

Experimental Analysis of the Prey Catching Behavior of *Hydromantes italicus* Dunn (Amphibia, Plethodontidae)

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Summary. 1. The Italian bolitoglossine salamander *Hydromantes italicus* shows a periodic cave life. In spring and in the fall it leaves the caves after which it lives under stones, in leaves and crevices. Inside the limestone caves, *H. i.* can be found both in the zone of dim light near the entrance and in total darkness. 2. Corresponding to these two environments there are two guidance systems of the prey catching behavior: one visual and one olfactory. 3. The visually guided prey catching behavior is determined by the stimulus parameters: velocity, size, contrast, and ambient illumination. Continuously moving objects are effective within a velocity range of 0.05 to 6 cm/s with an optimum at 1.25 cm/s (Fig. 2). Stimuli moving stepwise elicit fixation of the prey and complete approach more frequently than continuously moving stimuli. The prey size which elicits prey catching ranges from 0.5 to 10 mm² with an optimum size between 2.5–5.0 mm² (Fig. 3). The prey catching behavior is hardly impaired by a decrease in ambient illumination down to 0.03 cd/m². Beyond 0.03 cd/m², the prey catching activity decreases sharply, but there are still responses at an illumination level of 0.003 cd/m² (Fig. 4). 4. *H. i.* also responds to stationary non-smelling visual stimuli following stimulation by smell or movement. *H. i.* is able to detect prey by smell only both in total darkness and in the light (Fig. 5A). In the light, the prey catching behavior with regard to smelling objects is inhibited by the absence of visual contrast (Fig. 5B).

I. Introduction

Within the last two decades the prey catching behavior of the amphibia has become a favorite object of behavioral and physiological research. Most of these studies have dealt with anurans (for a review see Ewert, 1973, 1976). It was only recently that urodeles have attracted attention (Cronly-Dillon and Galand, 1966; Himstedt, 1967; Grüsser-Cornehls and Himstedt, 1973). Most of these studies, however, concentrated on European salamanders.

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So far no physiological or behavioral research has been done on the prey catching behavior of the largest family of the urodeles, the Plethodontidae or lungless salamanders (23 genera, more than 210 species), even though within this group the most diverse morphological and physiological adaptations can be found. Among the Plethodontidae, the Bolitoglossini or tongue projecting salamanders again form the most diverse and numerous group.

For the studies in the present paper the Italian cave salamander *Hydromantes italicus* was chosen. Together with *Hydromantes genei*, which lives on Sardinia, *Hydromantes italicus* is the only representative of the Plethodontidae outside the new world. *Hydromantes italicus* lives mainly in limestone caves of the French Maritime Alps and the northern Apennines. The limestone caves guarantee a rather stable temperature and high moisture. The animals leave the caves in spring and in the fall when the outside conditions of temperature, moisture and food are favorable, and then they live under stones and leaves and in crevices. Morphologically, the tongue of the Bolitoglossini represents a highly complicated and specialized mechanism (Wake, 1966; Wake and Lombard, 1973, 1975), which enables the Bolitoglossini to catch even fast moving prey. Both its tongue and its specific way of life, which requires an adaptation to dim light (outside the caves and near the entrance of the caves) as well as to total darkness (inside the caves), make *Hydromantes italicus* especially suited for sensory guidance studies of the prey catching behavior. The purpose of the present study was a quantitative analysis of the visual releasers of the prey catching behavior, and an investigation of the extent to which other sensory modalities take part in the guidance of this behavior.

II. Material and Methods

A. Animals

The salamanders were captured during the summers of 1972 and 1973 from limestone caves of the Alpi Apuane in the northern Apennines. The animals were maintained in terraria measuring $20 \times 14 \times 16$ cm, which contained a thick layer of foam rubber at the bottom and several smaller pieces of foam rubber. The terraria were kept air-tight by means of a glass-plate cover in order to maintain a high humidity (more than 90%). The sides of the terraria were covered with opaque plastic foil. The terraria were sprayed with water every day and were thoroughly cleaned every week. They were housed in a room with a constant temperature of 12 °C. The animals were fed mainly on a diet of house flies, less frequently on fly larvae or *Drosophila*. 2-3 house flies for each animal per week proved completely sufficient.

B. Procedure

1. The Visually Guided Prey Catching Behavior

a) *Stimulus Velocity*. The experiments with different stimulus velocities were performed in an experimental terrarium measuring $20 \times 20 \times 10$ cm. Disks of black cardboard with a diameter of 5 mm were used as prey dummies. The disks were fixed on a white plastic tape (stimulus background contrast $C=0.95$), so that they could be moved behind a window measuring 10×1 cm, at one side of the terrarium. The tape was driven by a regulated electromotor with 10 different speeds. Distance marks were placed on the bottom of the terrarium in order to measure the angular velocity of the dummies. Ten animals were used, one animal per experiment. The following were

considered as positive responses: 1. fixation of the prey (F), 2. complete approach (A), and 3. tongue projection (P). Up to ten experiments were carried out per animal at each respective speed. Two positive responses were considered sufficient demonstration that the respective animal responded to the given speed. The experiments with stimuli moving stepwise were performed by means of an astable multivibrator which turned the electromotor on and off. The ratio of motion time and rest time was 1:10.

b) Stimulus Size. In order to determine the minimum, optimum, and maximum sizes of the prey, black squares of cardboard on white background ($C=0.95$) varying in size from 0.5 to 15 mm² were used as dummies. The squares were moved in a quivering fashion at a speed of 3 cm/s and at a distance of 3 cm from the animal. Every animal was faced with the stimulus up to 10 times. Two positive responses were considered to be sufficient evidence for a reaction to the stimulus.

c) Illumination. The experiments to clarify the relationship between the visually guided prey catching behavior and illumination were made within a completely darkened room. The terrarium was illuminated by a diaprojector, whose light was reflected by a white polystyrene plate measuring 50 × 50 cm. The plate was situated obliquely above the terrarium. The different luminous densities were obtained by means of a set of neutral density filters (Schott, types NG 4, 9, 11), which were put into the path of rays of the projector. The stimuli moved forward stepwise at a propulsion speed of 6 cm/s. Only the responses A (complete approach) and P (tongue projection) were counted. The animals had been kept in darkness for at least two hours before the beginning of the experiment.

d) Stationary Visual Stimulus Pattern. In order to study the responses to stationary visual stimuli, two dark disks of cardboard with a diameter of 4 mm were placed on a white background ($C=0.95$) at one side of the terrarium and at a distance of 3.5 cm from each other. The animals were lured, by means of a moving dummy, to a central position with respect to the stationary stimuli and at shooting distance from them. The moving dummy was then taken away, before the animals were able to shoot with their tongues. The experiments were performed with 10 animals. 3 experiments per animal were carried out.

2. Prey Catching in Darkness

For these experiments house flies were fixed on a needle which hung into the terrarium. The needle was connected to a loudspeaker (Isophon BPSL 100) membrane, which itself was connected to an oscilloscope. The prey on the needle was situated high enough above the bottom of the terrarium so that the animals could reach the prey using the tongue only. Whenever the animals shot their tongues against the prey the movement of the needle induced a movement in the loudspeaker membrane and this in turn could be seen as a deflection of the electron beam on the oscilloscope screen. In each experiment 3 animals were used at any one time. The maximum duration of one experiment was 30 min. Each group of animals was tested 10 times.

3. Stationary Smelling Prey Objects in Light

The experiments were made in soft daylight. As prey objects, 3 squashed flies were used. The experimental conditions were the same as those for the preceding experiments.

4. Smelling Prey Objects with and without Visual Contrast

A piece of acrylic glass measuring 13 × 6 cm, with holes 5 mm in diameter at both sides and in the middle, was placed against one side of the terrarium. The holes had a depth of 4 mm and were situated 1 cm above the bottom of the terrarium. Black and white pieces of cardboard were placed behind the holes so that they got acquired either a black or a white background. The holes at the sides were filled with a pulp of squashed and lightly homogenized flies. These

prey objects formed a clear contrast to the white background, but were hardly visible on the black background. The hole in the middle, which always had a white background, was filled with a piece of black plastic the size of a fly. 30 experiments were made with prey objects, with and without visual contrast respectively. Only those experiments were counted in which the animals showed a complete approach to the prey and remained in front of it for at least 15 s. The maximum duration of each experiment was 30 min. Each experiment was carried out with one animal.

III. Results

A. The Visually Guided Prey Catching Behavior

The sequence of the visually guided prey catching behavior in *Hydromantes italicus* can be divided into fixation, approach (with or without correcting turns of the head), a short stop at the shooting distance, and tongue projection. The fixation is achieved by a moderately quick turn of the head towards the object moving within the animal's visual field. Often the animals follow the prey for a certain time only with their heads. The velocity of the approach greatly depends on the velocity or the intensity with which the prey moves. After having reached the shooting distance (2–4 cm) the tongue projection does not occur immediately in most cases, but the animals wait in front of the prey, move their heads slowly forward for some mm, and only then project their tongues. If, however, a prey moves very quickly, the animals may shoot at it while they are in full motion. They may even catch a laterally passing prey by an abrupt turn of the head, in which case they very often project the tongue laterally, sometimes of an angle of more than 45° to the head axis. Such lateral tongue projections also occur, as motion picture analyses show, in other Bolitoglossini.

The tongue skeleton, consisting of the basibranchiale, the two first and second ceratobranchialia, and the two epibranchialia, is projected out of the mouth three-dimensionally folded (Wake and Lombard, 1973, 1975). The reach of the tongue is 3–4 cm in *Hydromantes italicus* and up to 5 cm in *Hydromantes shastae* and *brunus*.

Figure 1 shows four characteristic stages of the tongue in action. As exact motion picture analyses show (Wake and Roth, in prep.) the tongue projection from the mouth to the prey over an average shooting distance of 2.5 cm takes about $1/100$ s, the gluing of the prey and the retraction of the tongue lasts about $1/13$ – $1/11$ s. Experiments with tropical Bolitoglossini show that some representatives of the genus *Bolitoglossa* (e.g. *Bolitoglossa rufescens*, *B. adspersa*) perform the whole capture process in $1/64$ – $1/128$ s. These tropical salamanders, however, are about half as long as *Hydromantes italicus* and, additionally, their tongues are shorter in relation to their body length.

B. Variation of Different Visual Stimulus Parameters of a Prey Dummy

1. Velocity

a) *Experiments with Continuously Moving Dummies.* As shown in Figure 2 the animals responded to a minimum velocity of 0.05 cm/s with regard to fixation

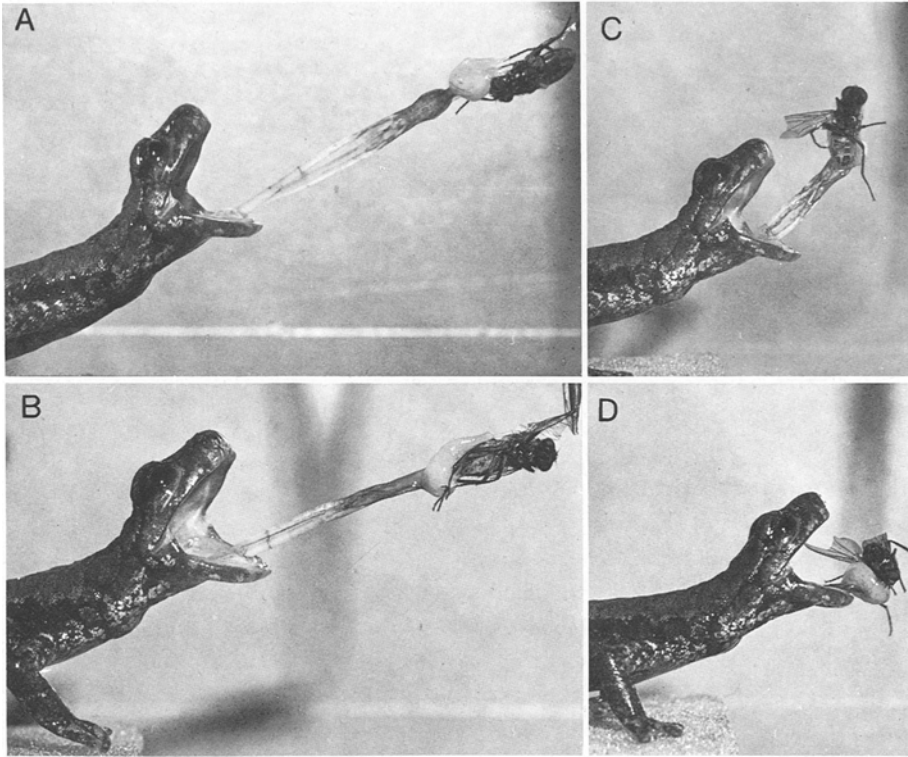


Fig. 1A–D. Tongue projection in *Hydromantes italicus*. **A** Early stage of retraction. The tongue shows about $\frac{3}{4}$ of its full length. **B** Later stage of retraction. The tongue pad has just contracted a little. **C** Late stage of retraction. The tongue is turned 90°. The elements of the tongue skeleton can be seen very clearly. **D** End of retraction. The prey is glued to the contracted tongue pad

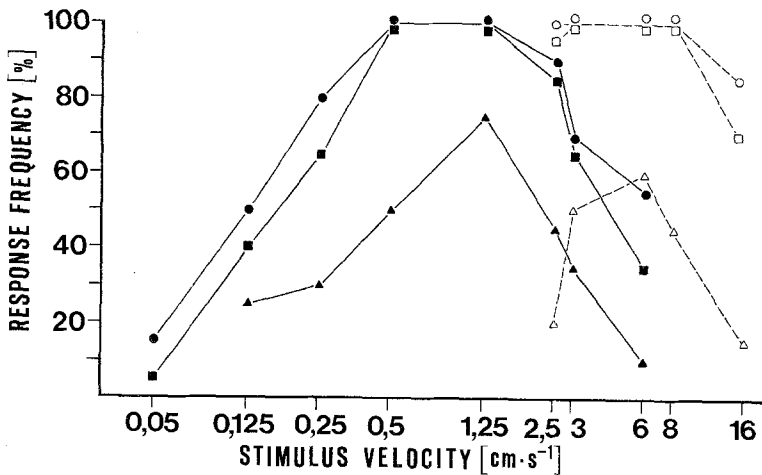


Fig. 2. Dependence of prey catching responses on stimulus velocity.—continuously moving stimulus, --- stepwise moving stimulus, ● ○ fixation, ■ □ complete approach, ▲ △ tongue projection

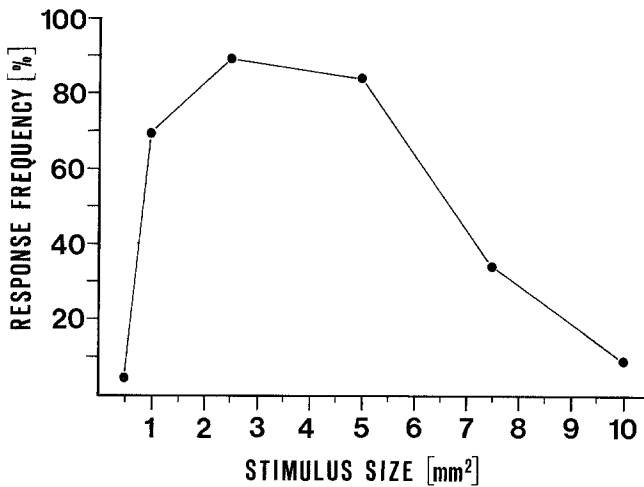


Fig. 3. Dependence of prey catching responses on stimulus size

(F) and complete approach (A) and a maximum velocity of 6 cm/s for F, A and tongue projection (P). The differences between the curves of F, A, and P show clearly that these response types have different stimulus thresholds respectively.

b) Experiments with Dummies Moving Stepwise. Figure 2 (broken lines) shows that the response curves have approximately the same shape as those of the preceding experiments, only shifted towards a propulsion velocity which is 4-6 times higher. The real dislocation velocity of the stimulus, however, is 10 times lower than the propulsion velocity. The range of the optimum velocity of stepwise moving stimuli concerning the responses F and A is broader than that of continuously moving stimuli. This could indicate a higher stimulus effectiveness. On the other hand, the number of P was lower than in the preceding experiments.

2. Influence of Stimulus Size

Figure 3 shows that the animals responded to a minimum size of 0.5 mm² and to a maximum size of 10 mm². A clear optimum was situated in between 2.5 and 5 mm². It is remarkable that the animals actually responded to stimulus sizes, which they would not have been able to swallow as natural prey. Even *Calliphora*, whose size is equivalent to a dummy size of about 7.5 mm², cannot be devoured by a small *Hydromantes*. The size interval from 1 to 5 mm², which is the optimum, corresponds fairly well to the sizes of *Drosophila* and *Musca domestica*, which in captivity are the preferred prey animals.

3. Influence of Illumination

As shown in Figure 4, a decrease in illumination down to 0.03 cd/m² scarcely impairs the prey catching activity of *Hydromantes italicus*. Below that level

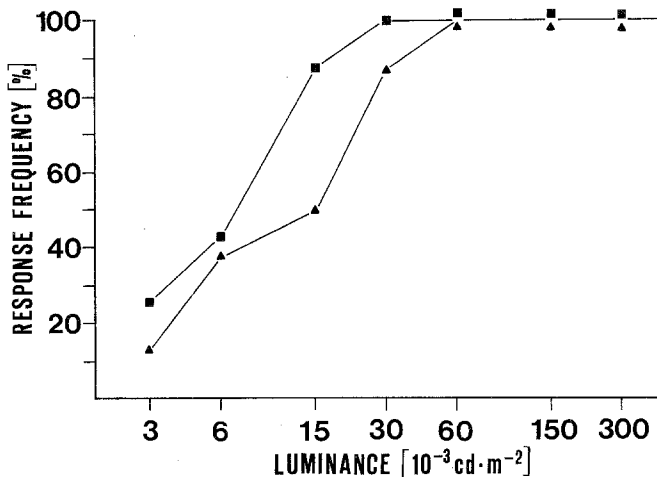


Fig. 4. Dependence of prey catching responses on luminance. ■ complete approach, ▲ tongue projection

of illumination, however, the activity decreases strongly, but still occurs at a level of 0.003 cd/m^2 . Below this level it was impossible to discriminate exactly a complete approach and other movements, even after long adaptation to the darkness. Tongue projection, which would still have been detectable, did not occur anymore.

4. Responses towards Stationary Visual Stimuli

The animals were lured towards the stationary stimuli using a moving dummy, which was then removed. In 23 out of 30 cases the animals stared for an average of 2 min at the point where the dummy had been moved, then turned either to the right hand or left hand stationary stimulus, stared at it and then shot straight at it. In the remaining 7 cases the animals stared ahead for an average of 4.5 min, then turned away without paying any attention to the stationary stimuli. A shooting at the point, where the dummy had been moved, in the sense of a “vacuum activity”, as described by Hinsche (1935) for anurans, was never observed.

C. The Olfactory Guided Prey Catching Behavior

1. Prey Catching in Darkness

The first series of experiments were carried out with 3 living house flies attached to the needle. The animals showed 27 responses (90%). In order to exclude localization of the prey by sound or by air movement, 3 dead flies were used as prey in the next series of experiments. The result was 26 responses (86%). The third series of experiments was made with a pulp of 3 dead flies, cooled

down to the temperature of the terrarium so as to exclude shape detection or infrared localization. The animals showed 24 responses (80%). In 30 control experiments using a piece of plastic similar in size to the natural prey, no responses could be registered (see Fig. 5A). The results show that *Hydromantes italicus* is able to detect and to catch prey in total darkness by smell only. One cannot exclude the possibility of the interaction of other sense modalities, such as sound or vibration, to effect the localization of living prey in darkness, but these factors are not essential, as the experiments show. The time intervals from the beginning of the experiments to the first response were evenly distributed between 1 min and the maximum time of 30 min. How quickly the animals were able to localize the prey in darkness seemed to depend strongly on the respective state of activity of the animals. That is, on whether the animals were wandering around the terrarium and chanced upon the prey in a relatively short time, or whether they remained quietly in a corner of the terrarium being attracted to the prey by smell only.

2. Responses towards Stationary Smelling Objects in Light

The animals localized the prey in 28 out of 30 experiments and shot at it with their tongues. The experiments usually took the following course: the animals wandering around eventually found themselves near the prey. They stopped, moved their heads from side to side as if they were looking for the origin of the smell. Then they directed their heads at the prey, showed olfactory test position characteristic of salamanders, and slowly approached it. In a few cases having just passed the prey, they stopped, moved back, and turned their heads to the prey. In rare instances there was a direct approach from a distance of 6–7 cm. Remarkably enough, practically no animals shot at the prey immediately after complete approach, on the contrary, before shooting it would

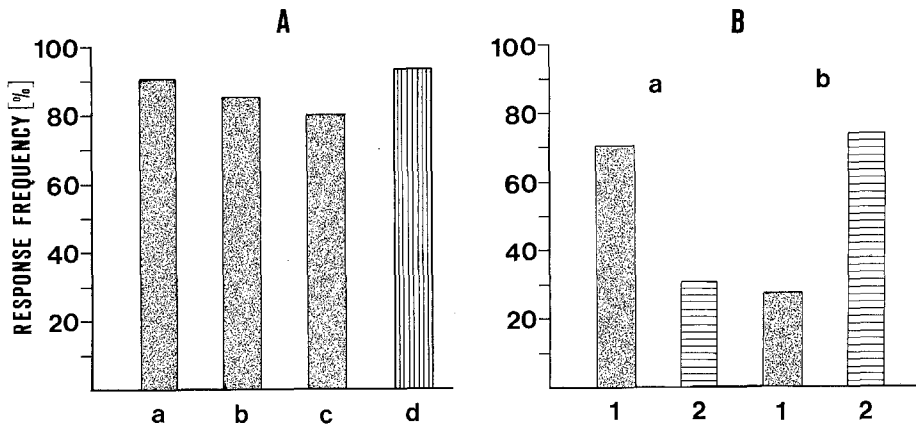


Fig. 5. **A** Prey catching responses to smelling prey. a–c in darkness, d in light. a: living house flies. b: dead flies. c, d: squashed and homogenised flies. **B** Prey catching responses to non-moving, smelling prey. a: with visual contrast. b: without visual contrast. 1: complete approach with tongue projection. 2: complete approach without tongue projection

remain in front of it for a certain time. In most cases this time lasted more than 15 s and sometimes longer than 10 min. During this delay the animals often moved back and forth for some mm, then again adopted the olfactory test position and turned away for a short time before finally catching the prey.

D. Interaction between Visual and Olfactory Stimuli

The experiments with smelling prey objects with and without visual contrast showed (see Fig. 5B) that after complete approach and exact olfactory localization, the animals responded in 70% of cases to prey with background contrast and in 23% of cases to prey without contrast. Very remarkably the animals sometimes remained in front of the prey without contrast for an extremely long time (up to 20 min) without shooting at it. They often approached the prey until they touched it with their snouts, then they moved back, showed the olfactory test position, moved their heads from side to side, before finally turning away.

IV. Discussion

Hydromantes italicus has, apparently due to climatic changes, developed a periodic life in caves without, however, becoming a cave animal proper, like some other Plethodontidae. This has produced an adaptation both to life in dim light outside the caves and near the entrance of the caves and to life in total darkness deep inside the caves. Accordingly, *Hydromantes italicus* possesses two guidance mechanisms for prey catching behavior: one visual and one olfactory. In principle both these mechanisms would secure the feeding in both environments independently of each other. The visually guided prey catching behavior depends on the following stimulus parameters: size, velocity, background contrast, and illumination. Present experiments indicate that the orientation and the shape of the stimulus also play an essential role, as they do for some anurans (Ewert, 1973, 1976).

As shown in Table 1, *Hydromantes italicus* has a lower minimum and a significantly higher maximum movement sensitivity than European salamanders. The optimum is thereby shifted to higher stimulus velocities, especially with regard to the angular velocity of the stimulus. Anurans do not show such high movement sensitivity either. Behavioral experiments with the toad *Bufo bufo* demonstrate that these animals show an optimum prey catching activity at a stimulus velocity of 30–60°/s and that the number of responses decreases sharply beyond 100°/s (Ewert, in prep.). Correspondingly, neurophysiological studies of Finkelstein and Grüsser (1965) demonstrate that in *Rana esculenta* the responses of class-2-ganglion cells decrease sharply beyond a stimulus velocity of 100°/s and that at 140°/s there is almost no response.

The experiments with various stimulus velocities revealed that in *Hydromantes italicus* fixation and complete approach is more easily elicited by stimuli moving stepwise than by continuously moving stimuli. These findings are

Table 1. The data for *Triturus vulgaris* and *Salamandra salamandra* are taken from Himstedt (1967). D=distance from subject to stimulus

	Minimum	Optimum	Maximum
<i>Hydromantes italicus</i>	0.05 cm/s 0.24°/s (D=12 cm)	0.5–2.5 cm/s 4.8–72°/s (D=6–2 cm)	6 cm/s 172°/s (D=2 cm)
<i>Triturus vulgaris</i>	0.05 cm/s 1°/s	0.5–1.5 cm/s 5–20°/s	2 cm/s 45°/s
<i>Salamandra salamandra</i>	0.5 cm/s 0.5°/s	0.5–1 cm/s 5–15°/s	2 cm/s 40°/s

confirmed by present experiments with various movement patterns. In *Hydromantes italicus* as well as in *Hydromantes genei* stimuli of optimum size (4 mm²) moving stepwise were significantly more effective than continuously moving stimuli, even with regard to tongue projection (Roth, in prep.). On the other hand, experiments of Grüsser et al. (1967) with *Rana esculenta* showed that the type of movement (e.g. linear, non-linear, irregular) of the stimulus in the ERF of class 2 neurones does not influence the exponent of the velocity function. Similar experiments with *Bufo bufo* indicate that higher efficiency of non-linear stimulus movements does not appear at the level of retina neurones but at the level of tectum neurones (Ewert, pers. comm.). Therefore movement pattern discrimination may be performed by “higher” neural mechanisms as it is the case for shape pattern recognition (Ewert, 1973). The question of the respective neural mechanisms of movement pattern discrimination in urodeles, especially in Plethodontidae, will be treated in future experiments.

The experiments with stationary visual stimuli show that stimulus movement is an important but not decisive factor for the release of tongue projection. That is, the animals will respond even to non-moving stimuli if they are stimulated high enough (e.g. by smell or by previous stimulus movements), but mostly after a characteristic delay which in some cases can last up to 20 min. Visual contrast, however, seems to play a more important role. The experiments with stationary smelling prey with and without visual contrast showed that after precise olfactory localisation the animals responded only in 23% of cases to prey without contrast. These results seem to disagree with those derived from the experiments on prey catching in darkness. In the latter experiments, the animals responded in 80% of cases, even though there was no visual contrast of the prey owing to the darkness. Perhaps the prey catching releasing mechanisms take into consideration the general possibility of detecting the prey visually. In total darkness, the parameter of background contrast is not “postulated”, and therefore the olfactory stimulus alone is able to release tongue projection, which is not the case in prey catching behavior under light.

The experiments on prey catching in darkness show that *Hydromantes italicus* is able to detect prey by smell only. Recent experiments and observations have demonstrated that besides *Hydromantes italicus*, *Hydromantes genei*, *Hydromantes shastae*, and the tropical salamanders *Bolitoglossa rufescens* and *Chirop-*

terotriton bromeliacia have the same ability. In all these animals, it was possible to elicit prey catching using only a piece of filter paper on which some body liquid of squashed house flies or *Drosophila* was placed.

On the basis of the results of the present paper it is possible to give a list of stimulus parameters, in order of effectivity, which elicit prey catching in *Hydromantes italicus*. The most effective stimulus is no doubt a moving visual prey object within certain limits of velocity, size and contrast, for which certain movement and shape patterns are more efficient than others. The presence or absence of smell apparently plays no essential role for the efficiency of moving objects. The next most efficient stimulus is a stationary smelling prey object with visual contrast (for example a motionless or dead prey animal). A non-moving and non-smelling prey object can elicit prey catching only after visual or olfactory stimulation. Only in rare cases in the light, can a smelling prey object, invisible to the animal, elicit prey catching, apparently after strong stimulation. Normally the presence of visual contrast seems to be necessary for release of prey catching behavior under light.

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