

Do Toads Plan Routes? A Study of the Detour Behaviour of *Bufo viridis*

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Accepted December 1, 1981

Summary. 1. Given the right circumstances, toads will detour round a paling fence to reach their prey on the other side. In programming this manoeuvre, toads take into account both the position of the fence and the distance of the prey (Fig. 1). Should there be a gap in the fence, which offers a more direct approach, toads will aim for that instead (Fig. 2).

2. The argument developed in this paper is that, when a toad decides upon a particular approach, it is guided by the sum of its reactions to several individual features of the situation, such as the length of the fence, the presence or absence of gaps, the gaps' width (Fig. 7) and their proximity to the prey (Fig. 11) and to the toad's long axis (Fig. 10). When there are several possible approaches, toads will select the gap (or edge) which has the most 'attractive' combination of features.

3. The relative attraction of gaps can be manipulated and toads will then shift their preference. Normally, toads head for the gap lying closest to the prey and to their long axis (Figs. 9a and 12b). However, if the relative salience of a more peripheral gap is increased the bias towards the closer gap is reduced (Fig. 9b).

4. Toads tend to choose the closest gap even when it is inappropriate to do so. They seem unable to use the spatial information potentially available to them to pick out the shortest, unobstructed path to their prey. The major support for this view comes from the way they treat double fences composed of two rows of palings. With both fences unbroken, toads usually detour around them (Fig. 2d). However, when a gap is inserted in the front fence, they will often aim for that, regardless that the rear fence blocks their subsequent approach (Figs. 2c and 4). If palings are added to join the ends of the two fences, toads continue to aim for the gap, though once they have entered the space between the two fences, all they can do is to retrace their steps.

5. It is not that toads are blind to the rear fence. They can detect gaps in it (Fig. 8a) and their behaviour is influenced by the distance between the rear fence and their prey (Fig. 6). Nonetheless, a gap restricted to the front fence is still treated as a gap, but as less attractive than one extending through both fences (Fig. 8b). And, if such a gap is close to the toad's midline and the prey, then toads are drawn to it, rather than to the ends of the fence.

Introduction

Toads are equipped with good spatial vision. They are capable of measuring depth accurately (Ingle 1976a; Collett 1977) and suggest by their behaviour that within a small sphere of space around them they may perceive the real sizes of objects and the distances between them (Lock and Collett 1979, 1980). This information helps in discriminating prey from predator (Ewert and Gebauer 1973; Ingle and Cook 1977), in recognising mates (Kondrashev 1976) and in circumnavigating obstacles (Lock and Collett 1979, 1980).

In people, an accurate assessment of the layout of objects in their immediate environment permits them to plan routes between any two points (Thomson 1981), and to solve numerous spatial problems. Toads are adept at negotiating barriers of various kinds (Ingle 1971, 1976a; Lock and Collett 1979, 1980). They can, for instance, make an accurate detour around an obstacle to reach food on the other side. Detours of this kind are programmed before a toad starts its approach. And, in a sense, toads in such situations are also planning their route. The major issue raised here is the meaning of this term when applied to a toad. To what extent can it use the three-dimensional information, which is poten-

tially available to it, to compute an economical and clear path to its prey?

To answer this question, an analysis has been made of the way toads cope with a variety of barriers. The conclusion that will emerge in the course of the subsequent discussion is that one can account for a toad's strategy in dealing with barriers in terms of rules, which rely on information derived from local features in its surroundings. There is no sign that the toad can assess whether the rules it uses will actually enable it to reach its goal in any particular situation: the rules seem to be applied automatically, regardless of whether they will work. Although the rules themselves are simple enough, the experiments also show that the information toads extract about the spatial arrangement of the barriers and prey is surprisingly sophisticated.

Materials and Methods

About 15 *Bufo viridis* acted as experimental subjects. The toads were originally caught in Turkey and bought from a commercial supplier (Xenopus Ltd.). They were housed in communal, foam-lined tanks and maintained on a diet of locusts and meal worms. This species remains lively in captivity. Individuals have now been kept for three years with no apparent deterioration. It is clearly important to have animals alert and in good condition, when conducting tests which attempt to explore the limits of their capacities.

Most of the experiments involved observing how the toad approached its prey, when one or more picket fences obstructed a direct path to the food. The picket fences were made of pieces of dowel or wire 30 cm high and 0.5 cm or 0.25 cm diameter, inserted into holes in the floor of a black painted arena. The prey consisted of several active meal worms confined within a transparent container. During periods of experimentation toads were usually tested daily and were then given between 3 and 10 trials. At this time they were fed only in the arena, usually with no more than one meal worm at the beginning and one at the end of an experimental session.

At the beginning of each trial a toad was lured with a moving dummy to a suitable position in front of the barrier and the direction in which it approached the barrier or food was noted. There was never any doubt that the animal was intent on reaching its prey, and, when a fence barred its way, it would try to push through. Its behaviour was sufficiently clear-cut that direct observation sufficed, except for two experiments in which more detailed information was needed. Tests were then recorded on videotape and the toad's approach analysed frame-by-frame. About 10 toads were tested in each experimental condition and the total number of trials for each condition varied between 50 and 100. The few exceptions to this procedure are noted in the Results. The χ^2 test was used to assess the statistical significance of the findings.

Results

Detours Around a Single Fence

When a toad is positioned so that a fence composed of vertical palings separates it from its prey, the animal will often aim directly for one end of the fence, and then detour round it to reach the prey on the

other side (Ingle 1971; Lock and Collett 1979). One such detour is illustrated on the right side of the barrier of Fig. 1a. The position of the toad has been drawn every 200 ms: its head being represented by a circle and its orientation by a line. The detour is performed in two stages with a 3.5 s pause between the two. L shaped opaque barriers were placed behind the fence, as shown by the lines in Fig. 1, so that once the toad had set off it no longer had any sight of the prey. Thus in so far as the second stage is aimed at the food, it must rely on information that the toad has picked up before it started out.

Ingle (1971) noticed that at the end of a detour the toad turns so that it faces in the approximate direction of the prey. This indicates that in executing a detour a toad takes the position of both prey and fence into account. The same behaviour can be seen in Fig. 1a. Here, however, the barrier prevents the toad from seeing the prey after its first step or two. In this case an accurate turn implies that the toad must record the distance of the prey before beginning its detour and incorporate the information into its programme.

To see whether this is indeed the case tests were conducted with the prey at different distances from the fence and with the opaque barriers positioned as indicated in Fig. 1a. Toads started 10 cm from the fence, with the prey either 10 cm or 22 cm behind it. Their position at the end of each leg of the detour was recorded. Examples of these positions are shown to the left of the fence in Fig. 1a.

The dashed lines indicate approaches with the prey at 10 cm, the unbroken lines approaches to prey at 22 cm.

In order to plot how accurately the toad faced the prey after turning, a line (shown dotted in Fig. 1a) was drawn through its long axis and extended until it intersected a second line perpendicular to the fence, passing through the container of prey. The distance of this point of intersection from the fence (the fixation distance) was measured, and the distribution of these distances is plotted in Fig. 1b. The stepped distributions show the fixation distances at the end of the first stage, both of detours which stop then and of those which continue on to a second stage. The filled circles represent fixation distances at the end of the second stage. Although the precision of the turns is not great, the distribution for the 10 cm (top) and 22 cm (bottom) prey distances are clearly different. Two parameters of the toad's approach contribute to the value of the fixation distance: first, the length of its approach and secondly the amount it turns at the end. Scrutiny of all the results confirms what can already be seen in Fig. 1a, that both factors vary with prey distance. The conclusion drawn from

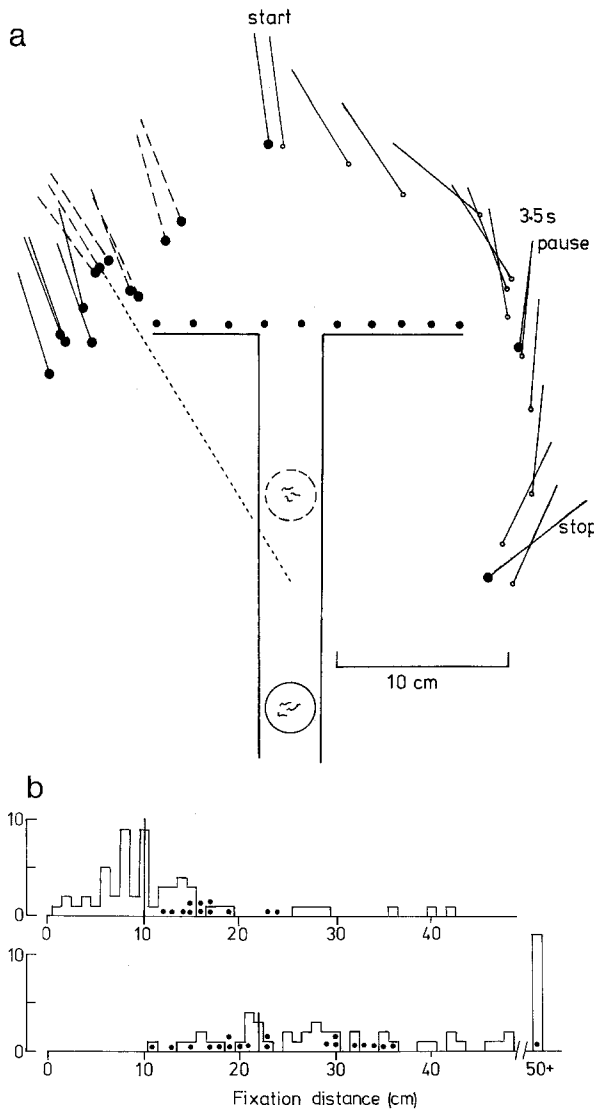


Fig. 1a, b. Detours round a picket fence to reach prey positioned either 10 cm or 22 cm behind. **a** Plan view of fence (filled circles) and of opaque barriers (lines) which are placed to prevent the toads from seeing the prey once they have left the start position. The course of one detour is drawn to the right of the barrier, with the toad's position shown every 200 ms. Toad's orientation indicated by the line, the position of its head by the circle. Filled circles indicate when toad is stationary. Note toad is turned towards prey when it has stopped moving. To left of barrier are shown end positions of detours. Dashed line indicates prey is at 10 cm, unbroken line prey at 22 cm. End of dotted line gives 'fixation distance' from fence, as defined in text. **b** Histogram of fixation distances at end of approach. Top distribution: prey at 10 cm. Bottom distribution: prey at 22 cm. Stepped distribution shows detours, which ended after one stage, or the first leg of those that continued. Dots show fixation distances at the end of the second stage. There is a clear difference between the top and bottom distributions implying that toads include prey distance when programming their detour

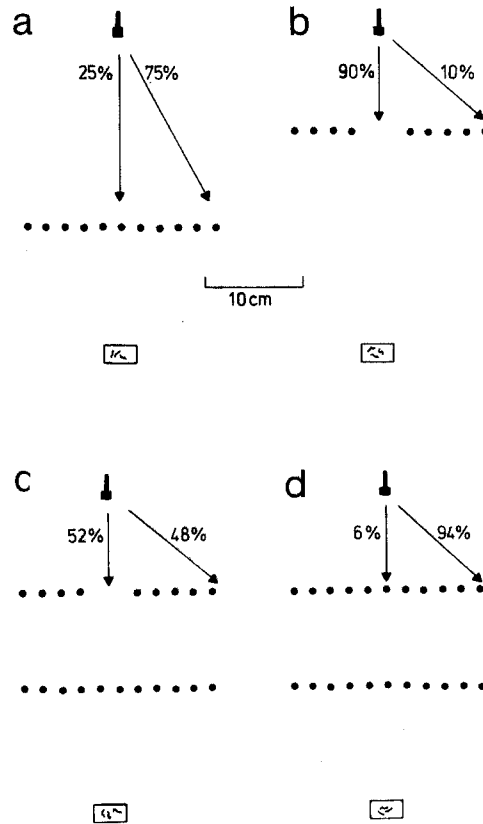
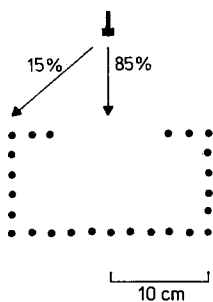


Fig. 2a-d. Approaches to prey with single and double barriers interposed. In each case, the 'hammer' indicates the toad's starting position and orientation, the filled circles show the fence, and the arrows summarise the directions of the approaches. For this and all similar illustrations, the results are given in terms of the percentage of approaches made in a particular direction. **a** Single fence with prey 12 cm behind. **b** Single fence with 6 cm gap and with prey 22 cm behind. **c** Double fence composed from single fences of **a** and **b**. **d** Double fence with no gap. In **c** toad makes for gap on about half of the trials, even though rear fence still blocks approach. Directions of approach in **c** differ significantly from those of **a**, **b** and **d** ($P < 0.001$ in each case)

this is that in planning detours toads need information not only concerning the fence but also about the distance and position of the prey.

Detours Around Double Fences

If a gap is inserted into a single fence, toads will usually aim directly at that, instead of detouring round the edge (Lock and Collett 1980). Figure 2b shows, for example, that with a 5.5 cm gap set within a 20 cm fence 90% of approaches are aimed at the gap. Double fences composed of two parallel rows of palings provide an interesting test situation. Gaps can be introduced into one fence, but not into the other. The question can then be asked: does the toad plan its route, taking into account the whole configuration of both fences? Is it able to choose an approach



(2)

Fig. 3. Approaches to prey behind 'cage'. Cage formed from double fence with palings connecting the ends. Toads still aim for gap in front fence. This suggests that toads do not work out the consequences of a particular approach, but are simply attracted toward certain local features in their environment

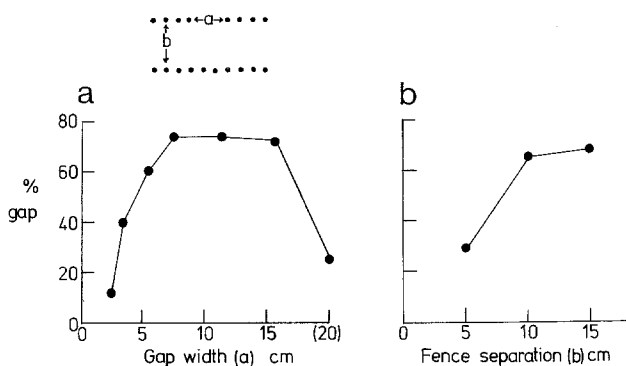


Fig. 4a, b. Double fences with varying gap-widths and fence-separations. **a** % trials aimed at gap plotted against the width of the gap in the front fence. Fence is 20 cm wide, so that when the gap is widened to 20 cm all the palings have been removed. Separation between fences is 10 cm and prey lies 12 cm behind rear fence. **b** % trials aimed at gap plotted against fence-separation. Gap-width 6 cm, prey 12 cm behind rear fence

that gives it an unobstructed path to its prey, or is its route governed by how it responds to individual features in one or other fence? The second alternative provides a closer description of the toad's performance. With a gap in the front fence, but not in the rear, the toad often aims directly for the gap, despite the second fence that still effectively blocks its approach to the prey. However, when the front fence is removed entirely, or the gap in it is filled, most of the toad's approaches are detours (Fig. 2a and d), indicating that the maladaptive behaviour is caused by the toad's response to the gap.

A more dramatic demonstration that toads do not work out the consequences of embarking on a particular approach was achieved by adding palings to connect the two ends of both fences. Now, if the toads decided to pass through the gap, they entered what was almost a cage. The extra palings, however,

did not reduce the number of approaches aimed at the gap (compare Figs. 3 and 4).

When a toad faces a single fence, it tends to detour round if the gap is narrower than the width of its head, and to aim for the gap should the gap be wider. With double fences the toad also approaches gaps more readily as they are made wider (Fig. 4a). This is somewhat surprising, for one might have expected that as gap-width is increased beyond some optimum, the front fence will become less obtrusive, and that as a result the toad's approach will be governed by the rear fence, so that the proportion of detours will increase. But, in fact, the toad mostly aims for the gap, even when the gap is so large that the front fence consists of nothing but a pair of palings at each end. It is striking, that the detours which are made, are still aimed at the end of the front fence, rather than at the rear fence, which is clearly visible through the gap.

The bottom of the front fence is lower in the toad's visual field than the bottom of the rear fence. To make sure that the gap can be detected against the backdrop of the rear fence, toads were also tested with the front fence raised 2 cm above the floor of the arena. This procedure was used for 7.5 and 11.5 cm gap-widths and the proportion of approaches aimed at the gap (70%) was unaffected.

As the two fences are brought closer together, the gap in the front fence exerts a less powerful effect on the toad's approach, and the toad more often detours round the fence (Fig. 4b).

The findings summarised in Fig. 2 and 3 are interesting on two counts. First, they indicate that a toad is able to keep separate the information that it obtains from different depth planes; the rear fence does not prevent the detection of a gap in the front fence. Secondly, it implies that toads do not seek out a clear path to their food, rather they make for the nearest gap, regardless of whether this provides a direct passage. The experiments described below were designed to find out what a toad notices about the spatial arrangement of the two fences and prey. Does the toad's failure to behave sensibly arise from a lack of information about sizes and distances, or is it because of the way the toad uses that information?

Density Changes Within a Single Fence

When projected on to a single surface, such as the toad's retina, the arrangement of two fences with a gap in one is equivalent to a change in the density and thickness of the palings. One thus needs to explore whether the toad is reacting to density changes, rather than to the three-dimensional arrangement of the two fences. Toads were tested with single fences,

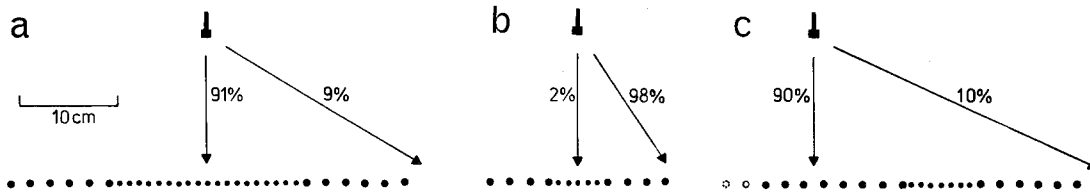


Fig. 5. Approaches to single fences in which density of palings and their thickness changes. Prey 12 cm behind fence, along line passing through toad's long axis, toads never approach density change as though they see it as equivalent to a change in depth. Open circles indicate where full extent of fence is not shown

formed of two thicknesses of palings, with the spacing between the thinner palings half that of the thicker.

In Fig. 5a the fence is so wide that normally toads will not detour round the end, but attempt to reach the prey directly through the fence (see below, p. 266). The density decreased some 10 cm from the midline. If the density-decrease were seen as an edge, one might expect approaches to be aimed at the region of fence where the density changed. This never happened. The situations of Fig. 5b and c are equivalent to the projection on to a single surface of a fence with a gap, which seen from the toad's starting point is exactly filled by a second more distant fence. Toads never approached the region of increased density as though they saw it equivalent to a fence behind a gap. In a fourth variant toads faced an 8 cm gap in a 20 cm fence with the projection of the rear fence mimicked by 12 cm of closely spaced thin palings placed right behind the fence and raised some 1.75 cm above the floor of the arena. Toads mostly detoured round the edge of the fence, rarely aiming at the 'gap', indicating again that toads do not see density changes within a single plane in the same way that they view a real three-dimensional situation.

Double Fences: Do Toads Know the Distance Between the Prey and the Rear Fence?

With single fences the toad's behaviour depends on the separation between fence and worm (Lock and Collett 1979). Detours are made more often, if the prey lies a long way behind the fence, than if it is close, when the toad aims directly for the prey, attempting to reach it through the fence. By manipulating the distance between the worms and the rear fence, one can thus ask whether the toad has any appreciation of the separation between the two, despite the presence of a masking fence in front.

Figure 6 illustrates such an experiment. The left-hand column shows tests, in which the gap in the front fence was offset from the midline, so that the toad had to view the prey through both fences. In the right column, the gap in the front fence lay in line with the prey. As the prey is brought from in front of the back fence (top row) to the rear of it,

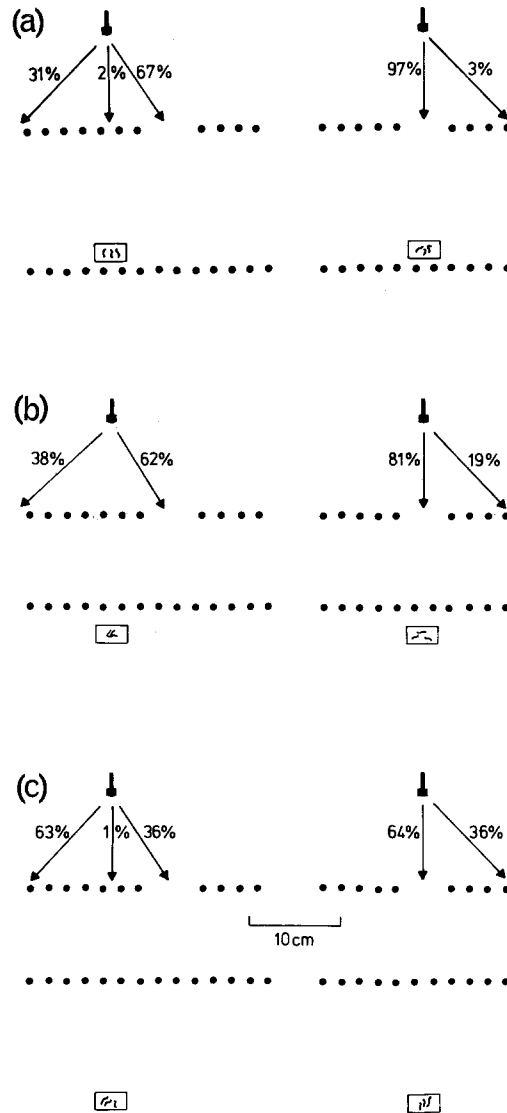


Fig. 6a-c. Approaches to double fences with different separations between prey and rear fence. *Left:* gaps in front fence are to the side of toad's midline and prey. *Right:* toad views prey through gap in front fence. **a** Prey 2 cm in front of rear fence. **b** Prey 2 cm behind rear fence. **c** Prey 12 cm behind rear fence. As prey is moved further behind fence, so fewer approaches aimed at gap, from which it is concluded that toads appreciate, to some degree, the distance between rear fence and prey

and the separation increased, there is a significant drop in the proportion of approaches aimed at the gap ($P < 0.001$, left column: $P < 0.01$, right column. Top two rows are compared with bottom row). It is not the distance of the prey from the front fence that lessens the frequency of approaches to the gap, because, if the rear fence is removed (Fig. 2b), almost all approaches are aimed at the gap. It is as though the back fence tells the toad to detour, while the gap in front says approach. As the separation between the back fence and prey grows, so the back fence becomes more effective. These results suggest, then, that the front fence does not prevent the toad knowing to some degree the distance between back fence and prey.

Offset Gaps in Single and Double Fences

Toads treat long fences differently from short ones. If the fence is long, toads are reluctant to detour around the end, and usually aim straight for the prey, ignoring the presence of the fence (Lock and Collett 1980). However, if a gap is placed to one side of the food, toads will detour through that. Although to us a gap in line with the food might seem the same as a gap to one side, in terms of the toad's decisions and behaviour the situation is different. A gap in line presents a direct pathway to its food, and, if the fence is short, the toad chooses between approaching the food directly through the gap, or detouring round the end. On the other hand, a gap to the side offers a possible detour. In this case, when the fence is long, the toad's choice is between a detour through the gap or a direct approach. So long as toads are no further than 20 cm from the fence, they seem to measure a gap's real width, when deciding whether a gap in line with the food is large enough to pass through (Lock and Collett 1980). And, it is worth asking whether toads also measure the real width of gaps used for detours, rather than the angle the gaps subtend at the retina.

Toads started either 7.5 cm or 15 cm from the fence, and the width of the gap was varied. The proportion of trials on which the toad detoured through the gap, instead of attempting to approach the prey directly, grew as the gap was widened. When gap-width is measured in cm (Fig. 7a, left), the starting distance has little effect on the relation between gap-width and the toad's choice of approach. However, when gap-width is measured in degrees subtended at the retina (Fig. 7a, right), the curves for the two starting distances differ significantly ($P < 0.001$). Thus, toads behave as though they measure the real width of a gap, whether they use it for a direct approach or for a detour.

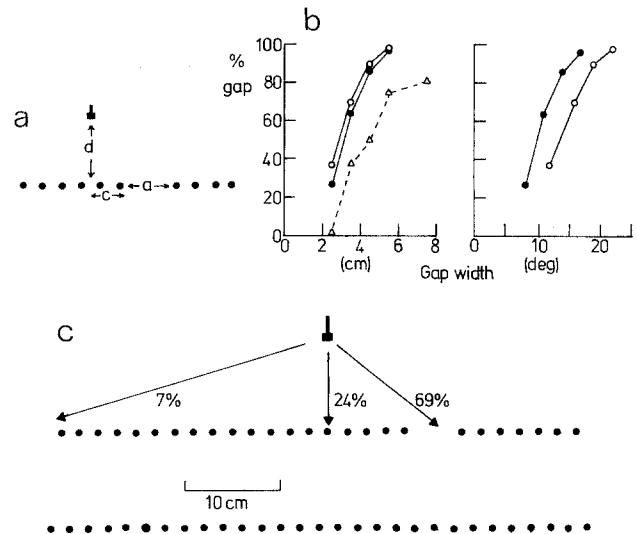


Fig. 7a-c. Approaches to offset gaps. **a** Plan view of position of fence and toad. Prey is positioned directly in line with toad's long axis and 12 cm behind fence. Fence is 60 cm long. **a** width of gap; **c** distance by which gap is offset, **d** distance between toad and fence. **b** % trials on which toads approach gap plotted against gap-width. *Left*: gap-width measured in cm. *Right*: gap-width measured in degrees subtended at toad's retina. *Filled circles*: $d = 15$ cm, $c = 4.5$ cm. *Open circles*: $d = 7.5$ cm, $c = 4.5$ cm. *Triangles*: $d = 10$ cm, $c = 8.5$ cm. Toad approaches gap more often, as width increases. Starting distance makes little difference to plot, if width measured in cm, and a significant difference, if width measured in degrees ($P < 0.001$). Thus, for these starting distances, toad behaves as though it estimates the physical width of offset gaps. **c** Double fence with offset gap in front. Despite unbroken rear fence, toad still aims high proportion of approaches towards gap

Gaps offset from the midline are approached less enthusiastically than those providing a direct path. Figure 7a includes data for gaps placed at two distances from the midline. As the gap is moved further away, toads require larger gaps before they are willing to approach them.

Figure 7b illustrates that when a second fence is erected behind the first, toads continue to aim for the gap, undeterred by the extra barrier separating them from their prey. These similarities between offset gaps and those in line with the prey allow one to use offset gaps to probe further what toads appreciate about the rear fence.

Do Toads Notice Gaps in the Rear Fence?

If toads see the individual fences which compose a double fence as distinct entities, they should also detect gaps in the rear fence. Two types of test were run to see whether they notice such gaps. In the first, toads approached an unbroken front fence with a gap in the back fence set to one side of the midline. The animals' performance was somewhat erratic. In one set of experiments toads aimed directly for the gap on a substantial proportion of trials (30%), indi-

cating that they do see gaps of this kind. However, when the test was repeated the following year, the frequency of trials aimed at the gap was too low to be significant.

A more reliable method of showing that toads notice gaps in the rear fence turned out to be the way in which such gaps bias the toad's choice between two symmetrically placed gaps in the front fence. One arrangement can be seen in Fig. 8a. Toads usually aim for one of the gaps in the front fence, and on the majority of trials they choose the gap which lies on the same side as the gap in the rear fence. The angular separation between gaps in the two fences seems unimportant. Several angular distances (as viewed from the toad's starting point) have been tried, and the toad's choice was always biased to the side of the rear gap.

Although this last result makes it unlikely, it might still be argued that toads do not notice gaps in the rear fence, but that they measure the density of bars resulting from the superimposition of the two fences, and that they are drawn to the gap embedded in an area of relatively low density. This possibility was tested directly with a single fence in which were two symmetrically placed offset gaps, one flanked by thin, high density palings, the other by thick, low density ones. Toads showed no preference for one gap over the other.

The argument so far is that toads behave stupidly in the situations of Figs. 2 and 3, not because they do not see the rear fence, but because the rules guiding their behaviour are not designed to cope with such complex situations.

Gaps in Line

This section and the next are concerned with what causes a toad to prefer one route to another. A gap's width is one important feature that determines whether a gap will attract a toad's approach. As we will see, other attributes also have a powerful influence on the toad's choice of route and help to account for the way it approaches double fences. In the previous test the animal saw the rear gap between the palings of the front fence. However, when the front and rear gaps were aligned, so that viewed from the toad's starting point they fell on the same line of sight, the rear gap acted more powerfully in steering the toad's approach. This can best be shown when the toad faces two gaps in the rear fence; one in line with a gap in the front fence, the other not (Fig. 8b). The toad then prefers to approach the side on which there is a clear path through the two fences.

For the tests illustrated in Fig. 8a and b the prey was placed 12 cm behind the rear fence. Should the

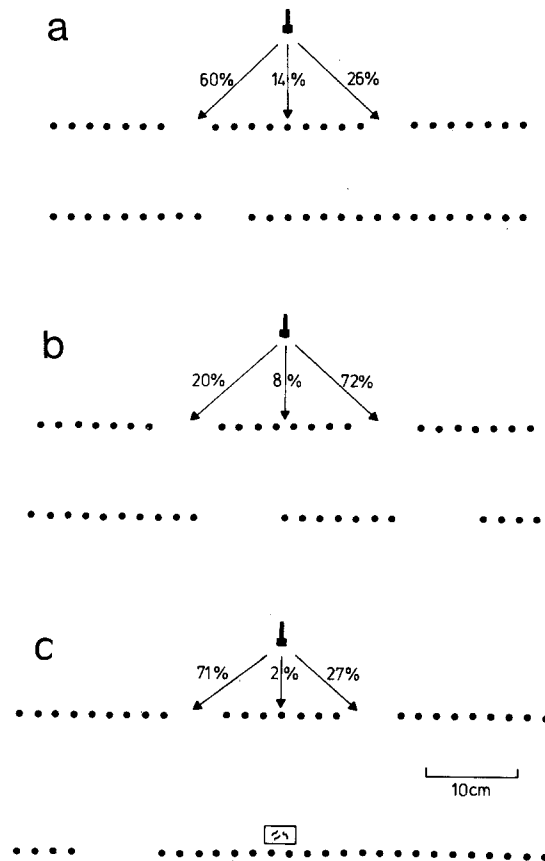


Fig. 8a-c. Approaches to double fences with symmetrically placed offset gaps in front fence and various offset gaps in rear fence. **a** Single offset gap in rear fence. Prey in line with long axis of toad, 12 cm behind rear fence. Toads tend to approach gap in front fence on same side as gap in rear fence, indicating that they see the rear gap. Note in this and all such asymmetrical tests, toads were tested with asymmetrical gap positioned to left on some trials and to right on others. **b** Two gaps in rear fence. On one side the toad views gap in rear fence through the gap in the front fence and, on the other side, the rear gap is seen through the palings. Prey 12 cm behind rear fence. Approaches are strongly biased to side on which gaps in two fences are aligned. **c** Single fence in rear fence aligned with front gap on one side. Separation between fences 15 cm. Prey is 2 cm in front of rear fence. Nonetheless, toads are still biased towards aligned gaps

prey be placed in front, as in Fig. 8c, the toad is still biased to the side of a gap in the rear fence, although such a bias is now of no help in reaching the prey. A more extreme version of Fig. 8c was also tested. In this case (not illustrated) the fences were separated by 20 cm and the prey was positioned 7.5 cm in front of the rear fence. Toads were equally strongly biased toward the gap through which could be seen a gap in the rear fence. 68% of the approaches were aimed at the gaps in line, 9% at the gap on the other side, and on 23% of trials toads directed their approach directly at the prey. This suggests that toads have not computed which side provides an easier path to their prey. It is simply that certain

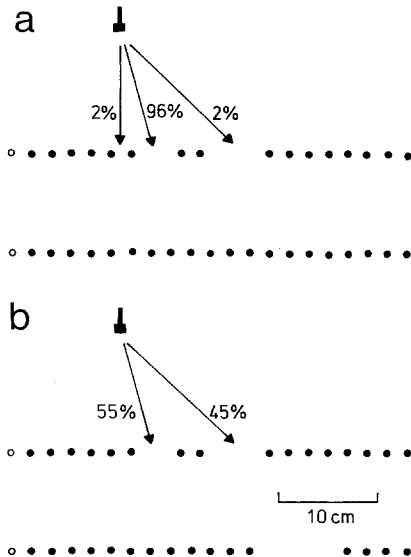


Fig. 9a, b. Approaches to double fence with two gaps in front fence, to one side of midline. Prey positioned in line with toad's long axis, 12 cm behind rear fence. **a** No gap in rear fence. **b** Gap in rear fence viewed through more peripheral of two gaps in front fence. Fences continue for 14 cm to left of open circles. In **a**, toads approach the nearer gap on almost all trials, indicating that the proximity of the gap to their long axis and/or prey is a powerful influence. In **b** rear gap has considerably reduced this bias

gaps (for instance those in line) are more powerfully attractive than others.

Choosing Between Gaps

The previous section showed that toads preferred to approach gaps which continued through both fences over gaps which were just let into the front one. This preference leads one back to the question: why should they then aim for gaps in the front fence when there is an easy path to the side, as they do in the situation of Figs. 2 and 3? The answer is that, when a toad faces a fence with two gaps, it is drawn more strongly by the one that is closer to its midline and to its prey.

Figure 9a shows the toad's response to a double fence with two gaps in the front fence to one side of the midline. Approaches were almost all directed towards the nearer of the two gaps. This bias is significantly reduced ($P < 0.001$) by inserting a gap in the rear fence in line with the more peripheral of the two gaps (Fig. 9b). But the preference is not reversed. Proximity is thus a very powerful influence.

In order to assess how much of the effect is due to the proximity of the gap to the midline and how much to its proximity to the prey, the two factors must be dissociated. In the previous tests, toads were lured into position and faced the prey, before deciding how to deal with the fence. They were now asked

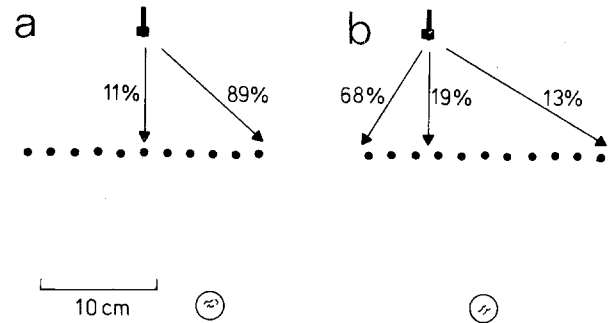


Fig. 10a, b. Approaches to single fences with toads positioned so that they do not face the prey. **a** Toad faces middle of fence with prey offset to one side. Approaches are mostly aimed at edge of fence closer to prey ($P < 0.001$). **b** Prey in line with middle of fence with toad to one side. Most approaches aimed at end of fence nearer to toad ($P < 0.001$). In both cases the results include those for the arrangement shown and for its mirror symmetrical partner. Toads are thus biased both by the position of the gap with respect to their midline and by the position of the prey

to make a choice when the worm was not directly in front. Although sometimes the toads turned to the prey before approaching the fence, often they aimed directly for one or other end of the fence from the position in which they had been left. Only those trials on which toads did not orient towards the prey are included in the results summarised in Figs. 10 and 11.

When toads face the mid-point of the fence and the prey is located to one side (Fig. 10a), they tend to detour round the edge that is closer to the prey. Conversely, if the prey is behind the centre of the fence and toads are positioned slightly to one side, facing the fence head on, approaches are aimed at the edge nearer to the midline (Fig. 10b). The experiment was also repeated with the toad starting at the same position, but with the prey shifted some 2 cm closer to the further edge. This meant that, from the toad's starting position, the angular separations between the prey and each edge were equal. In this case also (not illustrated), toads aim a significantly ($P < 0.01$) greater proportion of approaches at the edge closer to their midline. These tests demonstrate that the toads' choice is governed both by the proximity of the edge to its midline and by the position of the prey. However, they do not establish whether toads measure the distance between edge and prey, and choose the shorter, or alternatively whether they are drawn to the prey and consequently that their approach is biased to the end of the fence lying on the same side of their midline.

One way of tackling this problem is to have two gaps on the same side of the midline, with prey positioned closer to one of them. Toads looked obliquely towards a fence with two gaps to their left and with

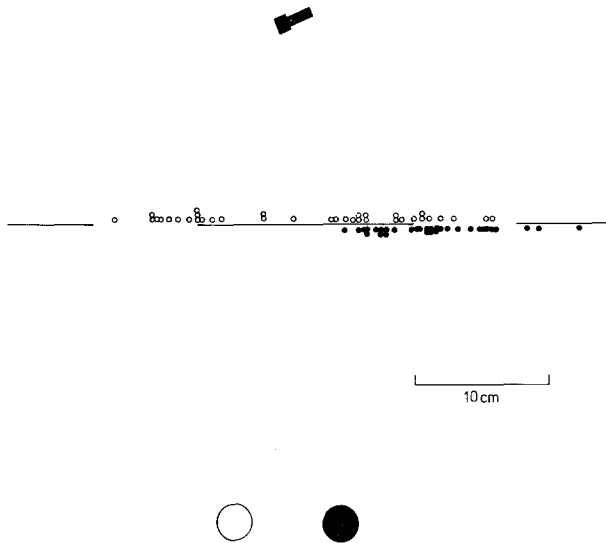


Fig. 11. Direction of approach when toads face fence obliquely. Fence indicated by *line*. Prey are placed either at position of *large open or filled circles*. *Small open and filled circles* show approaches to those two prey positions. For each approach, a *line* is drawn passing through the head at the start of the approach and at the end of the first stage. *Circles* show the intersection of this line with the fence. Approach directions differ for two prey positions: with prey to right, toads usually aim for gap that is closer to prey, but with prey to left toads aim for both gaps. It is concluded that the toads' approach is in part influenced by distance between prey and gap

the prey closer to one or other of the two (Fig. 11). Each approach was recorded on videotape and the starting and finishing positions noted. For analysis, a line was drawn from the midpoint between the eyes at the start of an approach to the midpoint between the eyes at the end. The intersection of this line with the fence for each approach is shown by the open and filled circles in Fig. 11. The small open circles record approaches with prey in the position marked by the large open circle, the small filled circles mark approaches with the prey position shown by the large filled circle.

The results are odd. Toads consistently make for the more peripheral gap when prey is closer to that. However, approaches can be directed at either gap when the prey is nearer to the other one. Nonetheless, the toads' behaviour does depend on prey position and to some extent they are drawn to the gap that is closer to the prey, suggesting that distance between gap and prey is one factor influencing approach direction. We are still left with the possibility that the toad is also pulled towards the side on which the prey lies, and that other things being equal, the toad will direct its approach to gaps on that side of its midline.

To summarise this section: two factors have been uncovered which influence a toad's choice of gap or

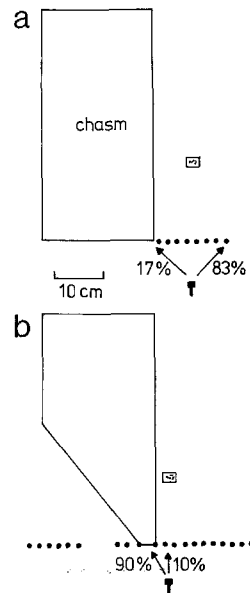


Fig. 12a, b. Interaction between fence and chasm. **a** Chasm to left or right of fence. Toads usually approach other end of fence, so avoiding chasm. **b** Two gaps in fence to one side of toad, with chasm arranged so that it is seen through the closer gap, but not the further. Fence continues for a total of 30 cm on the other side. Despite chasm, toads aim most approaches at closer gap

edge: the gap's proximity to the toad's midline and the gap's proximity to the prey. Between them, they are quite sufficient to mislead the toads into the 'cage' shown in Fig. 3.

Chasms and Fences

Chasms or holes in the ground are treated very differently from fences. If they are deep but not too broad, toads leap over them to reach prey on the other side. However, if they look too wide to jump, toads almost never detour round them, but merely stop at the edge or turn away, even when the side of the hole offers a clearly visible alternative path (Lock and Collett 1979). Nonetheless, chasms do influence the direction of a toad's detour. When a chasm is situated to one side of the fence, as in Fig. 12a, toads mostly detour to the other side.

Despite this strong bias, a chasm does not alter the toads' preference for gaps close to its midline. In the test illustrated in Fig. 12b, a chasm could be seen through the closer gap, but not through the further one. Toads usually approached the closer gap. Of the few approaches that were directed elsewhere, none were aimed at the further gap.

Interpretation of the interaction between chasms and gaps is difficult, and one should beware of concluding that the toad sees the chasm as blocking a

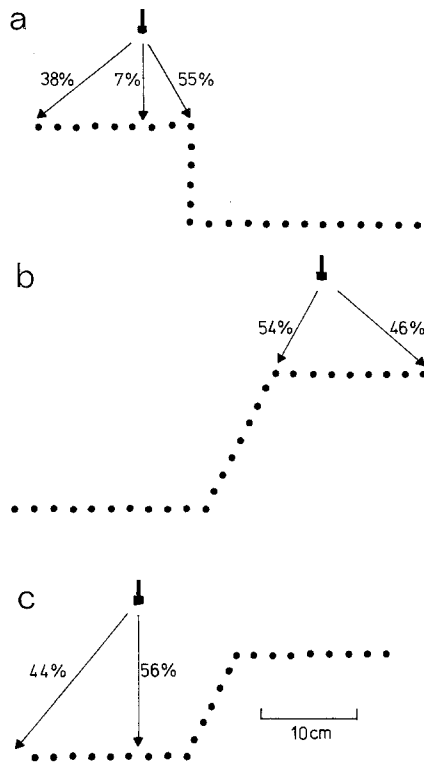


Fig. 13a-c. Approaches to fences which change depth. Prey is 10 cm behind rear fence in line with toad's long axis. **a** Right angle corner with fence turning away from toad. Many approaches aimed at corner. **b** 60° angle. Last 14 cm of rear segment of fence is not shown. Toads also aim many approaches at corner. **c** 60° angle. Toad placed so that angle brings fence towards toad. In this case no approaches aimed at corner

particular detour. The chasm may just make the toad avoid an approach to that side.

Single Fences with Change of Depth Plane

The way toads negotiate double fences emphasises that they are attracted towards points in the fence that do not necessarily provide free passage to the prey. This is also brought out by their behaviour when a single fence abruptly changes its depth plane. Toads will then often aim for the point at which a straight fence bends away from them (Fig. 13a and b), but they never approach corners, if the fence changes direction towards them (Fig. 13c). As a control experiment toads can be positioned asymmetrically in front of a straight fence of the same length. They then very rarely detour round the further edge.

The detection of such a point of inflection suggests that the animal not only perceives the positions of each individual paling, but also to some extent the direction in space of a row of them. In a normal environment inflections of this kind presumably indicate the corner of an object such as a boulder blocking

their way. It is a good strategy to aim for corners, since they are likely to point to a path round.

Discussion

Two somewhat contradictory facets of spatial vision in toads have been stressed here. The first is that toads know a great deal about the spatial layout of their environment. It had been found earlier that *Bufo viridis* (Lock and Collett 1980) behaves as though it appreciates the real width of fences and of gaps within them. The tests with double fences imply that toads are also able to segregate information from different depth planes: a paling fence in one plane does not prevent the detection of gaps in another. Moreover, their decisions and actions show that at any one time, toads may be influenced by several spatial measurements, which can be obtained from different depth planes. For instance, the path taken when negotiating a fence depends on the length of the fence, the position and width of any gap in it, and the distance between fence and prey.

The second aspect of their spatial vision is that toads are bad at formulating plans of action which require them to integrate the spatial information which is at their disposal. They can answer questions like: Is this gap passable? How far is the prey? Does it lie behind the fence? But they do not appear to have the flexibility to combine such measurements in order to compare the path length of different routes, for instance, or to reject routes that do not provide an unbroken path to the prey.

This inability is seen very clearly in the tests with double fences, when a toad, by rigidly following the rule: 'aim for the nearest gap', fails to choose the optimal path and is then trapped between the two fences. It isn't that the rear fence is not detected, or that the toad is unaware of the position of the prey relative to the fence. Tests have shown that the toad does notice these things. Where it seems to fall down, is in understanding the consequences of making a particular approach. One question for the future is whether a toad is any better at route planning in other situations, such as returning home or going to a favourite foraging spot. It will be of some interest to examine the powers of spatial reasoning of other animals with somewhat more highly developed fore-brains, using similar methods, to ask if they are able to judge the quality of a potential route, or whether, like toads approaching prey, they blindly apply a limited set of procedures.

Undoubtedly, there are more factors to be identified that govern how a toad negotiates barriers. Nonetheless, even a partial list gives a flavour of the animal's mode of operation. Its approach toward prey

positioned behind a paling fence can be roughly summarised as follows. Aim for a gap in the barrier. (A gap in this case also includes the ends). If there is a choice, select the most salient. If there is no suitable gap, aim for the prey.

Direct support for the hypothesis that the toad's choice of approach depends simply on the relative attraction of the available gaps comes from Fig. 9. Here it is shown that the toad's preference for a closer gap can be reduced by increasing the salience of a more peripheral one. Several features of a particular gap add their own contributions to its overall attraction. The gap's width and its proximity to the prey and to the toad's long axis are the ones that the present results have emphasised.

A second fence does not, on the face of it, complicate matters. A gap in the front fence is still seen as a gap, but less attractive than one extending through both fences. Although these rules are insufficient to solve the problems set by double fences, in simpler situations they will often be quite adequate to bring a toad efficiently to its prey.

Set out in this way, the toad's choice of approach is reminiscent of the way it selects which prey to aim for, should several move simultaneously within its visual field. Its preference is then for prey that are a short distance away and close to its midline (cf. Ingle 1976b). One way of modelling prey choice, as Didday (1976) and Lara and Arbib (1981) have done, is to associate with each prey item a signal of a size which depends in part on the prey's position – signals are stronger for prey items perceived to be close. Inhibitory interactions then limit the toad's response to the strongest of these signals. The behavioural outcome of such a choice is an approach made in a particular direction. This is most naturally specified in terms of radial coordinates originating at the animal's head, corresponding, for instance, to the coordinate system of the sensory-motor map found on the surface and in the deeper layers of the tectum of many species (Ingle and Sprague 1975).

While such a general scheme can probably account for the way toads select between alternative approaches when confronted with a barrier, their three-dimensional perception of the situation demands a more elaborate representation than that provided by a two-dimensional map of the kind seen in the tectum. In the first place, a toad, when assessing the width

of a gap or its position in the fence, seems to be aware of the real size of the fence and of gaps within it – small angular separations at long distances are seen as equivalent to large angular separations at short distances. A toad's response to double fences also emphasizes the need for us to understand its neural representation of objects in depth. Not only are the two fences seen in separate depth planes, but there are also interactions which depend on the depth relationship between them. Thus, both fences exert an influence on the toad's behaviour, but that of the front fence is stronger. Gaps in it are more powerful in attracting a toad's approach than those in the rear. And, somehow, the front fence, even with very wide gaps, is capable of partially suppressing the toad's response to the rear one.

Acknowledgements. I thank Michael Arbib, David Finch and Michael Land for their comments on the paper, Jo Harper for typing and the Nuffield Foundation for financial support.

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