the fact that the Simulander model is concerned only with a small part of the rich behavioral patterns living salamanders exhibit. Its duty is to suggest general principles of information processing in brains (e.g., the coarse coding mechanism), applied to the specific task of orientation movement. According to this concept, perceptional problems like figure-background discrimination, predator-prey discrimination, etc. are not taken into account. In this context, Simulander may be seen as the instantiation of a schema for prey capture in amphibians. Schema theory was introduced by Arbib (Arbib 1989; Arbib and Cobas 1991) to tackle the extensive task of explaining complex animal behavior: schemas are functional units in the brain which interact to produce the behavior observed. Schemas may be instantiated by different neural mechanisms; further animal experiments serve to select among these. A set of models called "Rana computatrix" has been developed to account for the behavior of frogs and toads including detour behavior and prey acquisition (Arbib 1989; House 1989). Salamander behavior and brain architecture have not been considered so far. Simulander yields a different approach to prey capture behavior including the modeling of realistic receptive fields sizes and a neural network architecture derived from experimental data.

Tongu-projecting plethondontid salamanders (Bolitoglossini) exhibit a "sit-and-wait" (or "ambush") feeding strategy. In many cases, their first reaction to a prey observed is a turning movement of the head to fixate the object binocularly. Usually, this orientation movement is performed with the head alone. Typical prey are collembolans, mites, and even dipterans moving at high speed (Roth 1987).

Simulander is a feedforward neural network simulating this orientation movement. The model starts at the level of the optic tectum and performs head movements

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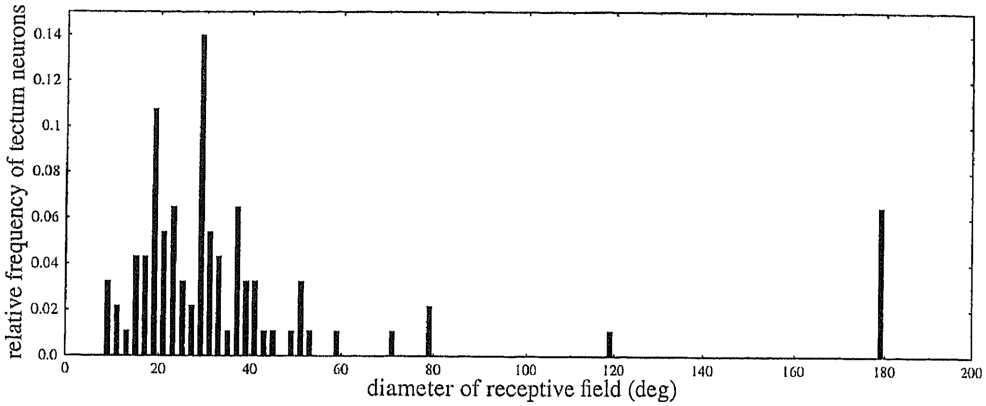


Fig. 1 Distribution of tectum neuron receptive field sizes in *Hydromantes italicus* (Wiggers 1991; Wiggers et al., this volume)

which are released by an irregularly moving model prey. It incorporates physiological, anatomical and behavioral data most of which are gained from recent experiments in *Hydromantes italicus* (Wiggers 1991; Wiggers et al., this volume). Nevertheless, it may be viewed as a model for both urodeles and anurans, since the enclosed features are considered to be general principles of information processing in amphibians:

1. The network layers resemble cell types that have been anatomically identified: the input layer consists of tectal neurons; there are motor neuron and interneuron layers which correspond to neuron populations in the brainstem of salamanders (Roth et al. 1988; Wake et al. 1988; Matsushima et al. 1989). The head movement is performed by four neck muscles.
2. Receptive field sizes of the tectal neurons in the input layer and their distribution in the Simulander's visual field are directly taken from experimental data. Since only the direction of the prey object is considered but not its distance, those neurons which are part of the crossed retinotectal pathway (projection from the left retina to the right tectum hemisphere and vice versa) are taken into account.
3. The firing rates of tectal neurons are adapted from electrophysiological experiments. They vary with angular size and angular velocity of the prey (Wiggers 1991; Wiggers et al., this volume).
4. In bolitoglossine salamanders, a fast connection from retinal ganglion cells to brainstem motor neurons exists (Matsushima and Roth 1990), probably with only two synapses in between (Dicke 1992). This feature seems to be important for the animals' fast reaction and their high success in prey capture. The fast connection is used in the network model.
5. The principle of inhibition of antagonistic muscles is realized: whenever a neck muscle is activated, the corresponding antagonistic muscle is inhibited by interneurons.
6. A population code for muscle activation is implemented.

The network is constructed as follows. Its structure is prescribed according to the above-mentioned empirical data, while the synaptic strengths and muscle strengths are determined by an evolution strategy during a learning phase. Once the network is established, several tests on model performance and model predictions as to biological experiments can be made.

The main questions are (1) whether the Simulander network is capable of localizing a small, irregularly moving prey, and (2) how many tectal neurons are needed for this task. Emphasis is laid on the problem of coarse coding: on the one hand, in behavioral experiments, salamanders exhibit high visuomotor acuity: they are able to localize mites of 0.5 mm size at distances of 15–20 cm and to snap at them accurately with their projectile tongue achieving high success rates (Roth 1987). On the other hand, electrophysiological measurements demonstrate that tectum neurons have large receptive fields (Fig. 1); their mean diameter is about 41°, and there are numerous receptive fields 180° in diameter, especially in the lateral visual field (Wiggers et al., this volume). How do these observations fit together? It is obvious that the high visual resolution observed at the behavioral level is not achieved by single neurons: The firing of a single neuron indicates that an object is located somewhere in the corresponding receptive field. Its exact position, however, cannot be inferred provided that the neuron's firing rate does not change with stimulus position as has been observed in salamander experiments. Instead, distributed information processing seems to play an important role in the visual system. The cooperation of many neurons leads to the angular resolution necessary for the control of the projectile tongue, i.e. for prey capture. Heiligenberg (1987) and Baldi and Heiligenberg (1988) suggest a coarse coding model to account for the phenomenon of hyperacuity. In this model, high resolution is due to the fact that the sensory units' firing rates precisely depend on the position of the stimulus in the receptive field. Theoretically, the stimulus variable can be calculated from the output of two units only. Furthermore, the units are arranged equidistantly in sensory space; a disturbance of this arrangement leads to performance errors and results in a decrease in resolution. The firing rates of tectum neurons in the model presented here do not depend on the stimulus position in the receptive field: when the prey crosses a receptive field boundary, the corresponding neuron starts firing at a rate *f*, which is a function of stimulus velocity and stimulus size only. Angular resolution, then, is a consequence of the overlap of the receptive fields. As mentioned above, the arrangement of the receptive fields in the visual field is taken from experimental data and is, thus, somewhat random. In this context, model performance is achieved by a self-organizing process which is implemented as a random learning strategy.

In the next step, the model network is subjected to a loss of neurons, and the resulting loss of visual resolution is investigated.

Whereas several classes of tectal neurons with large receptive fields (diameter > 120°) e.g. classes T2, T4, T6, have been identified in anurans (Grüsser–Cornehls 1984), their influence on angular resolution has not been considered so far. Since it is possible in the Simulander model to selectively eliminate neurons with large receptive fields, their significance for angular resolution can be analysed.

The removal of one of the Simulander's tectal hemispheres corresponds to experiments with monocular salamanders. The prey capture behavior of these animals (Roth 1976, 1987; Wiggers 1991) can be compared to model predictions.

Electric stimulation experiments in toads reveal the absence of a motor map in the optic tectum in the sense that stimulation of a tectal site leads to a turning movement of a definite angle (Jordan et al. 1990). Model performance is consistent with observations made in these experiments.

The model

The modelled test scene

In Fig. 2, the modelled test scene is depicted. A salamander sits in front of a 20 × 10 × 10 cm terrarium; it can only move its head. The salamander is described by the position of its neck (which is fixed) and by the head axis which points to the center of its visual field.

Inside the terrarium, a prey of size 0.6 cm moves at a mean speed of $v_{\mathrm{mean}} = 2.1$ cm/s. The movement can be described as follows: for a time interval (1.5 ± 0.5 s) (the respective value is determined by a random number generator) the prey moves along a straight line, then changes its speed and direction at random values ($\Delta v_{\mathrm{mean}} = 0.5$ cm/s, mean angular deviation $\Delta\alpha_{\mathrm{mean}} =$ 20°), thus moving along another straight line, etc. The irregularity is introduced to prevent the salamander from getting adapted to a particular movement pattern.

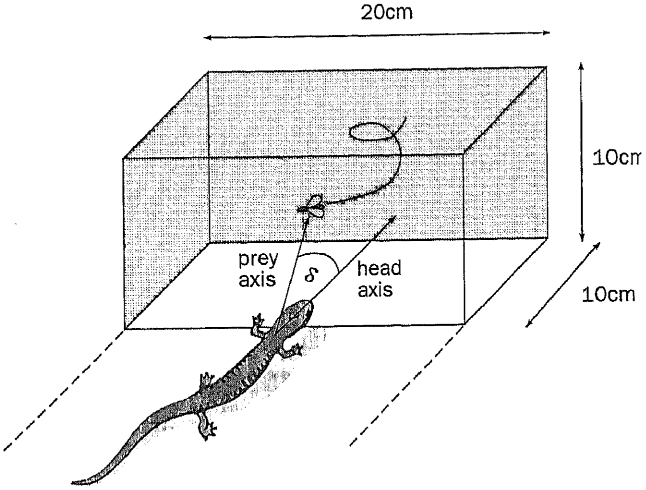


Fig. 2 The test scene

Network design

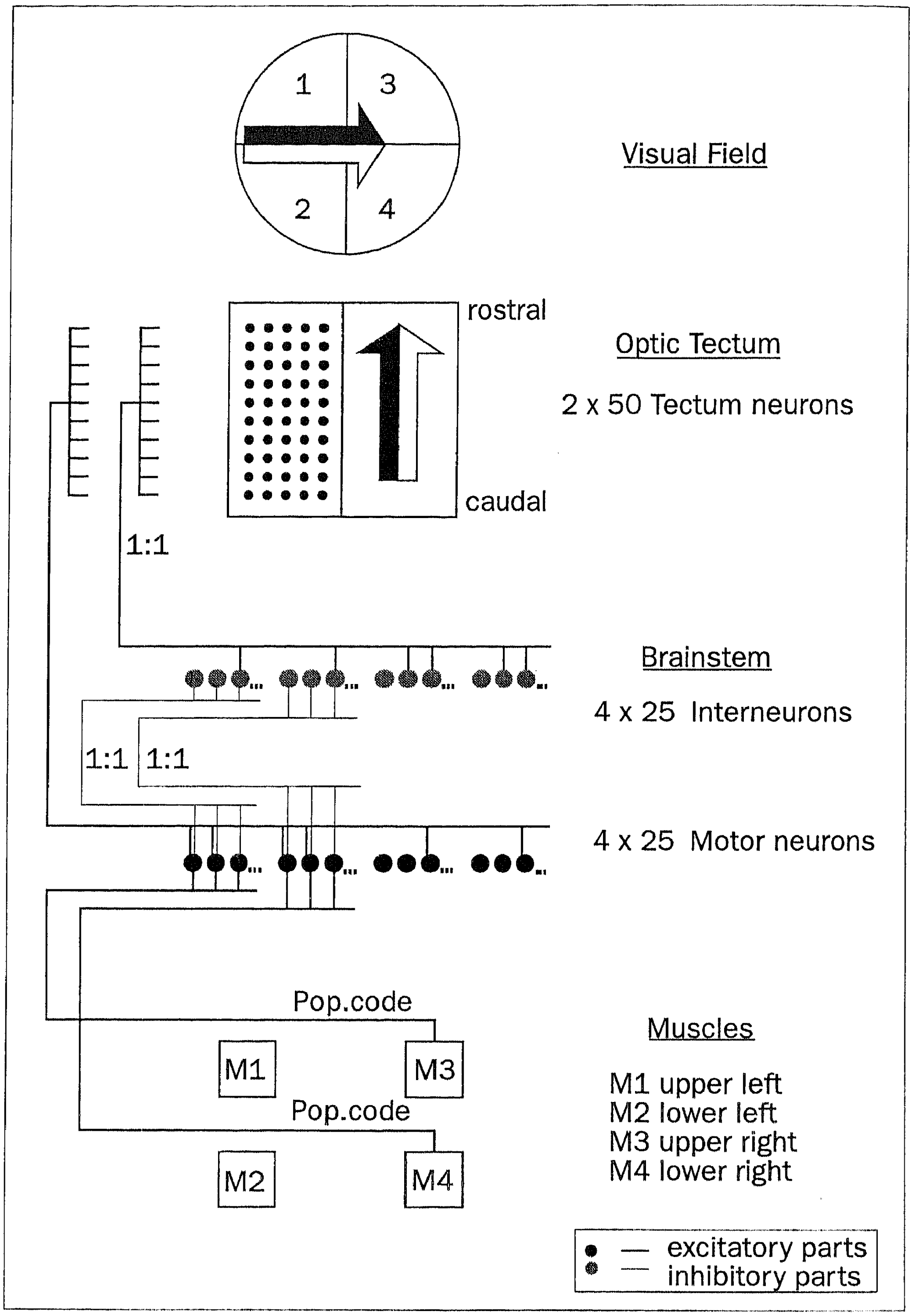
Figure 3 shows the structure of the neural network. At the top, the visual field is drawn schematically; it is divided into four parts which play a role in the topology of the network (see below). The arrows indicate the contralateral retinotectal sensory maps present in the optic tectum. The network consists of 300 neurons: 100 input neurons representing tectum neurons, 100 interneurons, and 100 motor neurons resembling neurons in the rostral spinal cord. The neurons are connected according to a feedforward topology. Head movements are performed by four muscles. The network is symmetric relative to the vertical midline; in biological terms, there is a symmetry between the brain hemispheres and between the left and right muscles. The symmetry includes localization of the respective fields, neuron connections, synaptic weights, and muscle strengths. The network dynamics is calculated in discretized time steps $\Delta t = 0.2$ s.

Input layer

The tectum neurons in the input layer are modelled according to measurements in *Hydromantes italicus* (Wiggers 1991; Wiggers et al., this volume). Figure 4 shows the distribution of receptive field centers in the visual field. Most receptive fields are situated in the binocular part of the visual field. Field sizes are taken from Fig. 1.

Whenever the prey crosses a receptive field, the corresponding neuron fires at a rate *f*; otherwise, it is

Fig. 3 Structure of the neural network; for explanation, see text



silent:

$$f_T = \begin{cases} f, & \text{prey is in the receptive field} \\ 0, & \text{otherwise.} \end{cases} \qquad (1)$$

f is a function of stimulus angular velocity and stimulus angular diameter; it is interpolated from biological data. The resulting function is drawn in Fig. 5. Each tectum neuron activates one motor neuron and one interneuron.

Muscles

Four muscles M1, . . . , M4 are needed to move the head. Each muscle turns the head into the direction

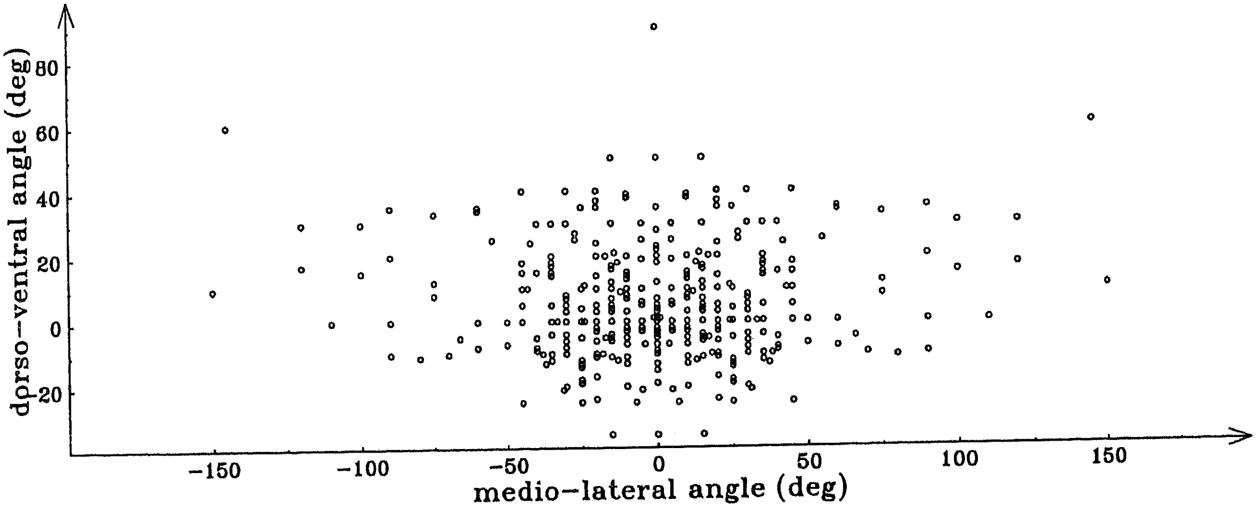


Fig. 4 Distribution of the tectum neurons' receptive field centers in *Hydromantes italicus* (Wiggers 1991; Wiggers et al., this volume)

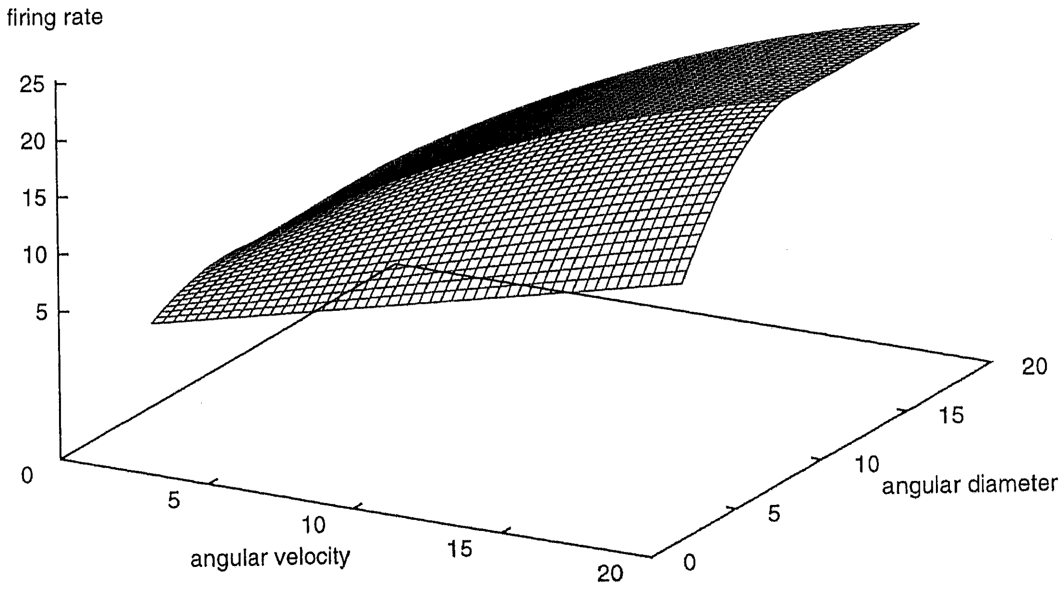


Fig. 5 Tectum neuron firing rates *f* as a function of stimulus angular velocity (deg/s) and stimulus angular size (deg)

indicated by the respective number in the visual field: e.g., an activation of M1 results in a turn to the upper left. M1/M4 and M2/M3 are pairs of antagonists. The muscles are innervated by 25 motor neurons each. The turning angle $\Delta\varphi_i$ resulting from the contraction of muscle Mi (i = 1,. . .,4) depends on the number of active motor neurons as well as on their firing rates:

$$\Delta\varphi_i = k_i \frac{\sum_{j=1}^{25} w_{ij}x_j}{25} \Delta t \; (i = 1, \ldots, 4) \qquad (2)$$

with Δt: time step (0.2 s), k_i: muscle strength of muscle Mi, x_j: firing rate of motor neuron #j ($j = 1, \ldots, 25$), w_{ij}: strength of neuromuscular synapse between motor neuron #j and muscle Mi. Equation (2) can be regarded as the implementation of a population code for muscle activation. The total head movement results from the four angles $\Delta\varphi_i$ calculated this way.

Motor neuron layer

The motor neurons are divided into four groups ("pools") with 25 neurons each that innervate the muscles. The neurons are activated by tectum neurons in a 1:1 connection. At the same time, each motor neuron is inhibited by one interneuron. The motor

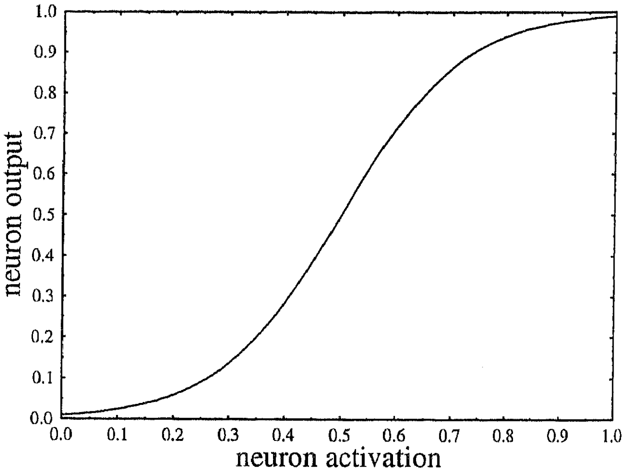


Fig. 6 The Fermi function

neuron activation is transformed into the motor neuron output ("firing rate") via a Fermi function (Fig. 6). The choice of the Fermi function is not imperative here; another transformation function would lead to essentially the same network performance.

Interneuron layer

The interneurons are likewise divided into four groups. Each interneuron is activated by one tectum neuron. As with the motor neurons, the activation is transformed into a firing rate by the Fermi function. The interneurons are 1:1-connected to the motor neurons with negative synaptic weights, i.e. they have an inhibitory effect.

Overall connectivity

The neural connections described are not arbitrary; instead, a coarse topology is implemented. The motor neuron and the interneuron to which a tectum neuron is connected are determined by the position of the receptive field center of the latter in the visual field. For example, if the center is located in quadrant 1, then the tectum neuron activates one of the motor neurons that innervate muscle M1. At the same time, the tectum neuron activates an interneuron that inhibits a motor neuron belonging to the motor pool of M3, thus inhibiting the antagonist of M1.

Note that most tectum neuron-motor neuron connections drawn in Fig. 3 belong to muscles M3 and M4; however, some belong to M1 and M2 as well (the same structure is valid in the mirrored half of the network which is not depicted). They resemble the crossed and the uncrossed descending pathways, respectively. In the model, the latter are due to the fact that the visual hemifields extend beyond the vertical midline: each contralateral retinotectal fiber carries information about all of the four quadrants. This property is conveyed to the tectal hemispheres, and according to the network connectivity described all muscles are activated by each hemisphere.

Training of the network

The neural network contains 2 × 200 synaptic weights and 2 × 2 muscle strengths (two in each case are identical because of the network symmetry) which have to be determined in order to make the model fulfil its task. During a training phase, the values of these parameters are calculated with an evolution strategy (Rechenberg 1973; Bäck et al. 1991). This algorithm which is based on a random search in parameter space is not supposed to imitate biological evolution; rather, it can be seen as a mathematical method for parameter optimization. We used a (1 + 1)-ES which we slightly modified in order to adapt it to our problem.

Synaptic weights are restricted to the interval [0; 1], muscle strengths to [0; 10]. The algorithm starts with a random set of parameters.

For a given set of parameters, the fitness of the network is determined. Two different fitness functions are used that are nearly equivalent: the mean square angle δ^2 between prey axis and head axis (cf. Fig. 1) and the mean "success rate", i.e. the fraction of time in which the head axis intersects the 0.6 cm-sized prey. Both functions are calculated by iterating the system for a time T. T is raised during the training procedure: Starting with small iteration times in order to leave those regions in parameter space which lead to bad network performances, T is finally raised to 20,000 s to reveal slight performance differences among the best networks. In each case, the sequence of training patterns consists of a number N of prey positions and the respective positions of th head axis ($N = 100{,}000$ for $T = 20{,}000$). Thus, a high number of "prey-head-configurations" is presented to the network. These configurations are partially determined by a random number generator (prey movement) and partially determined by the network itself, since the network is responsible for the head movement. During training time T, the model prey moves irregularly inside the terrarium thus probing a representative part of it. For networks exhibiting high performance, the angle between head axis and prey axis is small in most cases, but there are also training patterns with large angles.

Next, some parameters are changed. These "mutations" are performed as follows: A subset of parameters is chosen with the help of a random number generator. The values of these parameters are changed using equally distributed random numbers. The fitness of the network originating from these mutations is determined and compared to the fitness of the previous one. The fittest network survives and serves as a basis for further mutations, while the other network is discarded ("selection"). Then, the next mutations are calculated, etc.

A typical training phase takes nearly three days of calculation on an IBM work station. About 10,000 networks were tested, out of which about 40 led to an increase in fitness. In order to get an impression of the achievable network performance, several training phases were executed with different initial values for synaptic weights and muscle strengths. In each case, nearly the same final values of the fitness functions were achieved. The final parameters turned out to be different, however. From a mathematical point of view, we can conclude that there are many local minima of the fitness functions in this high-dimensional space which are nearly equivalent. The network drops into one of these, showing a typical performance and a typical distribution of parameter values.

Results and discussion

General performance

Once the neural network has been trained as described above, the model salamander is capable of following the prey with its head. Calculations show that the head axis intersects the irregularly moving prey in about (86.3 ± 0.3)% of the time. To calculate the standard deviation, we performed 500 test runs of 20,000 s each using the best network obtained from the evolution algorithm. The small value of 0.3% demonstrates the generalization capability of the network: the test runs consist of sequences of prey-head-configurations not presented to the network during the training phase. Another means of testing network performance and generalization capability is to observe the network behavior using prey at rest. Emphasis may be laid on configurations with large angles between prey axis and head axis, since such patterns don't occur very often during the training phase. The Simulander network copes with such situations in most cases (see below).

The high network performance achieved demonstrates that 100 tectum neurons are sufficient to yield the angular resolution necessary to fulfil the task. The result is remarkable because of two reasons: the receptive fields of the tectum neurons are quite large, and neural connections do not show a special topology except the classification according to the quadrants of the visual field.

A reduction of the number of tectum neurons leads to a decrease in network performance. The resulting fitness depends on the number of remaining neurons as well as their properties like position and size of the receptive fields. In some cases, a success rate of 70% is achieved with 75 tectum neurons only, while in other cases, the success rate drops of 45% with 95 tectum neurons.

Although plethondontid salamanders have comparatively few tectum neurons, the number of cells involved in prey capture far exceeds the number of tectum neurons used in the model. This is because only a small part of the visual behavior is simulated here. Furthermore, there may be a redundancy in biological systems which leads to a more reliable behavior and to an insensitivity against neuron failure.

Distributed representation

Analysis of the synaptic weights as determined by the evolution strategy shows how information about prey locus is passed to the muscles. The couplings between tectum neurons and motor neurons/interneurons are of special interest: they indicate whether there is a relation between properties of the receptive fields and importance of the corresponding tectum neurons. Some results are shown in Fig. 7. In Fig. 7a, the synaptic weights (tectum neurons to motor neurons) are plotted against the diameter of the receptive fields. While the distribution of receptive field diameters is taken from biological data (cf. Fig. 1), the coupling strengths are calculated during the training phase of the network. They are distributed over the entire unit interval for all diameters; there is no correlation between synaptic weights and receptive field diameters. The same holds for the relationship between synaptic weights (tectum neurons to motor neurons) and dorso-ventral angles of the receptive field centers (Fig. 7b). Analyses of further parameters such as the medio-lateral position of the receptive field center or the angular distance between the receptive field center and the center of the visual field yield similar results. The remaining synaptic weights (tectum neurons to interneurons, interneurons to motor neurons, motor neuron to muscles) exhibit no significant tendency either.

These results show that all neurons participate in the information processing. The information about prey locus is distributed over the whole neuron layer at each processing stage. This accounts for the fact that at the behavioral level salamanders are able to localize prey precisely while their single neurons show a relative unspecific activity.

Importance of large receptive fields

Another means of determining the role played by single neurons and neuron populations in the orienting behavior is to remove them from the model network. In two test series, the influence of removal of neurons with large receptive fields and with small receptive fields was investigated. The results are shown in Fig. 8: The network fitness decreases as more and more neurons are inactivated. It is remarkable that the destruction of large field neurons leads to an immediate decrease in

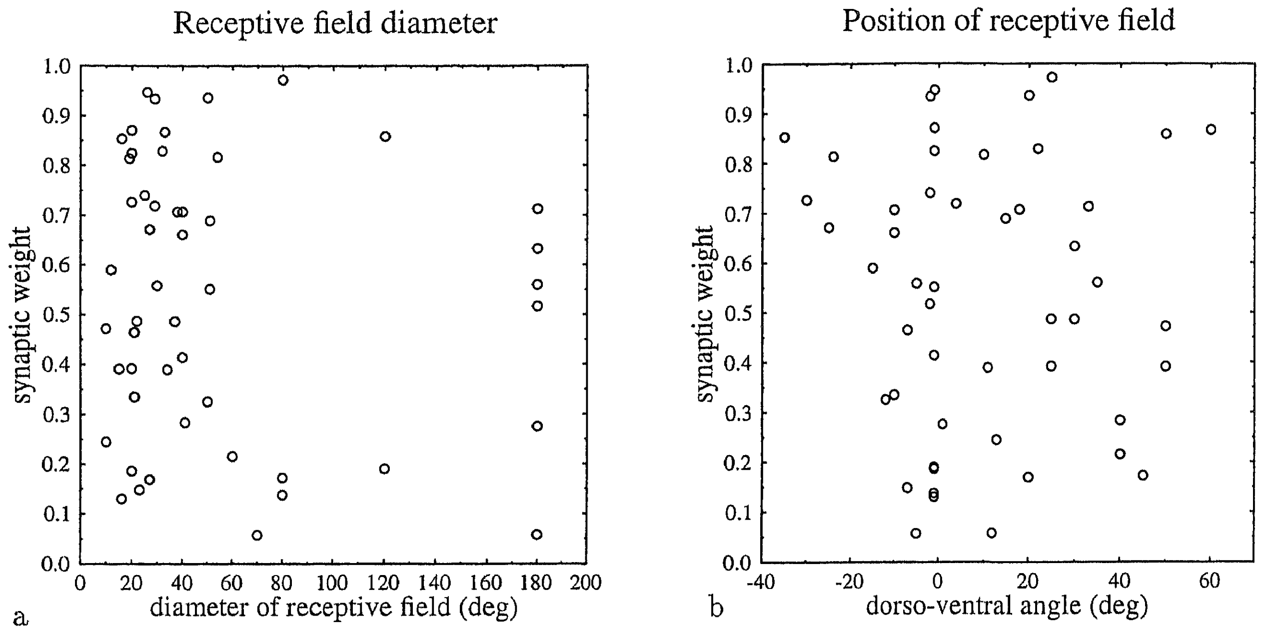


Fig. 7 Examples for distributed representation: synaptic weights (tectum neurons to motor neurons) as a function of **a** diameter, **b** position of the respective field

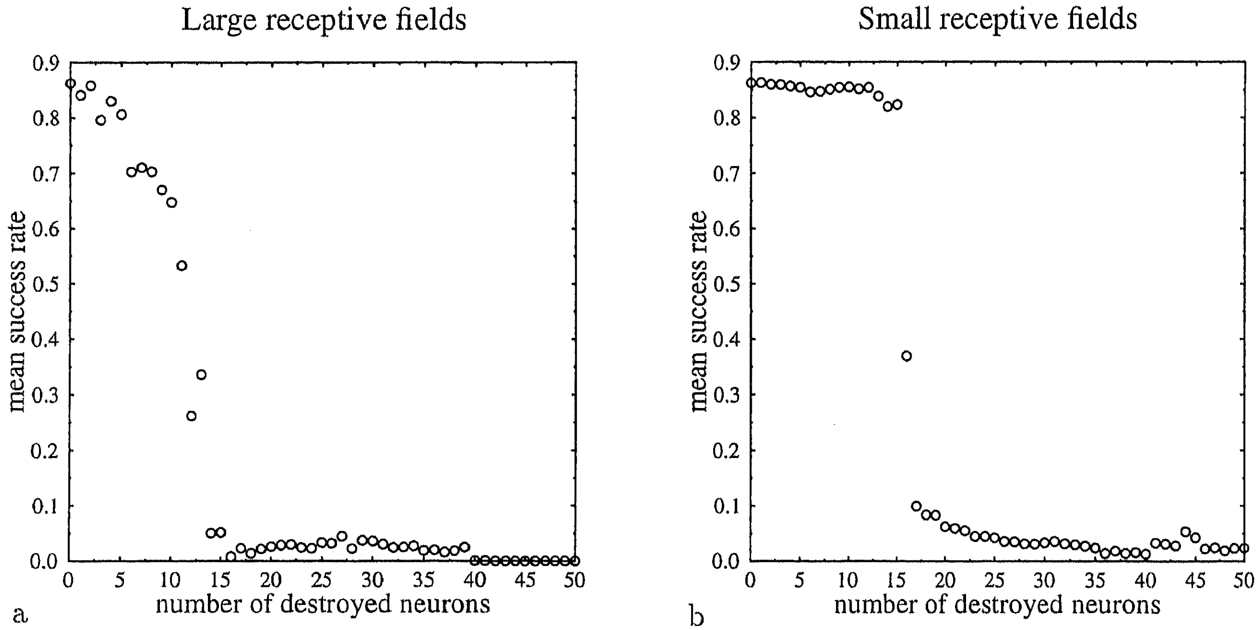


Fig. 8 Effects of destruction of tectum neurons. **a** Large receptive fields; **b** small receptive fields

network performance which is not the case with the destruction of small field neurons. In a similar experiment, the network underwent a training phase after the destruction of 25 tectum neurons. Here, the results are even more significant: the removal of small field neurons leads to a network with a success rate of 49%, while removal of large field neurons results in a success rate of about 1%.

Although these results may partially be due to the smaller number of large field neurons in the network, they reveal a general principle of information processing in brains: large field tectum neurons play an important role in prey localization. More than small receptive field neurons they seem to be suitable for this task. In this context, high angular resolution does not take place on single neuron level, but is a property of neuron populations.

Analytical calculation of the angular resolution obtained by McCulloch-Pitts neurons with different receptive field sizes support these findings (Eurich et al., unpublished): for a given number of neurons, the finest resolution is achieved by receptive fields with 180° in diameter! Theoretically, less than 800 neurons are sufficient to yield the resolution necessary to catch very small prey (0.5 mm in size) at maximal reach of the projectile tongue (4–5 cm in *Hydromantes italicus*, Roth 1987).

The importance of large receptive field neurons does not contradict the fact that all neurons participate in information processing (see above). Rather, the neural population is absolutely necessary since information about prey locus is not concentrated in single neurons. In the Simulander network, small receptive field neurons take part in object localization as well, but they do not play a major role as one perhaps would have expected: otherwise, their removal would have a greater effect, since we removed a good part of them.

Motionless prey; monocular salamanders

Although the Simulander network was designed for moving prey, it copes with motionless prey as well. Problems arise only for some prey positions in the terrarium: a non-moving prey elicits lower firing rates in the tectum neurons (cf. Fig. 5) which results in lower activity of the whole network and in weaker muscle contraction. In most cases, however, the Simulander turns its head correctly, centering the prey in the visual field. Figure 9a shows a typical movement: the angle between head axis and prey axis is plotted against time. In about 5 s, the head moves into the correct position. A means of testing the model quantitatively is to compare this trajectory to movement patterns gained from biological experiments. This has not been done so far.

The prey capture behavior in monocular salamanders has been studied in detail (Roth 1976, 1987; Wiggers 1991). Figure 10 shows a typical situation: the salamander approaches the prey, but the prey is not centered in the visual field; instead, it is located on the same side as the animal's blind eye.

Because in the Simulander model only the contralateral retinotectal projections are used, monocularization of an animal corresponds to the removal of one hemisphere of the model tectum. The response of the

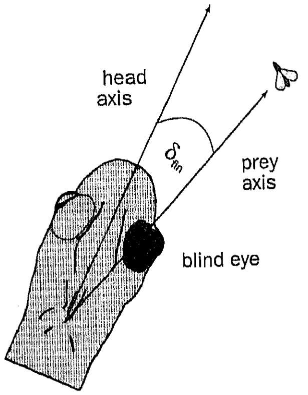


Fig. 10 Prey catching behavior of monocular salamanders

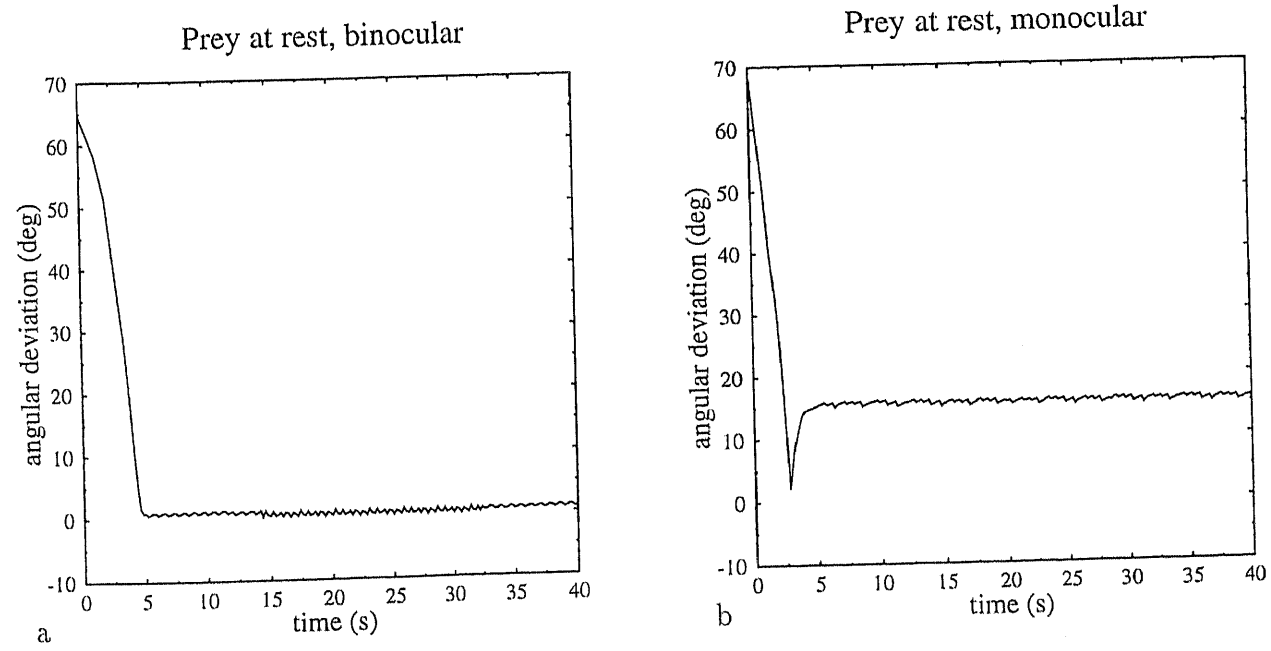


Fig. 9 Convergence behavior of the Simulander model with prey at rest. **a** Binocular salamander; **b** monocular salamander

network to a prey at rest is shown in Fig. 9b. At time $t = 0$, the angle between head axis and prey axis is 70° with the prey on the side opposite to the blind eye. Head movement is performed as expected from biological measurements: after 5 s, a final position is reached with the prey on the blind side. There is an angle of about 15° between head axis and prey axis. The minimum of the curve at $t = 2.5$ s results from the fact that the head axis has to cross the prey axis during the orientation movement described. The reason for the behavior of the network can be derived from the network structure (Fig. 3). Assume that the Simulander's left eye is blind; this corresponds to a "silent" right tectum hemisphere. As a consequence, motor neurons are activated by left-hemisphere tectum neurons only. Some of these motor neurons belong to muscles M1 and M2 (elicited by rostral tectal neurons), but most motor neurons belong to M3 and M4. Thus, the Simulander's head tends to move to the right, leaving the prey on the left side.

The Simulander behavior with a lesioned hemisphere is a model prediction that was not considered when the network was constructed. This fact corroborates the validity of the model.

Comparison with electrical stimulation experiments

Ewert (1967) investigated behavioral responses released by electrical stimulation of the optic tectum in toads (*Bufo bufo*). Depending on the tectal site of stimulation, the toads perform turning movements in different directions. Electrical stimulation experiments were made by Jordan et al. (1990) in order to answer the question if there is a tectal motor map that relates a definite turning angle to each tectal coordinate. Their results suggest that such a motor map does not exist in the toad's tectum. These observations seem to uncover principles of information processing which are valid in anurans and urodeles. They can be explained by the Simulander model as far as prey capture is concerned.

The direction of the turning movement depends on the site of stimulation. Stimulation of the rostral tectum elicits ipsiversive turns, while contraversive turns are elicited by stimulation of the middle and caudal tectum. In the Simulander model, the situation is as follows. Because of the retinotopic map in the tectum, stimulation of the rostral part corresponds to an activation of tectal neurons whose receptive field centers are situated in the central, mainly ipisilateral visual field. According to the network topology, these tectum neurons activate motor neurons belonging to muscles that elicit ipsiversive turns. On the other hand, activation of tectal neurons in the middle and caudal optic tectum leads to the activation of motor neurons belonging to muscles performing contraversive turns.

In the experiments, it was observed that the turning angle is a monotonically increasing function of stimulus current amplitude and frequency. In the model, increasing amplitude or frequency corresponds to a higher activity of tectum neurons which results in a higher activation of motor neurons and consequently in a stronger muscle contraction (see Eq. 2).

In the experiments, turns began immediately after the onset of stimulation and ceased immediately after its end. The reason for this is evident from the model as well. The muscles are activated as long as tectum neurons are active, i.e. during stimulation. The activation of a group of neurons at a certain spot in the optic tectum corresponds to a prey somewhere in the visual field. As a consequence, the salamander performs an orientation movement to center the object. During normal prey capture, this behavior would result in the spot of activation shifting toward the rostral tectum, where the turning movement ceases, because the prey is in the middle of the visual field. However, if the tectum is stimulated electrically, the spot of activation is fixed so that the prey stays at the same position in the visual field even when the orientation movement is performed. Therefore, the movement continues.

It was also observed that simultaneous stimulation of two tectal sites elicits intermediate turns. This is exactly what the model predicts: Activity of two groups of tectum neurons leads to activation of two groups of interneurons and motor neurons, respectively, and a compromise in muscle contraction is found.

Outlook

The Simulander network may serve as the basis of a more elaborate model for prey capture in amphibians, especially in salamanders. The following features may be added:

- Proprioception. In the present model, the head can be turned into arbitrary positions. This is unrealistic. A simple feedback mechanism can solve the problem.
- Depth perception. In conjunction with the contralateral retino tectal projections, ipsilateral projections are present in bolitoglossine salamanders (Rettig and Roth 1986; Wiggers 1991; Wiggers et al., this volume) and can be used to yield information about the prey distance (stereoscopic vision).
- Control of the projectile tongue. It is suggestive to introduce the feeding response into the Simulander model using contralateral and ipsilateral retinotopic mappings. The distance between prey and horopter serves as a criterion for the release of tongue projection. Control of the projectile tongue includes feeding distance and direction.
- Prey-trajectory extrapolation. In addition to the direct retinotectal projections mentioned above, two indirect retinotectal projections exist in the optic tectum (Wiggers 1991; Wiggers et al., this volume). They are mediated by the nucleus isthmi and have characteristic

time delays. In conjunction with the direct mappings, they may yield an extrapolation of the prey trajectory, which enables bolitoglossine salamanders to catch even fast-moving prey with high success.

- Prey classification. It is promising to implement a classification of prey according to criteria such as "tasty/unpalatable". The classification may be based either on the perception of visual details of the prey due to an increase in visual resolution gained by a higher number of tectum neurons, or on an evaluation of differences in prey movement patters. For this task, it is necessary to introduce several classes of tectum neurons differing in their responses to prey features such as contrast, shape, velocity, movement pattern (cf. Grüsser-Cornehls 1984; Roth 1987).
- Retinal ganglion cell output. The recent model starts at the level of the optic tectum. The Simulander network could be extended by adding a retinal layer which is connected to the tectal layer. With the help of an evolution strategy, it may be possible to calculate tectum neuron properties from the retinal output.
- Use of multiple prey stimuli. When more than one prey is presented to the salamander, it is necessary to introduce an attention mechanism. Otherwise, the network would not focus on one prey, but perform an intermediate movement pattern which is not observed in behavioral experiments.

The suggestions presented may not be all realized in one model. However, their implementation as neural networks will yield a better understanding of the neural mechanisms underlying the prey capture behavior in amphibians.

Declaration The experiments carried out for this paper comply with the 'Principles of animal care', publication No. 86-23, revised 1985 of the National Institute of Health and also with the 'Deutsches Tierschutzgesetz' Sect. 8 Abs. 1.

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