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Prey orienting in frogs: Accounting for variations in output with stimulus distance

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Summary. We have studied the responses of leopard frogs, *Rana pipiens*, to live mealworms presented at different distances on the mid-sagittal plane. The response of normal frogs to stimuli at nearer distances consists of a direct snap whose amplitude increases with stimulus distance. For greater distances, the response consists of a forward hop whose amplitude also varies with stimulus distance. Over an intermediate range of distances, responses may be either snaps or hops. Whichever response occurs is of appropriate amplitude. The distance at which frogs switch from predominantly snapping responses to predominantly hopping responses increases with body size.

Like normal frogs, unilaterally blinded frogs respond to stimuli at nearer distances with snaps whose amplitude varies with stimulus distance, switch from snapping to hopping over an intermediate range of distances, and respond to stimuli at greater distances with hops whose amplitude also increases with stimulus distance. In many cases, unilateral blinding did however result in a decrease in the distance at which the frogs switched from snapping to hopping. Such changes were not accompanied by the changes in snap or hop amplitude which would be expected if unilateral blinding resulted in generalized changes in distance judgement. Normal variations in snap amplitude and switches from snapping to hopping were also observed in frogs subjected to unilateral eye removal prior to the metamorphic eye migration which creates the adult binocular visual field.

These results imply that neither distance discrimination nor any of the kinds of variation in motor output which occur with increasing stimulus distance necessarily depend on binocular cues. The behaviors studied also appear to be largely independent of normal binocular experience. More generally, our results suggest that the movement triggered by a stimulus at a particular location is not determined entirely by the retinal and superficial tectal region activated but rather reflects a combination of a retinal local sign signal with other kinds of information. The latter probably include signals related to stimulus distance and body posture, and may include signals related to body size as well.

Introduction

Studies of prey capture behavior in the frog have led to significant insights into the nature of the neuronal organization underlying directed movement (Ewert et al. 1983; Grobstein et al. 1983; Ingle 1983), as well as into the mechanisms involved in the development of such organization (Sperry 1965; Hoskins et al. 1982). Although prey capture movements vary appropriately with variations in stimulus location in all three dimensions of space (Ingle 1970; Comer and Grobstein 1981), most studies have focused primarily on the turning component of prey capture motor output and on its variation with changes in stimulus angle on the horizontal plane. Recent work (Ingle 1982; Kostyk and Grobstein 1982a, b) suggests that the neuronal pathways involved in triggering the turning component of prey capture motor outputs may be substantially different from those involved in triggering the other components, those related to stimulus elevation and to distance. In this paper we report behavioral studies of the variations in prey capture motor output which occur with increasing stimulus distance in *Rana pipiens*. We also report observations to determine the dependence of such variations on binocular vision and on binocular experience. Our general concern was to determine wheth-

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er the responses to stimuli at particular distances are determined solely by the retinal loci activated by the stimulus or whether instead, as appears to be the case for responses to stimuli at given horizontal angles, the particular movements triggered reflect a combination of retinal local sign signals with additional information of other kinds (Grobstein et al. 1983; Grobstein 1983).

Ingle (1970) has shown that for appropriate stimuli located in front of a frog, prey capture movements may involve a snap, consisting of a forward lunge with an associated tongue flip, or of a hop, a forward displacement of the body without a tongue flip. A snap is almost invariably used for near stimuli. While casual observations clearly indicate that snap amplitude increases with stimulus distance, no quantitative study of this variation has been reported. As stimulus distance increases beyond a characteristic value there is a rather abrupt switch from snapping to hopping. Whether hop amplitude also varies with stimulus distance has not been studied. Of particular interest to us was the switch between snapping and hopping, which suggests that not only absolute distance but also some variable corresponding to 'within reach' is significant in understanding the linkage between stimulus location and motor output. If this is so, one would expect the distance at which the switch occurs to vary with body size. To determine whether this is the case, as well as to provide needed quantitative information on variations in snap and hop amplitudes, we have observed the responses of normal frogs of several different sizes to prey stimuli at varying distances.

Variation in motor output with stimulus distance is often presumed to depend on binocular cues although there is abundant evidence that monocular cues can be equally important and are in some cases the only cues available (Collett and Harkness 1982; Ingle 1976; Grobstein et al. 1983). Frontal stimuli are visible to both eyes of *Rana pipiens* (Fite 1973; Grobstein et al. 1980) and so binocular cues are potentially significant. While such cues are clearly used by the toad *Bufo marinus* (Collett 1977), available information on their importance in *Rana pipiens* is sketchy and somewhat conflicting. Unilaterally blinded frogs continue to exhibit a switch between snapping and hopping as stimulus distance increases (Ingle 1972). The distance at which the switch occurs, however, was reported in many animals to change after blinding. Whether this change resulted from a general alteration in distance judgement or represented instead an effect specific to the snap/hop transition is unclear. Ingle (1976) cites observations suggesting that unilaterally blinded frogs exhibit normal snap amplitudes for stimuli in front on the midline. Fite and Rego (1974) on the other hand reported increased numbers of pre-strike orientations and an increased error rate for such stimuli (see also Fite and Scalia 1976). Effects of unilateral blinding on hop amplitudes have not been reported. To clarify the effects of elimination of binocular cues, we have re-examined the responses of unilaterally blinded frogs to stimuli at various distances. We have also studied the behavior of several frogs subjected to unilateral enucleation at larval stages, prior to the metamorphic eye migration which creates a large binocular field, in order to determine whether normal binocular experience is necessary for the development of distance dependent variations in prey orienting.

Methods

Northern grass frogs and tadpoles, *Rana pipiens pipiens*, were obtained from commercial suppliers and maintained in the laboratory. Surgery, where necessary, was carried out under tricaine methanesulfonate anesthesia. Tadpoles, staged according to Taylor and Kollros (1946), were unilaterally enucleated by removal of one eyeball after the suspending extraocular tissue and the optic nerve were cut. In frogs, unilateral blinding was accomplished by removing a section of optic nerve at a location just outside the skull. The nerve was approached via an incision in the roof of the mouth. Recovery from this surgery was rapid, making it possible to test animals within days of blinding.

Behavioral testing involved presentation of stimuli on the substrate at a predetermined series of distances along the midsagittal plane in front of the frog. Distances were measured from a point between the frog's eyes, using a ruler positioned on the substrate. The stimuli consisted of live mealworms. In an effort to maximize the frequency with which frogs responded, we selected active worms, drawing them from a population of larger worms for larger frogs and one of smaller worms for smaller frogs. The range of worm sizes was much less than that of frog sizes and there was substantial variation in worm size within each of the two populations, making it highly unlikely that variations in stimulus size played any role in our findings.

Worms were held in a pair of forceps at the selected distance until the frog either snapped or hopped. The diagnostic feature used to identify a snap was a protrusion of the tongue. The protrusion was readily detected visually and usually left a wet mark on the substrate. Forward movements lacking such a tongue protrusion were characterized as hops. While tongue protrusion is the most unambiguous criterion for distinguishing between a snap and a hop, the two kinds of movements differ in other ways as well. The snap for example involves a transient outward and downward projection of the head which is absent in a hop. Depending on stimulus location, successful prey capture may involve either a single snap or a sequence of hops and snaps. In the latter case, our primary concern was with the first of the series of episodic movements. Individual snaps and hops appear to be ballistic movements which, once triggered, proceede independently of visual reafference related to target location (Comer and Grobstein 1981).

Response amplitudes, like stimulus distances, were read from the substrate ruler. Response amplitude in the case of hops was defined as the forward displacement of the reference point between the frog's eyes which resulted from the first completed movement. In some animals, we also observed subsequent movements up to the completion of prey capture. In the case of snaps, response amplitude was defined as the distance from the reference point between the frog's eyes prior to movement to the farthest point on the substrate reached by the tongue during the movement. The distance was measured to the wet spot left by the tongue, except in cases where such a spot was absent because the tongue hit the worm. In these cases snap amplitude, in our initial studies, was recorded as equal to stimulus distance. This procedure assumes, consistent with our visual impression, that snap trajectories have a sufficient downward component so that overshooting snaps, if they ocurred, would not be interrupted by contact with the stimulus and as a result, fail to leave a wet mark at a greater distance. In our later studies, the stimuli were quickly removed after initiation of the response, and all measurements were made to wet marks left by the tongue. The two different procedures yielded quite similar results, indicating that the assumption underlying the first was valid.

Results

Normal behavior

Figure 1 illustrates variations in prey capture movements with stimulus distance as observed in a typical animal. For nearer stimuli, all responses were snaps; snap amplitudes increased linearly with stimulus distance. For stimuli at distances within an intermediate range, responses were either snaps or hops. Typically, there was a drop from a snap frequency of 90% or greater to one of 40% or less which occurred over a range of 3 to 4 cm. While decreasing in frequency, snap amplitudes continued to increase in amplitude throughout the intermediate range of distances. Beyond this range, 90% or more of the responses were hops. The hop amplitudes, like the snap amplitudes, were linearly related to stimulus distance. Both mean snap and mean hop distances clearly differed for 2 cm differences in stimulus distance, indicating that distance discrimination as well as the matching of movement to stimulus location are at least this precise.

A comparison of the snapping behavior in a small and in a large frog is illustrated in Fig. 2. It is evident that the distance at which snap frequency begins to fall off sharply is different in the two animals. Observations like those illustrated in Fig. 2 were made on a total of 19 animals ranging in length from 2.5 to 10 cm measured from the vent to the tip of the snout. These are summarized in Fig. 3. For each animal, the distance beyond which snap frequency dropped to 40% or less is plotted as a function of body size. While there was significant variation in this value for frogs of a given size, there was nonetheless a clear correlation between body size and the distance of the snap/hop transition, with the latter being about twice the former.

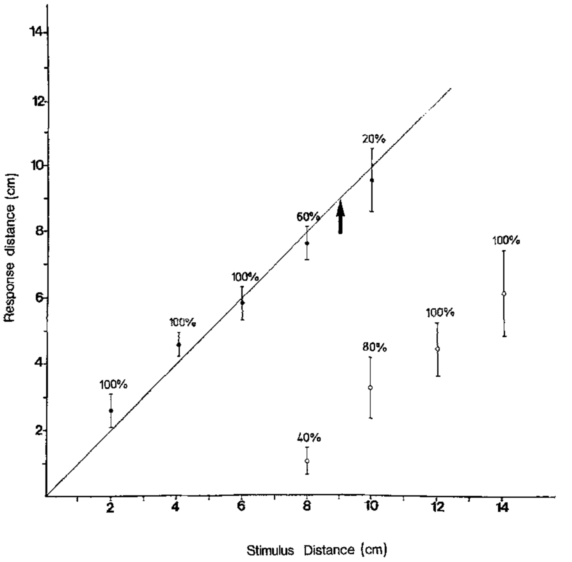

Fig. 1. Behavior of a normal frog. Response distance (ordinate) is shown as a function of stimulus distance (abscissa). Mean and standard deviation of snap amplitude is shown by filled circles and error bars. Mean and standard deviation of hops is shown by open circles and error bars. Points represent a minimum of ten trials at each distance. Numbers above error bars indicate percentage of trials on which a response of the kind indicated occurred. The transition distance, as defined in the text, is indicated by the arrow. The line at 45° represents equivalence between response distance and stimulus distance

Dependence on binocular cues

Figures 4 and 5 illustrate the behavior of two frogs before and after unilateral blinding. Similar observations were made on eight other animals. In all cases, the frogs continued to exhibit a switch between snapping and hopping over a range of distances which was comparable to that seen in normal animals. The actual distance at which the switch occurred however was often different before and after optic nerve section, as reported by Ingle (1972). In seven cases, including those illustrated, the distance decreased; in one it increased somewhat. Alterations in snap zone size were not attributable to generalized trauma associated with surgery. Transition distances remained abnormally low through repeated testing over several weeks. No change in transition distance was observed in a control animal subjected to identical surgery except that the optic nerve was left intact.

Of particular interest is that variations in the distance of the snap/hop transition were not neces-

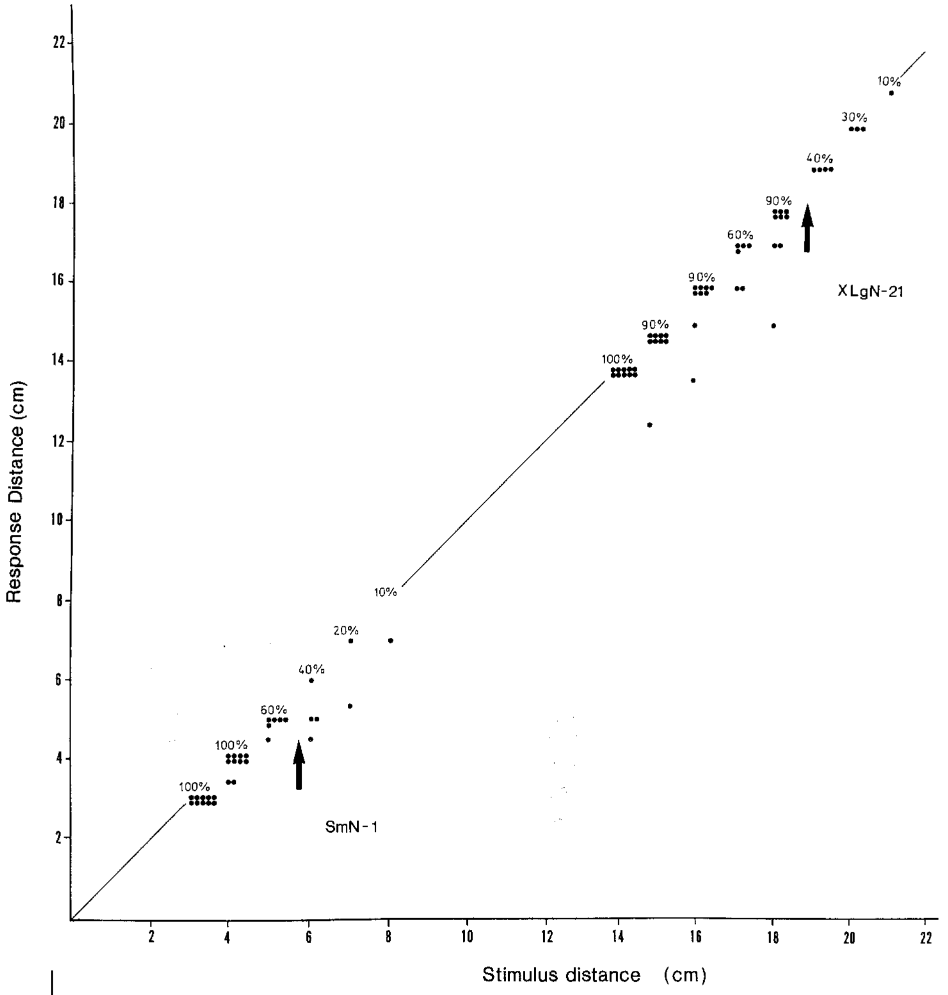

Fig. 2. Comparison of the snapping behavior of a small and a large frog. The behavior of both is shown on the same set of axes with ordinate, abscissa, and 45° line as in Fig. 1. The small frog (snout to vent length 2.5 cm) exhibited a snap/hop transition distance of 6 cm (left arrow). The large frog (snout to vent length 8 cm) exhibited a transition distance of 19 cm (right arrow). Points in the vicinity of the arrows for each frog represent the amplitudes of snaps on individual trials. Means and standard deviations are not shown since in these animals responses striking the stimulus were assigned an amplitude value equal to stimulus distance (see Methods). Numbers above the clusters of points show the percentage of trials on which a snap occurred. Observations on hop amplitudes were not made in these animals

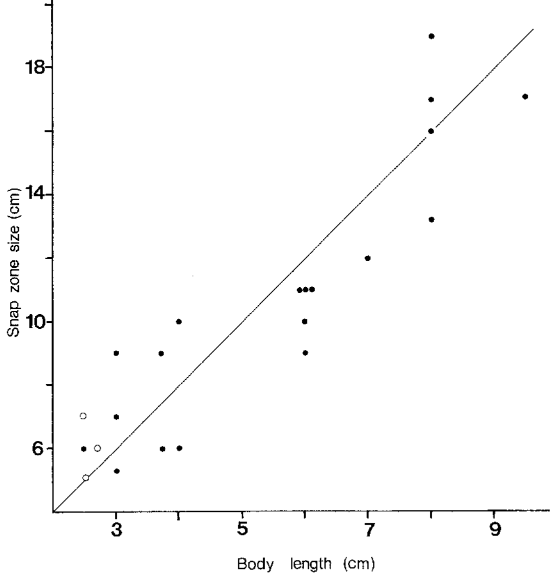

Fig. 3. Transition distance as a function of body size in a population of normal frogs. Each point shows the transition distance (ordinate) for a different frog whose size is indicated on the abscissa. Filled points are normal frogs. Open points represent the three juvenile frogs unilaterally enucleated prior to metamorphosis, as described in the text. The line at 45° corresponds to transition distances equal to twice body sizes

sarily accompanied by changes in the relation between stimulus distance and either hop or snap amplitude. Changes in snap amplitude were not observed in any animal. Jump amplitudes were studied in five of the six animals in which the transition distance decreased after optic nerve section. In one (Fig. 5), the hop amplitudes, like the snap amplitudes, were unchanged. In the other five, reductions in hop amplitude were observed (Fig. 4). While reduced, hop amplitudes in all cases continued to increase with stimulus distance, indicating that discrimination of stimulus distances was still present.

Reductions in the snap/hop transition distance were in general accompanied by an increase in the number of movements associated with successful prey capture. In normal animals, successful prey capture for stimuli at intermediate distances involves two movements, a hop followed by a snap. The amplitude of the hop is such as to reduce the distance to the stimulus so that it falls within the snap range. After optic nerve section, successful prey capture sequences frequently involved three

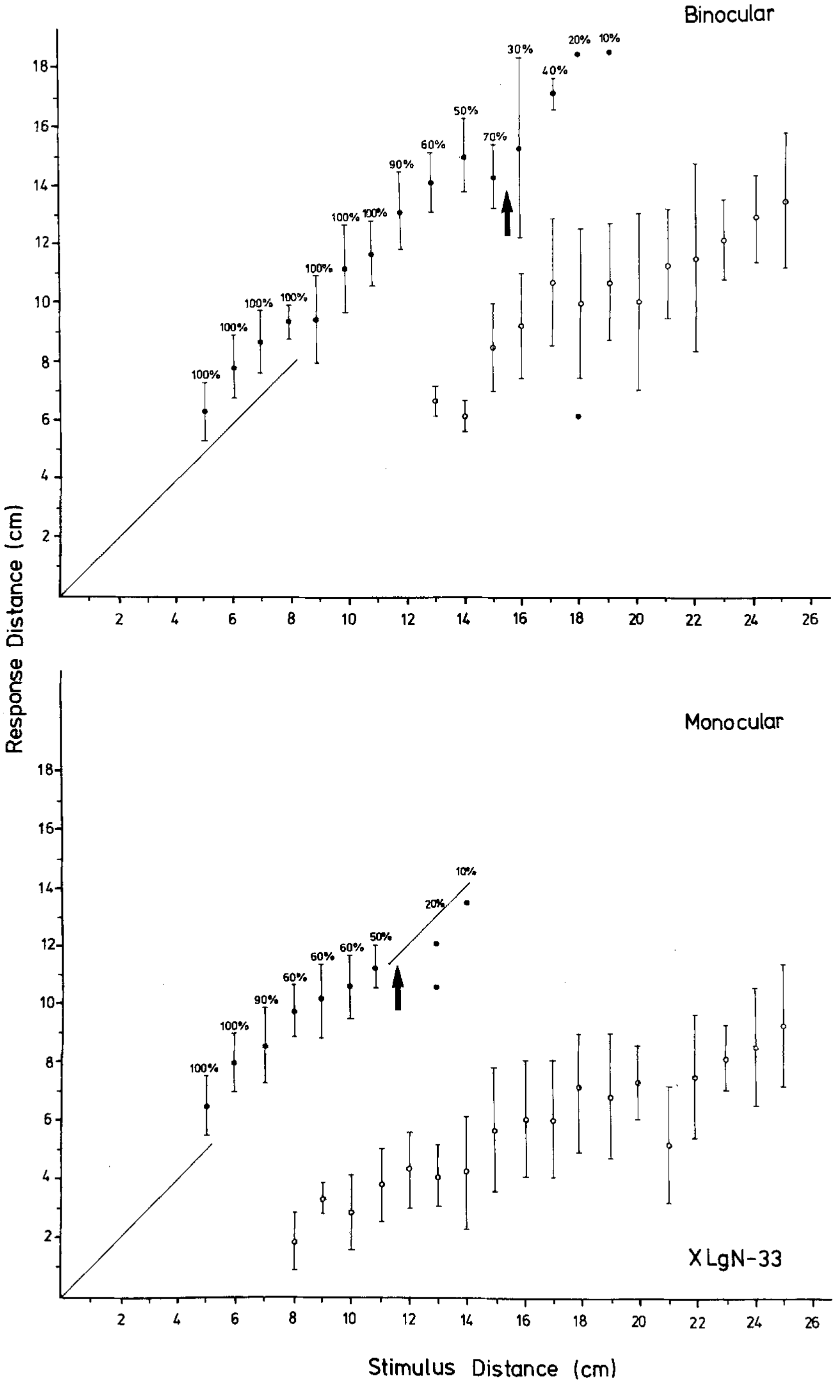

Fig. 4. Behavior of a frog before (Binocular) and after (Monocular) unilateral optic nerve crush. Conventions as in Fig. 1

movements, with two hops preceding the snap. The significance of this observation is considered in the Discussion.

Dependence on binocular experience

In addition to the adult frogs with one optic nerve sectioned, we also collected some data on three juvenile frogs that had had one eye removed prior to metamorphosis. The enucleations were done at stage XXI (Taylor and Kollros 1946) in one case and at stage XVII in the other two. Both stages are prior to the completion of the metamorphic eye migration which creates the adult binocular field. Hence none of these animals had normal binocular experience related to postmetamorphic eye position. Stage XXI is subsequent to the initial development of convergent input to the tectum from the ipsilateral eye; enucleations at this stage are reported not to effect development of this ipsi-

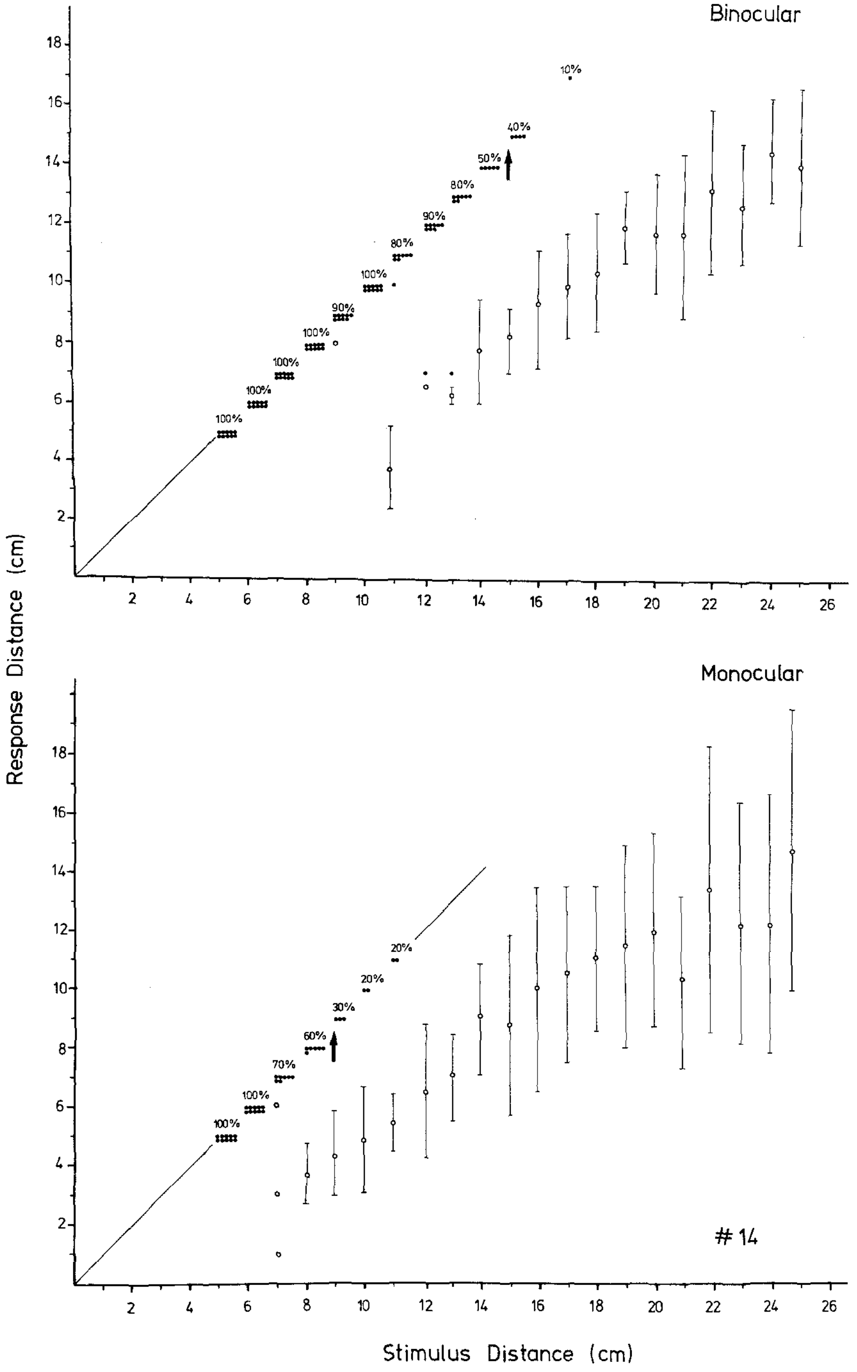

Fig. 5. Behavior of a second frog before (Binocular) and after (Monocular) unilateral optic nerve crush. Individual snap amplitudes rather than mean and standard deviation are shown as in Fig. 2. Other conventions as in Figs. 1 and 4

lateral projection (Jacobson 1971). Stage XVII is earlier, prior to the initial appearance of the ipsilateral projection; enucleations at this stage result in abnormalities in the ipsilateral pathway (Jacobson 1971). No evidence of abnormalities was apparent in the behavior of any of the enucleates, one of which is illustrated in Fig. 6. All three animals showed good variations in snap amplitude with stimulus distance as well as a clear snap/hop transition which occurred at a distance comparable to that seen in similarly sized normal frogs (Fig. 3).

Because of the small distances and the inability to compare behavior in binocular and monocular conditions, it is not possible to say whether in these enucleated animals, as in unilaterally blinded adults, small abnormalities in the distance of the snap/hop transition resulted from the absence of binocular vision. Hop amplitude was not studied

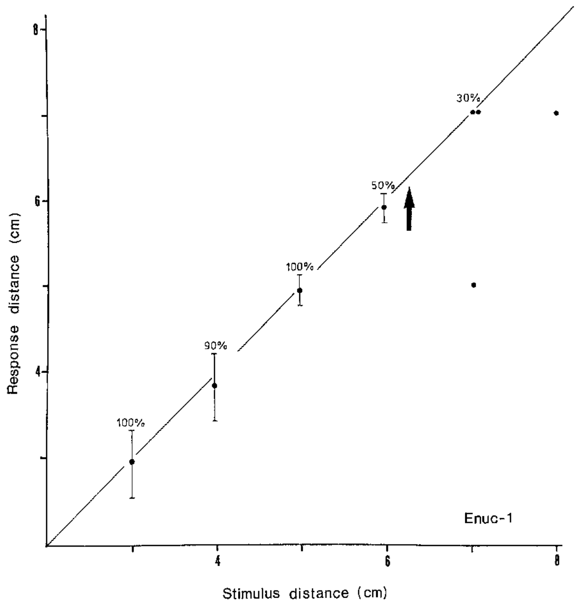

Fig. 6. Behavior of a juvenile frog unilaterally enucleated prior to metamorphosis (at stage XVII). Conventions as in Fig. 1 except that observations on hop amplitude were not made

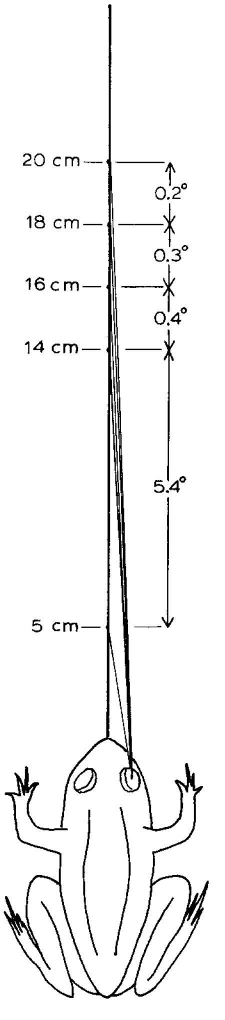

Fig. 7. Variations in the locus of retinal stimulation with increasing distance on the mid-sagittal plane. Illustrated is a schematic scale drawing of an 8 cm frog having an interocular spacing of 1.5 cm. Numbers to the right show differences in visual angle which correspond to distance intervals shown to the left. Transition distance for this frog would be in the range of 16 cm. Clear differences in the movements triggered by a stimulus are present for 2 cm differences in stimulus distance at and beyond this range, despite the fact that the corresponding variations in retinal locus amount as shown to less than a half of a degree

in the enucleated animals and hence we also cannot be certain whether this particular aspect of distance dependent behavior was normal. In general, however, our observations indicate that neither distance discrimination nor the behaviors studied depend on normal binocular experience. We also tested turning behavior in the two stage XVII animals, to determine whether the lack of binocular experience had any effect on the ability of the remaining eye to trigger turns both to the right and the left of the midline (cf. Kostyk and Grobstein 1982a). Neither animal displayed any inability to turn toward stimuli in the part of the frontal visual field contralateral to the remaining eye. This finding is consistent with an earlier one (Hoskins et al. 1982) also indicating insensitivity of this aspect of orienting behavior to abnormal binocular experience.

Discussion

Normal behavior

Our observations, confirming earlier ones (Ingle 1970), show that frog prey orienting movements for frontal stimuli may consist either of a direct snap or of a hop, with the former predominating for near stimuli and the latter for more distant ones. For distances within a transition zone, either motor pattern may occur. Our observations extend earlier ones by showing that the amplitude of both motor patterns varies with stimulus distance, and that the transition distance varies with body size.

Ingle (1970) originally suggested that the transition from snapping to hopping corresponded to a determination as to whether a stimulus was 'within reach'. Our finding that the transition, in normal frogs of a wide range of sizes, occurs at distance of about two body lengths is consistent with this suggestion. Our observations also exclude a possible alternate explanation of the transition, that it occurs at a distance beyond which the frog can no longer discriminate distances. The existence of variations in hop amplitude with variations in stimulus distance clearly indicates an ability to discriminate distances at values greater than that at which the transition occurs. Additional evidence for discrimination comes from the finding that most frogs snap accurately, albeit infrequently, at distances beyond that at which hopping becomes the dominant response. The infrequent large amplitude snaps do, however, also indicate that the transition distance does not in general correspond to that calling for the maximum possible amplitude of the snap motor output. While 'within reach' may thus not be the best term, our observations clearly confirm the more general point, that frogs make some kind of distinction between local and more distant sensory space, a discrimination in which body size is a significant factor. Possible ways in which such a discrimination might be made are considered below.

Our finding that snap amplitude is closely matched to stimulus distance in normal frogs is not unexpected. The results do however indicate that the matching is fairly precise and comparable to that observed in toads (Collett 1977). The snap clearly ought not to be thought of as an invariant consummatory movement but rather as a repertoire of movements that vary in amplitude. Our findings indicate that hop amplitude also varies with stimulus distance. While snap amplitude is in general equal to stimulus distance, hop amplitude is not. The effect of the increase in hop amplitude is to produce, for a range of stimulus distances, a roughly constant distance between frog and stimulus *after* the hop. This remaining distance, in normal frogs, is less than that at which the snap/hop transition occurs, suggesting that hop amplitude is programmed to bring the stimulus within range of a snap. Since snap range varies with body size, this indicates that hop amplitude for stimuli at given distances may also vary with body size. Our observations on hop amplitudes were made primarily on larger frogs. Additional study of hop amplitudes in frogs of a range of sizes is necessary to establish whether such variations occur.

Behavior of one-eyed frogs

Our observations on one-eyed frogs indicate that neither binocular cues nor binocular visual experience are necessary for discrimination of stimulus distances throughout the range tested. Our finding that snap amplitude was not affected by optic nerve section is consistent with a previous report on *Rana pipiens* (Ingle 1976). Parallel observations also exist for the toad, *Bufo marinus* (Collett 1977). Persistance of a snap/hop transition in one-eyed frogs has also been previously reported (Ingle 1972). Our findings extend previous reports by showing that binocular vision is not essential for discrimination of distances at the distances where hopping predominates, as well as within the range where snapping occurs. This is not to say that binocular cues are not normally available and used by the frog. Collett (1977) has shown that toads are capable of monocular depth discrimination but also use binocular cues when available. While the additional use of binocular cues by the frog is quite possible, our observations clearly indicate that adequate information for discrimination of stimulus distances and for triggering of all kinds of motor outputs must be available from monocular cues. Candidates include monitoring of accommodative state (Collett 1977; Jordan et al. 1980), as well as a variety of pictorial cues (Gibson 1950; Kaufman 1974).

As originally described by Ingle (1972), monocular blinding frequently resulted in a change in the distance at which the transition from snapping to hopping occurred. In most cases, unilateral optic nerve section resulted in animals hopping in response to stimuli at distances where snapping was the predominant response in the binocular condition. This change cannot be attributed to a loss of the ability to discriminate distances beyond some range, for the reasons discussed above. Nor can it be accounted for in terms of a generalized alteration in the determination of stimulus distance. One might imagine that monocular processing generally yields larger values for stimulus distance than does binocular processing, resulting for stimuli at intermediate locations in the triggering of a hop rather than a snap. Were this the case, however, one would expect under monocular conditions to also see increased snap amplitudes for nearer stimuli and increased hop amplitudes for more distant ones. Such increases were not observed. The fact that snap amplitudes were in all cases unchanged implies that distance values, at least over the range where snapping occurred, were the same under binocular and monocular conditions. In one animal, jump amplitudes too were unaltered, indicating that changes in the snap/hop transition distance can occur without observable changes in the determination of distance values anywhere within the tested range. Jump amplitudes decreased rather than increasing in the remaining animals. Whether this was due to a change in the distance values for longer distances or represented instead a shift in behavioral strategy for dealing with distant stimuli is unclear. In either case, our observations indicate that monocular blinding affects specifically the relation between stimulus location and motor output for longer distances, those where motor output is likely to be a function not of stimulus distance alone but of stimulus distance in relation to body size. The effects can be quite specifically on the snap/hop transition, which we have shown is in fact a function of relative rather than absolute stimulus distance.

Our observations on the behavior of one-eyed frogs also bear on the suggestion that hop amplitude may be programmed in relation to snap zone size; they clearly indicate that the normally observed relation between the two variables is not an inevitable one. As mentioned, in animals in which snap range was decreased by optic nerve section there was not a corresponding increase in hop amplitude. The result was that these animals, unlike normal frogs, frequently made two or more jumps before snapping. This may account for the earlier finding of increased numbers of pre-strike orientations in unilaterally blinded frogs (Fite and Rego 1974). The observations also suggest that there may have to be an active process which adjusts hop amplitude in relation to snap range or vice versa. Whether frogs in which snap range and jump amplitude are mismatched as a result of optic nerve section will adjust one or the other with time is under investigation.

General implications for understanding neuronal organization

The concept of 'retinal local sign' has been valuable in trying to understand the neuronal organization underlying anuran orienting behavior. A stimulus at a particular location activates a particular part of the retina. Information as to what retinal region has been activated is preserved by the topographic retinotectal projection. Simple models of the subsequent neuronal organization presume that such local sign information is adequate to specify the required movement and hypothesize that such a movement is the consequence of circuitry which associates with each tectal locus a distinctive and appropriate motor output (Grobstein et al. 1983). Since retinal local sign can vary in only two dimensions while stimulus location varies in three, some additional processing must be presumed to account for variations in movement associated with variations in stimulus distance. A combination of local sign signals from the two eyes so as to yield a distinctive locus of tectal activity might satisfy this requirement.

Our observations clearly indicate that the existence of neither the quantitative nor the qualitative variations in motor output that occur with increasing stimulus distance depend on the existence of a retinal local sign signal from both eyes. This makes it unlikely, though not impossible, that distance-related variations in motor output correspond to variations in retinal local sign signals. As illustrated in Fig. 7, variations in stimulus distance will, even in one-eyed animals, produce some variations in the retinal locus on which the stimulus is imaged. With increasing stimulus distance, however, these variations rapidly become quite small. At greater distances, significant differences in behaviour continue to be seen for 2 cm differences in stimulus distance; the corresponding differences in retinal locus represent a half degree or less. Given available information on ganglion cell and tectal cell receptive field sizes (Grüsser and Grüsser-Cornehls 1976), multiunit receptive field sizes in superficial tectum (cf. Adamson et al. 1984), and tectal magnification factors (Jacobson 1962), it seems highly improbable that these very small differences in retinal locus result in differences in the locus of tectal activation of sufficient magnitude to account for the observed variations in behavior. A necessary conclusion would seem to be that activation of a given superficial tectal locus is associated with a number of different movements, with the particular movement triggered by a given stimulus depending on a combination of retinal local sign information with other kinds of information related to stimulus distance.

While changes in stimulus distance will produce quite small changes in the retinal locus activated, much larger changes in retinal and hence tectal locus for a stimulus at a constant distance would result from small changes in head or eye position. Since movement amplitudes should remain similar in the face of such changes, there is additional reason for doubting that the normal correspondence between stimulus location and motor output can be accounted for in terms of a simple one to one linkage between superficial tectal locus and motor output. This consideration suggests that the output associated with activation of a given tectal region is probably influenced not only by additional information related to stimulus distance but also by information related to body posture (see also Ingle 1970). Both additional sources of information are probably necessary for determining turn amplitude as well (Grobstein et al. 1983).

Our observations specifically on the snap/hop transition provide still another reason for doubting that there is a one to one coupling between tectal locus activated and motor output. The switch between two qualitatively different motor patterns does not occur at a particular distance but rather over a range of distances. At a given distance within this range either snaps or hops may be triggered, suggesting that both kinds of motor output can be triggered from the same tectal locus. Whichever movement occurs is of appropriate amplitude. This makes it unlikely that the existence of two kinds of responses for stimuli at particular distances is an artifact resulting from small variations in the retinal and hence tectal locus activated. More interestingly, the observation, like the previously discussed behavior of one-eyed frogs, also implies that which of the two kinds of movements occurs is not determined solely by perceived stimulus distance.

That the snap/hop transition distance varies with body size provides further evidence that the switch from one kind of movement to the other is not a function of perceived stimulus distance alone. It might seem that the increased snap/hop transition distance in larger frogs could be attributed solely to an increased interocular spacing, since this increases the distance along the mid-sagittal plane which corresponds to a given retinal angle. Such an explanation presumes though that the transition from snapping to hopping is accounted for entirely by changes in the retinal local sign signal, a presumption which seems unlikely for the reasons discussed above. A more fundamental problem with such an explanation, as well as any other which similarly tries to account for the increasing transition distance in terms of a distance signal that scales with body size, is that they predict that changes in the transition distance should be accompanied by changes in output amplitude for stimuli at other distances. In fact, the variation in the snap/hop transition distance with body size, like the fluctuation in the distance in normal animals and the alteration in the distance following optic nerve section, occurs with no evidence of an altered distance signal, as judged by snap amplitudes.

To account for the snap/hop transition it seems necessary to presume that, in addition to a distance signal, some independently modifiable parameter is involved, one which varies with body size. The variation might be attributed to growth related changes in a pattern of connections specifically involved in establishing the transition distance. An alternate hypothesis is that besides those related to distance and posture, there is a third neural signal added to the retinal local sign signal, one carrying information about, and hence itself varying with, body size. The involvement of such a signal in determining the movement triggered by activation of a given retinal region would provide an explanation for variations in transition distance with body size without having to presume rearrangements of neural circuitry. The finding of alterations in snap range after unilateral optic nerve section suggests the intriguing possibility that binocular processing may be of significance in generating a signal related to body size.

In general, the present findings on variations in output with stimulus distance parallel earlier ones on the control of direction and angle of turn (Grobstein et al. 1983; Grobstein 1983; Kostyk and Grobstein, in preparation). Both imply a substantial sophistication in the neuronal circuitry underlying prey orienting behavior in the frog. While the topographic retinotectal projections create one to one correspondences between retinal and superficial tectal loci, the subsequent neuronal organization does not appear to be such as to establish a similar one to one correspondence between tectal locus and motor output. Instead the organization appears to be such as to associate a variety of possible movements with individual tectal loci. This makes sense given the recognition that retinal local sign information is insufficient to adequately specify stimulus location. The implication is that retinal local sign information must be combined with additional information in order to generate an appropriately directed movement. Whether the combining of relevant signals occurs in the tectum or subsequently is not yet clear. Neither is it clear whether the additional signals act in such a way as to yield neurons whose activity is related to stimulus location in a body coordinate frame or rather, as suggested by Lashley (1951), they act to alter ongoing patterns of activity and hence shift the networks activated by a retinal local sign signal. The phenomena observed in the frog, and the questions they raise, are not substantially different from those which characterize spatial localization processes in other vertebrates, including man. It thus seems likely that studies on the frog will continue to provide a source of generally significant insights into such processes.

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