BLACK AND WHITE PREFERENCES IN THE FROG, *RANA TEMPORARIA*, AND OTHER ANURA

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INTRODUCTION

A strong visually determined white preference has been demonstrated for many Anura when they are given a choice of going toward stimuli of different intensity, or of turning toward or away from a light source (Pearse, 1910; Muntz, 1962*b*). This preference is probably mediated by a system of 'on' fibres projecting to the diencephalon (Muntz, 1962*a*, *b*) and dependent on the development of the green rods of the retina (Muntz, 1963*a*, *b*).

However, when frogs were tested in a small jumping stand designed by Mrosovsky (1964) they showed a strong and unexpected black preference; the same was found using a Y-maze. These observations are reported here, together with attempts to discover some of the conditions that determine the white or black preference of Anura.

(1) *Experiments giving black preferences in the frog*

Methods

Two forms of apparatus were used. The first was a jumping stand described by Mrosovsky (1964). The animal was placed on a small light-grey platform. A transparent cover prevented escape upwards. By jumping forward a frog could drop into one of two water compartments, each surrounded by interchangeable panels, painted matt black or white. The drop from the platform into the water compartments made it easy to score when a choice had been made.

The second apparatus was an uncovered Y-maze made of frosted plastic (Perspex) containing water. The starting arm was 2 ft. long and 6 in. wide. At the choice point there were two arms, 1 ft. in length and 6 in. wide, placed at angles of 120° to the start arm; in these were inserted painted black and white panels covering the floor, walls and the ends of the arms. The maze was 1 ft. high and the water 4 in. deep. A frog was dropped into the water near the end of the starting arm. When more than half its body was in the black or the white arm a choice was considered to have been made. Usually the animals entered one or other arm completely.

Both pieces of apparatus were in a room illuminated by daylight and by a 150 W. bulb. The water temperature was about 20° C. in both cases. No particular measures were taken to adapt these animals to standard backgrounds. During the tests the animals were on a window bench in glass containers. Direct sunlight did not fall on the bench.

Fifty-nine *Rana temporaria* were obtained from dealers and tested within 36 hr. of arrival in the laboratory. Each frog was given eight trials. For half the animals the first four trials were in the maze and for the other half in the jumping stand. Black and white were presented equally often for each animal on the right and left of each apparatus in a randomized order. If no choice was made within 2 min. the trial was abandoned. The intervals between trials were approximately 15 min.

Results

There was no obvious order effect as regards which apparatus was used first, so the scores for a given apparatus were combined. Table 1 shows that for both situations there was a strong black preference, whether the total number of responses was considered, or whether each animal was classified on the responses it made as preferring black, white, or being without preference. There were no clear sex differences (see Table 2).

<div align="center">Table 1</div>

	Jumping stand	Y-maze
Number of black choices*	146	161
Number of white choices*	28	23
Trials abandoned after 2 min.*	62	52
Number of frogs going more to black than white	45	51
Number of frogs going equally to black and white	6	4
Number of frogs going more to white than black	3	2
Number of frogs not jumping	5	2

<div align="center">* Out of possible 236.</div>

<div align="center">Table 2</div>

	Jumping stand (%)	Y-maze (%)
Males	83	91
Females	85	86

Total of black choices expressed as a percentage of all choices made. There were twenty-eight males and thirty-one females.

<div align="center">(2) *Observations on other amphibia*</div>

Table 3 gives the results for various other amphibia tested in the jumping stand and maze in conditions similar to those described above. The past history of these animals was unknown; most of them had been in the laboratory for some weeks. There is no doubt of a predominant preference for black in the four species of Anura tested.

However, there was some indication that *R. esculenta* under these conditions may prefer black less strongly than *R. temporaria* (Table 3). And, when another ten *R. esculenta* were tested in another experiment in the jumping stand with a choice of blue or black painted surrounds to the water compartments, only fourteen out of the twenty-seven responses made were to the black, compared to thirty out of thirty-nine for ten *R. temporaria* tested at the same time.

(3) *Effects of altering jumping-stand conditions*

The most obvious difference between the conditions of the experiments reported above giving a black preference, and those of Muntz (1962*b*) and other authors giving a white preference, is that of the illumination level in the starting area. In the present experiments the frog made its choice from an illuminated platform, open except for a transparent cover (see p. 865). An experiment was carried out, therefore, to see if the black preference found under these conditions would be replaced by a white preference if the frog made its choice from a dark area. This was done by substituting

Table 3. *Black and white preferences of various Anura*

Species	Apparatus	No. of animals tested	No. of trials per animal	Black choices	White choices	Trials abandoned after 1½–3 min.	% Black choices
Xenopus laevis laevis	Y-maze	10	4	25	3	12	89
Bufo bufo	Y-maze	3	4	7	3	2	70
Rana esculenta	Jumping stand	8	2	10	4	2	71
R. esculenta	Jumping stand	3	4	10	2	0	83
R. esculenta	Y-maze	3	4	9	3	0	75
R. temporaria	Y-maze	6	4	23	0	1	100

Table 4. *Black and white preferences of* Rana temporaria *jumping from a covered or illuminated starting stand*

	No. of frogs	No. of black choices	No. of white choices	% Black	No. of trials abandoned after 2 min.
Covered stand	12	25	8	76	15
Illuminated stand	12	33	7	83	8

Table 5. *Effects of forcing trials on black and white preferences of* Rana temporaria *using covered or illuminated stands*

		Unforced trials				Forced trials after 2 min.			
	No. of frogs	No. of trials	Black choices	White choices	% Black	No. of trials	Black choices	White choices	% Black
Covered stand	12	24	23	1	96	24	12	12	50
Illuminated stand	12	44	40	4	91	4	4	0	100

an opaque cover for the usual transparent one and turning off the room light. Some light was of course reflected off the stimulus panels into the starting area. The opaque cover was placed over the stand as the frog was put in. Apart from this and from the fact that the conditions were standardized by light-adapting the animals for 24 hr. before testing, the experimental procedure was the same as that described on p. 866. Each animal was given four trials only. Table 4 compares the results for twenty-four *R. temporaria* with the dark and the illuminated starting area. The percentage of black choices made under both these conditions is almost the same. The relatively dark starting did not give a white preference. However, almost twice as many trials had to be abandoned with the dark start because the animals failed to jump within

the allotted 2 min. Another experiment was therefore carried out in which the frogs were forced to jump.

To force the frogs forward and out of the starting area a curved plaque was fitted against the back wall of the jumping platform. The experimenter moved this rapidly forward by means of an attached rod when a frog failed to jump in 2 min. Apart from the forcing, the experiment was the same as that just reported. Fresh *R. temporaria* were used. Table 5 gives the results.

There is some variability in the number of frogs that do not jump within 2 min. between the animals shown in Table 4 and those in Table 5 (see also Table 1). This could be a reflexion of geographical differences because subsequent investigation showed that the frogs of Table 4 came from Ireland, while those of Table 5 came from Germany.

However, in spite of the variability in the number of trials abandoned these experiments show that when jumping spontaneously from a darkened stand (mean latency = 48 sec., compared to 13 sec. for unforced trials from illuminated stand for animals from Table 5) the black preference, found in the experiments already reported, again occurred. But when the frogs that had not jumped were forced, they went into the black and white compartments equally. This 50 % black on the forced trials might be due to a reduced black preference, or to forcing eliminating choice on the part of the frog. The forced trials from the illuminated stand, all to the black, suggest that the frog does still choose when forced, but a greater number of such trials would be needed to establish this. Moreover, in those experiments with the covered stand it was sometimes noticed that a frog might already have its head over the edge of the stand pointing directly towards the side it eventually went into when forced.

(4) *Effects of forcing and lighting conditions on phototaxis and associated colour preferences*

In the experiments described above, darkening the starting box reduced the black preference when the animals were forced. But the white preference found by Pearse (1910) and Muntz (1962b) still did not occur. It is possible that the starting area was still not as dark as those used by these authors in that, although covered on top, it was painted light grey. Therefore a further experiment was run in which the starting area was painted black as well as being covered. Also, because it has been shown in *Xenopus* tadpoles (Wheeler, 1956) that previous adaptation to different lighting conditions affects phototactic behaviour, the animals in the present experiments were adapted to one of two extreme lighting conditions by being kept before testing either in a brightly lit white box or in a black box in the darkness. At the same time as testing preferences between stimuli of different intensity, investigations of colour preferences were made using the type of apparatus now shown to give negative phototaxis. A blue preference goes with the positive phototaxis (Muntz, 1962b), and it is likely that activation of the diencephalic projection system is the mechanism underlying this behaviour (Muntz, 1962a). Should an aversion to blue occur in the negative phototaxis situation, it would suggest that the same mechanism is being activated in these circumstances, but that there is a reversal of instructions as to what should be done about that activation.

METHODS

A modified version of the original jumping stand was made (Fig. 1). A cold-cathode tube mounted above the starting platform provided illumination but did not raise the temperature of this space above about 25° C. Two painted panels provided the stimuli. Spectro-photometric reflectance curves of the paints were provided by the National Physical Laboratory, Teddington, Middlesex. Both paints reflected light
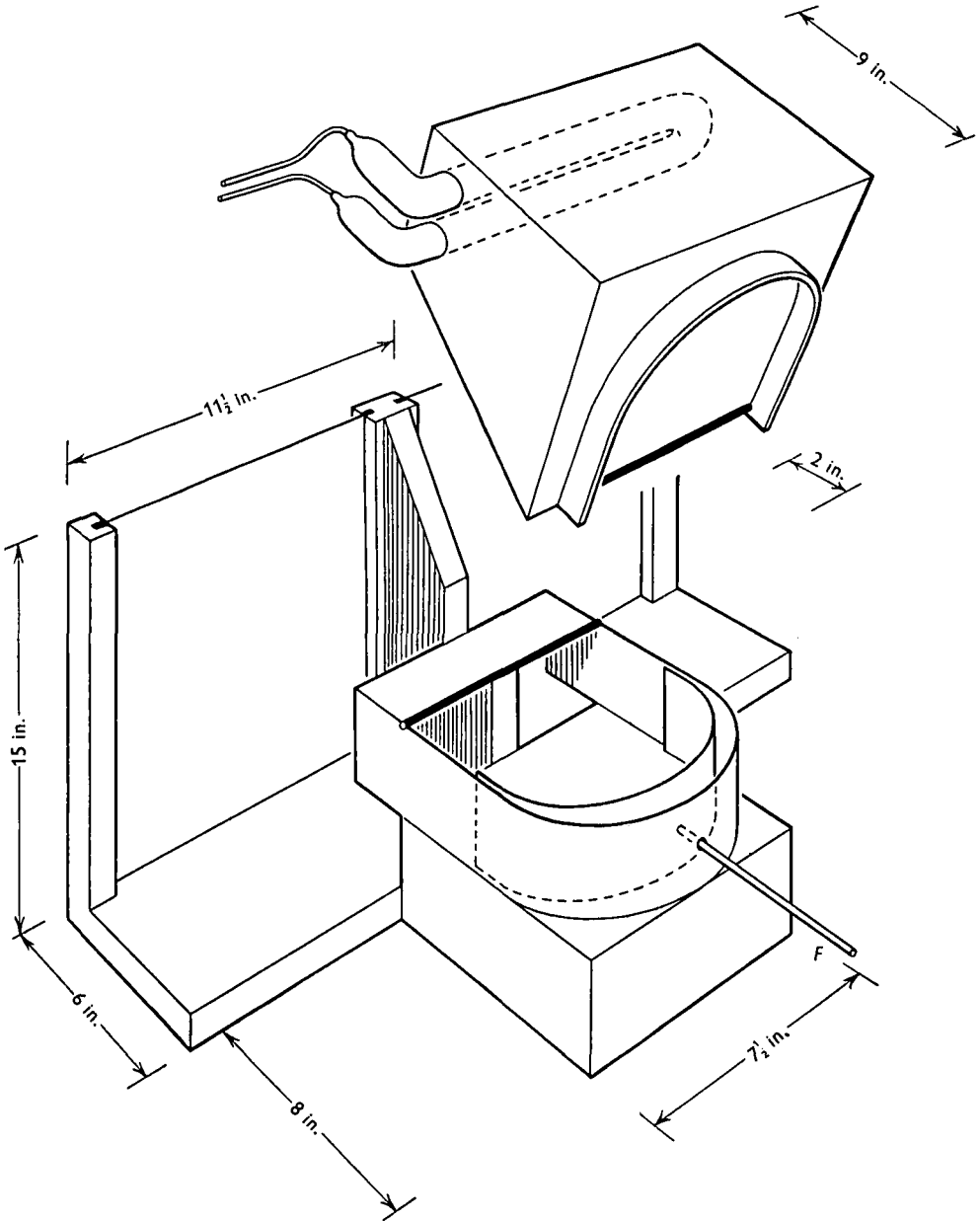

Fig. 1. Diagram of frog jumping stand. *F*, forcing rod; for details see text.

throughout the visible spectrum. In the case of the blue the maximum reflectance was at 470 mμ, and in the case of the green at 510 mμ. These panels were illuminated by means of 200 W. clear glass tungsten-filament bulbs, and the luminance of the panels was varied by altering the distance of the bulbs from them.

Distances for the bulbs were calculated to yield three conditions: (1) green and blue of equal luminance, (2) green brighter than blue, and (3) blue brighter than green. The colour temperature of the source was assumed to be 2878° K. throughout in the calculations. For condition (1) it was further assumed that the photopic sensitivity of the frog is the same as that of the standard C.I.E. observer.

Table 6. *Approximate absolute luminances under the different stimulating conditions*

	Luminances (ft.-lamberts) of the		Ratio of brighter to dimmer
Condition	Blue	Green	colour
Green brighter than blue	0·9	8·9	9·9
Green and blue of equal luminance	8·9	8·9	1·0
Blue brighter than green	14·0	2·9	4·8

In conditions (2) and (3) the distance of the bulbs were so calculated that the dimmer colours reflected less light than the brighter colour throughout the visible spectrum. Thus in condition (2) the green panel reflected more light than the blue panel at all wavelengths, even at 470 mμ (where the blue was maximally reflective), and similarly in condition (3) the blue reflected more light than the green even at 510 mμ. The purpose of this arrangement has been described in detail in Muntz (1963*a*, *b*). Briefly, the arrangement serves to distinguish blue discrimination as such from spectral sensitivity; if animals are positively phototactic but prefer blue to green under condition (2), this cannot merely be a case of heightened sensitivity in this part of the spectrum since the green panel reflects more light than the blue panel throughout the spectrum. A similar argument can be applied to condition (3): if animals are negatively phototactic but nevertheless prefer the blue to the green, this implies choice of blue as a colour.

Approximate absolute luminances were also calculated, assuming that a 200 W. bulb produces 1970 lumens (Cotton, 1957). Results of these calculations are shown in Table 6.

Twelve batches, each of sixteen frogs, *R. temporaria*, all males, were obtained from a dealer on different days between 25 June and 1 August. On arrival in the laboratory half of each batch was housed in a tank within a large white cardboard box lit with a 40 W. bulb about 27 in. above the frogs. The other half of each batch of animals was enclosed in a black cardboard box with no lamp. Running cold water through the tanks kept the frogs in both boxes at the same temperature to within a few degrees centigrade (21 ± 4° C.). After 24 hr. (plus or minus 1 hr.) adaptation in these boxes, the experiment was begun. The procedure for each batch was the same and the testing always took place between 1.0 and 5.0 p.m.

Three different choices were presented: green versus blue of greater intensity, green versus blue of equal intensity, green versus blue of lesser intensity. There were

two conditions in the starting box. In the first, the light above it was on and the inside of the box and all other surfaces visible to the frog were painted matt white. In the second, the light was off and all the surfaces were painted matt black. Nevertheless, light reflected from the stimulus panels gave some illumination inside the black starting box. Each batch of frogs was tested on one of the stimulus conditions and one of the starting-box conditions only. With six batches three stimulus choice conditions were tested against both starting-box conditions. Thus the design was a 2 by 2 by 3 analysis of variance design with two adaptation conditions, two starting-box conditions, and three stimulus-choice conditions. There were two replications giving a total of sixteen separate animals per cell.

Each animal was placed in the centre of the starting box. If no response was made within 2 min., the rod and attached metal plaque (see Fig. 1) were moved forward by the experimenter and a 'forced choice' scored. Each frog was given four trials. Intervals between trials were approximately 15 min., but were generally longer with the black start than the white because the animals were slower in jumping. The same experimenter handled all the animals.

RESULTS

Table 7 gives the percentage of occasions on which blue was chosen under the various conditions. The figures show that there was no aversion to blue; in fact blue was chosen in preference to green on all occasions except two out of the twelve different conditions. The two exceptions occurred when the green was darker and the frogs were jumping from the white starting area. In the dark starting-box conditions blue was chosen whether it was darker or lighter which, as was pointed out on p. 870, suggests blue discrimination as against spectral sensitivity.

Table 7

	White starting box (%)	Dark starting box (%)
Light-adapted		
Green *v*. darker blue	72*	53
Green *v*. blue of equal intensity	69*	59
Green *v*. brighter blue	45	61
Dark-adapted		
Green *v*. darker blue	69*	67*
Green *v*. blue of equal intensity	53	63
Green *v*. brighter blue	42	56

Percentage of trials (forced and unforced combined) on which the blue was chosen. Scores for each cell were based on sixty-four responses.

* Shows where, for a given cell, the choice for a colour is significant at the 0·05 level, two tailed, on a binomial distribution.

Although there were, therefore, indications of blue preference, the data also show that, other things being equal, the animals usually preferred the darker of two stimuli. This was the case under all conditions except the dark starting-box condition with light-adapted animals, since in all other cases the preference for blue increased as the blue became darker. Considering the light-adapted animals only, the starting-box

condition can be shown to be a factor affecting the animals' light–dark preference. The animals tested with the white starting box showed an increasing preference for blue as the blue became darker, whereas for the animals tested in the dark starting box the reverse was the case. An analysis of variance between the two conditions, scoring whether the darker or lighter of the two stimuli was selected, and excluding the condition of equal intensity, gave an F ratio of 8·2 (df 1, 60); this is significant at the 0·01 level. This difference between the two starting-box conditions only reached significance with the light-adapted frogs; a similar analysis for the dark-adapted frogs did not give an F ratio significant at the 0·05 level.

This experiment therefore confirms the previous experiments reported in this paper, showing that the dark starting box decreases the preference for the darker of two stimuli, although under the conditions used the preference for dark was only reversed under one set of conditions, namely light-adapted animals in the dark starting box.

Table 8

	White starting box (%)	Dark starting box (%)
Light-adapted		
Green v. darker blue	9	58
Green v. blue of equal intensity	9	36
Green v. brighter blue	17	59
Dark-adapted		
Green v. darker blue	14	69
Green v. blue of equal intensity	9	55
Green v. brighter blue	24	66

Percentage of trials that were forced after 2 min. Scores based on sixty-four trials per cell.

Another factor must now be considered: forcing. The results presented so far have been for forced and unforced trials combined. But in the dark starting-box conditions there were many more forced trials than in the white starting-box conditions (Table 8). The animals were staying in the dark starting box for at least 2 min., often on more than 50% of the trials. (The mean latency of all spontaneous jumps from the dark starting box (51 sec.) was also greater than that for all the spontaneous jumps from the white starting box (38 sec.).) It is perhaps better then to think of there being a positive phototropism (turning toward the light stimuli) which is only brought into evidence when the frog is stimulated to move by the rod from the back of the apparatus. It was, unfortunately, not possible to watch the frogs in this situation to confirm definitely to which stimuli they were turning on being placed in the box. Nevertheless, there is an apparent paradox. They tend to stay in the dark starting box much longer than animals tested in the white starting box. Yet the dark starting box gives the greater choice of the lighter of the two stimuli (as discussed above, see also Table 5) of the two starting conditions.

Table 9 shows the choices of the different stimuli that were made by the animals in the forced and unforced trials. The effect of forcing was particularly marked when the animals were choosing between the green and the dark blue stimuli; in every case under these conditions forcing greatly reduced the ratio of blue to green choices. In the case of the light-adapted animals in the dark starting box the preference was

Table 9. *Choice of stimuli on unforced and forced trials*

| | Light-adapted | | | | | | Dark-adapted | | | | | |
| | Unforced | | | Forced | | | Unforced | | | Forced | | |
	Blue	Green	Blue/green	Blue	Green	Blue/green	Blue	Green	Blue/green	Blue	Green	Blue/green
					Dark starting area							
Green *v.* darker blue	20	11	1·8	15	18	0·8	15	5	3·0	28	16	1·8
Green *v.* blue of equal intensity	24	17	1·4	14	9	1·6	18	11	1·6	22	13	1·7
Green *v.* bright blue	18	10	1·8	21	15	1·4	12	10	1·2	25	17	·1·5
					Light starting area							
Green *v.* darker blue	44	14	3·1	2	4	0·5	40	15	2·7	4	5	0·8
Green *v.* blue of equal intensity	43	16	2·7	2	3	0·7	33	26	1·3	2	3	0·7
Green *v.* bright blue	24	29	0·8	5	6	0·8	18	31	0·6	9	6	1·5
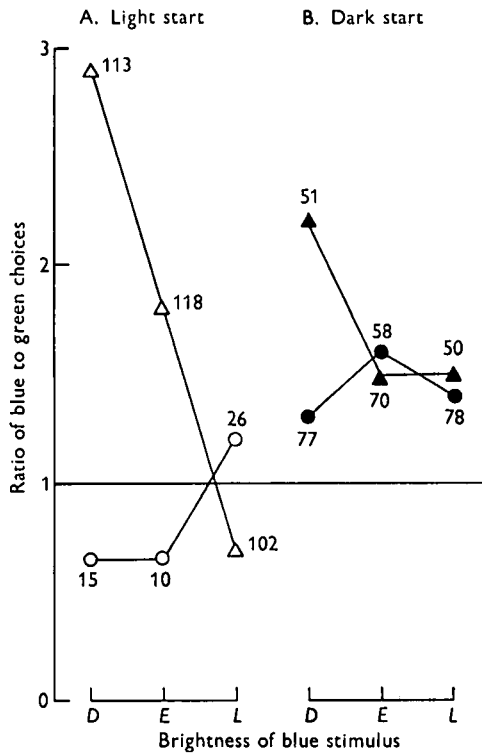
Fig. 2. Effect of forcing. (A) Animals tested with the white starting box. (B) Animals tested with the dark starting box. Circles, trials on which forcing took place; triangles, trials on which animals jumped spontaneously within 2 min. The figures beside each point show how many trials contributed to each point. *D*, dark blue; *E*, blue of equal luminance to the green; *L*, light blue. The horizontal line indicates equal choices of blue and green.

actually reversed; on unforced trials these animals chose the blue (the darker stimulus) more, and on forced trials the green (the lighter stimulus).

These data suggest that forcing decreases the preference for the darker stimulus, as was also shown previously (see Table 5). The rest of Table 9 bears out this conclusion, although the effect of forcing on the other stimulus pairs was not so marked. Thus in the unforced trials there was a tendency to choose blue more the darker it was, indicating a preference for darker stimuli. On the forced trials, however, the tendency was much reduced, and often reversed, indicating a decreased preference for the darker stimuli, or often a preference for the lighter stimuli. Both these tendencies were much more marked under the light starting-box conditions.

The effect of forcing is clearly brought out in Fig. 2, in which data from the dark-adapted and light-adapted animals have been pooled. A second point illustrated by this figure is the greater preference for blue under the dark starting-box conditions: all the points in Fig. 2B lie above the horizontal line, whereas only half the points lie above this line in Fig. 2A.

The results may be summarized as follows. On unforced trials darker blues were preferred to lighter blues irrespective of the starting-box conditions (preference for the darker stimulus), whereas on forced trials the reverse tended to occur (preference for the lighter stimulus). With a white starting box most animals jumped spontaneously within 2 min., whereas with the dark starting box there was a tendency not to jump until forced. The preference for blue was more marked in the dark starting-box conditions than in the light starting-box conditions.

DISCUSSION

Pearse (1910) states that blue is the most effective colour in the production of positively *phototropic* reactions. His animals had only to turn toward a stimulus to score; locomotion was not necessary. The present experiments also suggest that the reaction to light and blueness may be tropic rather than tactic, or to use Pearse's words 'mechanical stimulation furnishes the impulse to locomotion, while the light is effective in determining the direction of the movements'. This would be consistent with Torelle's (1903) finding that in certain conditions frogs may sit in a dark area facing out towards a light source. Forcing the animals out of a dark place should then give a positive reaction to light.

However, in the present experiments a strong positive reaction to light was not found on the forced trials. It appeared rather that forcing often reduced the choices of the darker stimuli to about 50 % (see Tables 5 and 9). This reduction could be due to choice on the part of the frog. But on the other hand, it could be dependent on a forcing procedure that did not give the frog the opportunity to score differently from 50 % between the lighter and darker stimuli. There are some indications that forcing does not prevent the frog choosing (see Table 9, e.g. twenty-eight dark blue to sixteen green scrored on the forced trials from the dark box, which just fails to reach significance at the 0·05 level on a binomial distribution). But to gain further information about the effects of forcing, a re-analysis was made of Muntz's (1962b) data (Table 10). This confirmed the results of the present experiments that forcing (the procedure was slightly different) increased the choice of the lighter of two stimuli. Forcing was

necessary on a large number ($>50\%$) of the trials; this is consistent with the results for the dark starting area in the present work.

But in Muntz's data (see Table 10) there was a definite positive phototaxis on the unforced trials, whereas the darker of the two stimuli was chosen more on unforced trials in the present experiments. There is, then, still some unknown factor (or factors) that must account for this discrepancy on unforced trials between the two procedures. Possibly this may concern the method of handling and the precise way in which the frog is placed in the starting area. The mean latency of the unforced trials from the dark start in the present experiments, as noted above, was 51 sec., while in Muntz's experiment it was <30 sec., because forcing took place after this time. The generally higher level of choices of lighter stimuli in Muntz's experiments might be associated with a greater readiness of his animals to move out of the starting area. In the present work forcing increased the score of the lighter stimuli, but probably this level did not rise above about 50% because the whole level of choices of the lighter stimuli was so low (see Table 1).

Table 10. *Data from Muntz* (1962*b*) *re-analysed to show choices of colours and darkness on forced and unforced trials*

(Each figure is out of a maximum possible of 96.)

	Blue	Blue/ Green	Green	Green/ Yellow	Orange	Red	Darkness	Mean
No. of unforced choices	28	29	18	18	19	18	10	20
No. of forced choices	54	36	24	28	29	20	5	28

The most straightforward result of the experiment on colour preference was the absence of any indication of aversion to blue in the situations giving negative photo-taxis. This demonstration therefore provides no evidence that there is a reversal of the consequences of activation of the diencephalic system described by Muntz (1962*a*). But it does not explain why the diencephalic system is not brought into action. One possible reason could be that in general illumination the on-receptors are already firing strongly and that a white surround to a water compartment, such as was used in some of the present experiments, would not increase the rate of firing sufficiently. However, this explanation does not take account of the possibility that the animal might look away from the darker toward the lighter of two stimuli, in which case the response of on-receptors should be somewhat augmented even in general illumination; or that blinking, which seems to occur often in frogs when they move, should be followed by firing in on-receptors. Nor does it cover the trend for the blue to be chosen more often the darker it was by frogs that were adapted to darkness and tested in the dark starting box (see Table 7).

There seems to be no reason why the on-receptors in the retina that are connected to the diencephalic neurons should not be at least partially activated in some of the conditions in the present experiments giving preferences for darker stimuli. If there is no reversal of the consequences of activating the diencephalic system, then some other mechanism mediating negative phototaxis must be predominating over it. The optic tectum contains cells giving an off-response and it is known that fibres pass from here to the diencephalon (Muntz 1962*a*). Further information about these fibres might be relevant. However if, in addition to a dark starting box, absence of

forcing the frogs (that is presumably absence of excessive fright) is important in bringing out the negative phototaxis, as was the case with the green versus dark blue in the dark starting box, then it may be difficult to investigate electro-physiologically the functioning of the diencephalic system in the appropriate conditions with any method involving the unanaesthetized animal under curare.

It is not surprising that the reactions of the frog to light should be plastic. To have an immutable phototaxis would restrict the animal to limited environments. But the exact value of the preferences under given conditions is less easy to assess. Muntz (1962b) has suggested that a blue preference will be useful to the frog because light over water tends to be relatively blue. The frog will be guided towards the water by its blue preference and positive reaction to light. This may perhaps hold for a frog startled in a covered place, e.g. sitting beneath foliage, but for an animal with cryptic coloration it would perhaps be safer to stay in unexposed places unless actually discovered or touched. Should this occur, escape into the open might be facilitated if the animal was already facing the light (positive phototropism). Once in the open, a black preference, as found in the present experiments, would assist the frog in reaching another concealed area. However, there are probably other complicating factors. For instance, the different results reported here for dark-adapted and light-adapted animals (Table 7) suggests the possibility that at night, during which a frog would become dark-adapted, there are different behavioural priorities.

SUMMARY

1. Conditions are described in which the frog, *Rana temporaria*, selects the darker of two stimuli.

2. Some similar observations are reported for other amphibians.

3. Further experiments suggested that a dark starting area is a factor tending to decrease negative phototaxis. Forcing the frogs from the dark starting area decreased the scores for the darker of two stimuli.

4. No strong positive phototaxis was found in the present experiments.

5. In conditions giving negative phototaxis there is a slight preference for blue over green.

6. These results are compared to previous work and discussed in relation to the possible underlying mechanism and their biological value.

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