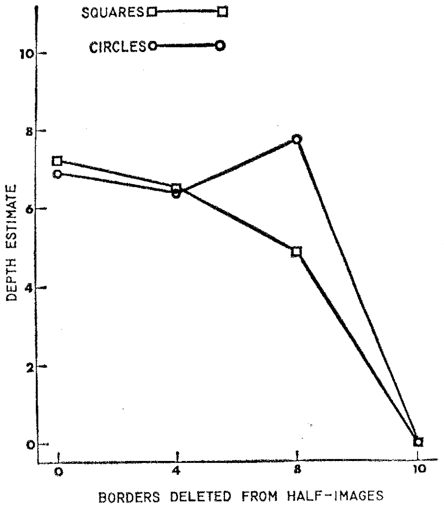

Fig. 2. The mean depth estimates based on eight observers for each experimental stereogram.

mean depth estimates for eight observers for each of the experimental stereograms. The depth estimates remained relatively stable despite the removal of the horizontal borders of dots from the square and circular patterns; however, depth was not reported when the stereograms contained no form disparity and had ten dot borders removed. Anomalous contours were reported *only* when the white planar surface appeared in depth, and none of the observers reported depth when viewing the control stereograms.

To assess the effects of dot configuration (square and circular) and the number of borders removed from each half-image upon the depth estimates, an analysis of variance was computed. The only significant factors were the subject ($F = 12.58$, 7/21 df, $P < .005$) and border deletion effects ($F = 88.09$, 3/21 df, $P < .005$). A Duncan's multiple range test revealed that only the depth estimates for the experimental half-images without any form disparity differed significantly from the other half-images with form disparity ($P < .001$). The slight enhancement of the depth effect for the circular pattern in the absence of the upper and lower quadrants of dots was not significant and was due to the fact that two observers had difficulty in reporting depth for the comparable square pattern ($t = 1.68$, 18 df, $P < .01$). The shape of the forms in depth remained the same regardless of the number of dot borders removed from the disparate half-images.

For those patterns with only vertical dot borders that produced depth, all observers reported that the vertical contours (straight and curved) were much sharper than the contours along the horizontal dimension of the planar surface in depth. The horizontal edges represent a striking example of visual contours in homogeneous space and indicate that contiguous dots in the stereoscopic field are not essential for the contour effects (*6*).

Similar stereoscopic depth and contour effects as reported above were also found with Julesz dot patterns (*1*) and Kaufman letter patterns (*2*) when all of the nondisparate background elements were deleted except for two vertical borders in each half-image.

The present results indicate that neither horizontal dot borders nor monocular recognition of disparate forms is essential for stereopsis and anomalous contour perception in dot and letter matrix targets. However, form disparity which can be produced by shifting laterally a central submatrix of dots (*1*), by superimposing a laterally shifted brightness pattern upon a matrix of nondisparate elements (*2*), or by the selective omission of elements in a visual pattern (*3*) is essential. The disparate form is detected from the combined monocular images and the location of the anomalous contours cannot be specified completely in terms of the characteristics of the change in gradient of the reflected light within the optical array.

The findings with matrix-defined disparate forms can be accommodated by traditional theories of stereopsis provided disparity is extended to include certain properties of visual arrays besides contours (*4*). The fact that with form-disparate stereograms depth is restricted to the corresponding yet spatially disparate feature of the visual display supports this conclusion. Furthermore, data on depth magnitude judgments indicate clearly that perceived depth varies directly as a function of the lateral displacement of the forms (*1, 3*).

That contour can be perceived in homogeneous space (*7*) suggests that new conceptualizations of contour processes are necessary.

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#### References and Notes

1. B. Julesz, *Bell System Tech. J.* **39**, 1125 (1960).
2. L. Kaufman and C. Pitblado, *Amer. J. Psychol.* **78**, 379 (1965).
3. R. B. Lawson and W. L. Gulick, *Vision Res.* **7**, 271 (1967).
4. K. N. Ogle, in *Psychology: A Study of a Science*, S. Koch, Ed. (McGraw-Hill, New York, 1959), vol. 1, p. 362.
5. Details of the Angermeier stereoscope may be obtained from the authors.
6. The stereoscopic effects are visually quite striking and the reader can see them with a hand stereoscope or simply by viewing the dot patterns cross-eyed.
7. T. Shipley, *Science* **150**, 348 (1965).
8. Supported by PHS grant NB 07301-01 to R.B.L., and by NSF grant GY146 for undergraduate research participation.

30 August 1967

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## Total Luminous Flux: A Possible Response Determinant for the Normal Monkey

Abstract. *Thirteen normal monkeys* (Macaca mulatta) *trained to discriminate between transilluminated figures of equal area and different luminance, and consequently different luminous flux, made similar numbers of errors during training on a new problem with the same luminance values but with targets equated for luminous flux. These findings together with results of "critical trials" suggest that the significant cue in the original problem was luminous flux. This behavior is strikingly similar to what has been reported for the monkey following exclusion of the geniculostriate system.*

It is well known that normal monkeys can be trained to discriminate between two figures of equal area (A) that differ in luminance (amount of light per unit area, B) and consequently also in luminous flux (total quantity of light, F) (*1*). Although it has been stated that a "brightness" or "intensity" discrimination (*2*) was established in this case (*3*), the experiment to be described suggests that this conclusion does not apply to all conditions of testing. In fact, there are several possible response determinants for this discrimination when transilluminated targets are used: (i) the absolute dimensions of one or the other stimulus, that is, the selection of one because of its own level of brightness or flux, without reference to the other figure;

(ii) the differences between the two targets in terms of the "more than" or the "less than" type of relationship, that is, the selection of one because it has more or less of a given parameter than the other; (iii) in this latter case, the monkey may be responding to differences in either luminance or luminous flux; (iv) if luminous flux of the targets were the cue, it might act as a parameter of the figures or by producing luminance and flux differences in the background, that is, the testing chamber. Because of this latter consideration, the animal's response in the present report is operationally labeled in reference to the position of the figures and not to the targets per se.

In the course of a study on visually guided behavior after brain lesions (*4*) we evaluated some of the abovementioned response determinants by training 13 normal monkeys on a series of two-choice discrimination problems, by use of the pulling-in technique (*5*). The experimental animal was free in a cage and was dark-adapted before the session was started (Fig. 1). Stimuli consisted of a pair of square apertures located in a plane parallel to the front of the cage at a distance of 38 cm. Their centers were 25 cm apart and 27 cm from the floor. These apertures were transilluminated by a single rectangular source of cool, white, fluorescent light of even luminance. Luminance and area of the stimuli were varied by means of neutral density filters and appropriate masks. Below each aperture there was a hidden food-well that the monkey could obtain by pulling from a thin nylon filament which in turn activated a microswitch connected to corresponding response indicators. In the intertrial period an opaque screen was lowered in front of the cage, the box containing the light source was raised, and both the position of the targets and the reward were changed according to a Gellerman series. All monkeys were given 50 trials per day and trained to a criterion of 90 percent correct responses in 200 trials on two discrimination problems, with the introduction of "critical trials" after each of the tasks was mastered.

The stimuli used for nine of the animals are illustrated in Fig. 2. In the first discrimination problem, figures of the same area differed in luminance and in luminous flux (B-F problem). Square *aB* was 2.10 cm$^2$ and 72.29 ft-lam (77.78 mlam); square *ab* was of the same area and 1.005 ft-lam (*6*). The resultant F values were 0.1636 and 0.0023 lumen respectively. In the second problem, the same *aB* target was opposed to a larger square *Ab* which was 141.60 cm$^2$ and 1.005 ft-lam. Since the luminance difference was the same as in the previous task, the targets now differed in luminance and area (B/A problem) but in an inverse proportion so that the F's were practically equal ($\Delta F/\bar{F} = 0.07$). The placement of the reward was determined by the position of square *aB* in both situations.

After achieving criterion performance on each of these tasks, ten "critical trials" were introduced. In these trials, the same *aB* figure was opposed to a square *AB* that had the same luminance but a larger area (141.60 cm$^2$) and consequently a greater luminous flux value (A-F trials). In fact, the flux relationship was reversed with respect to the B-F problem. While in this latter condition, square *aB* was the one with the greater F, in the A-F trials the same square had the lesser F. In each of these "critical trials" both food-wells were baited and a record was made of the number of responses to the position of *aB* and *AB* targets. The experimental design required the use of a constant order of testing and the same reward contingencies for all animals in order to evaluate the significant response determinants in the B-F problem.

Table 1. Error scores through criterion on the two discrimination problems, and percentage of responses to the position of the small square on ten "critical trials" following each problem. B-F indicates problem with stimuli of equal area differing in luminance and luminous flux. B/A denotes problem with stimuli of equal flux and an inverse area and luminance relationship. A-F represents trials with stimuli of equal luminance differing in area and luminous flux. Monkeys with identifying numbers 400 or below were tested with high photometric levels and those above 400 with low photometric levels. S.D., standard deviation.

| Monkey | B-F | A-F | B/A | A-F |
|---|---|---|---|---|
| 374 | 96 | 0 | 82 | 40 |
| 394 | 48 | 10 | 36 | 50 |
| 396 | 62 | 10 | 24 | 80 |
| 340 | 86 | 10 | 81 | 100 |
| 339 | 89 | 10 | 82 | |
| 398 | 83 | 20 | 61 | 100 |
| 400 | 89 | 30 | 158 | 100 |
| 395 | 128 | 30 | 114 | 90 |
| 341 | 136 | 40 | 60 | 50 |
| Mean | 91* | 17.8† | 78* | 76.3† |
| S.D. | 28 | 13.0 | 40 | 25.6 |
| 443 | 140 | 10 | 161 | 70 |
| 444 | 81 | 0 | 86 | 50 |
| 447 | 66 | 0 | 39 | 100 |
| 448 | 56 | 0 | 62 | 50 |
| Mean | 86‡ | 2.5§ | 87‡ | 67.5§ |
| S.D. | 39 | 5.0 | 53 | 7.9 |

* $t = 0.809$ ($P < .50$). † $t = 6.008$ ($P < .001$).
‡ $t = 0.030$ ($P > .90$). § $t = 5.327$ ($P < .005$).

The other four monkeys in the study were trained with similar problems and "critical trials" with a 1.45 neutral density filter (3.5 percent transmittance) at the source, thereby reducing the B values to 2.78 and 0.035 ft-lam, and the F values proportionately.

Table 1 presents the number of errors on the B-F and the B/A problem, including those made on criterion trials for both groups of animals, together with the percentage of responses to the position of the smaller square (*aB*) made on the A-F trials after each of the problems was mastered. All monkeys reached criterion level of performance on both tasks with the expected amount of variability in error scores among animals.

The analysis of the results obtained at high photometric levels revealed no significant group mean differences between error scores made on the B-F and B/A problems ($P < .40$). It is important to note that these results were obtained despite the fact that the location of the reward was determined by the position of the same target (*aB* square) in both conditions and, moreover, that luminance values were also maintained the same. The luminous flux, however, was equated for the two figures in the second problem.

The results on the A-F "critical trials" introduced after criterion had been achieved on the B-F problem showed that the average number of responses to the position of the smaller square (*aB*) was below 18 percent. More specifically, monkeys that were responding almost 100 percent to square *aB* on the B-F problem, selected the position of the larger square (*AB*) on 82 percent of the trials when confronted with the A-F condition. Following the B/A problem, the response pattern on the A-F trials shifted such that the average number of responses to the position of the smaller square (*aB*) increased to 77 percent. This difference in performance on the A-F trials after mastering one and the other problem was highly significant ($P < .001$).

Analysis of the data from the group of animals tested with low photometric values revealed results similar to those

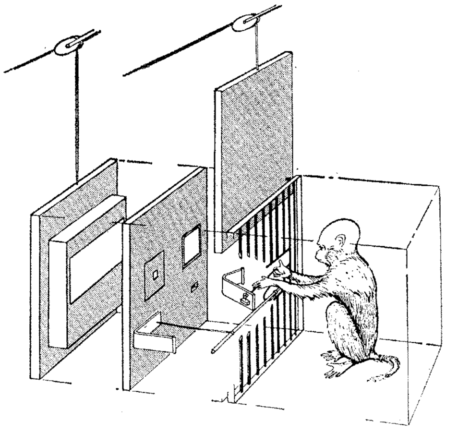


Fig. 1. Testing apparatus, with opaque enclosure indicated by broken lines, showing, from left to right, the light source, panel containing the stimulus apertures and movable food-wells, opaque sliding screen, and animal cage. A portion of the front of the cage has been removed in this drawing for clarity.

presented above. Moreover, error scores on the B-F and the B/A problems were practically equal, and the responses to the position of the smaller square (*aB*) on A-F trials following the B-F condition was only 2.5 percent. Comparison of performance of both groups of animals on each task revealed no significant difference for the two photometric levels used (B-F problem, $P < .80$; B/A problem, $P < .80$).

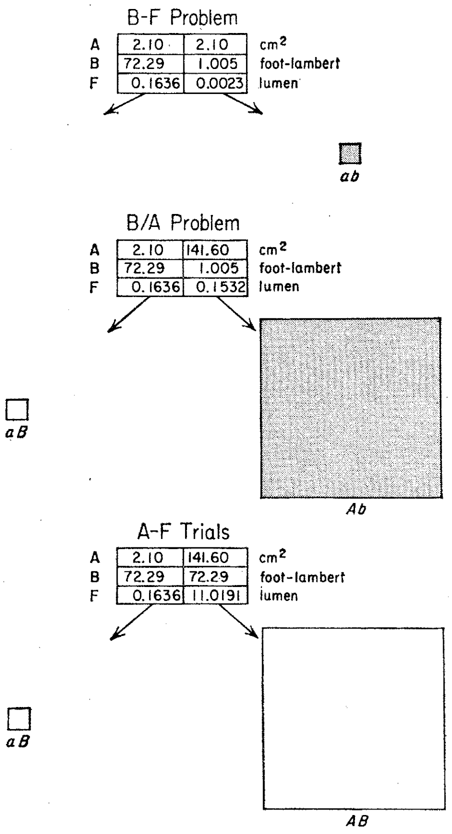
The present results may serve to define some of the response determinants for the normal monkey on what has been traditionally considered as a brightness discrimination. Our B-F situation is an example of such a discrimination problem, and some of the stimulus parameters that might have been used to solve this task can be ruled out in view of the animal's performance on A-F trials and the B/A problem.

First, the absolute dimensions of the stimuli can be eliminated because the same stimulus (*aB* square) which determined the position of the reward in the B-F condition was available and baited in the A-F trials, yet the animals did not respond to the position of this figure (*aB*) but rather to the other (*AB*). Moreover, there was no decrease in the number of errors made in the B/A problem, even though it followed the B-F problem and the identical figure (*aB*) determined the rewarded position in both. This result is compatible with other reports showing that animals tend to use the relationship between stimuli to make their selection (*5*).

Second, normal monkeys appear to ignore the luminance of the figures, and consequently their brightness, to solve the B-F problem (*7*). This follows from the finding that there was no reduction in the error scores obtained for the second task (B/A) where identical brightness differences were present. This is further supported by the animals' continuing to respond to the higher-flux target on the A-F trials, in spite of the fact that this figure was opposed to the one originally rewarded in the B-F situation. Therefore, by exclusion, the difference in luminous flux emitted by each figure in the B-F problem, either per se or through its influence on the background, appears to be the differential parameter of the stimuli upon which the discrimination was made. The correct response on the B-F problem was determined by the higher luminous flux and not by the higher luminance of figure *aB*.

These results do not support the conclusions of other investigators (*3*) who stated that equalizing the stimuli in luminous flux does not affect the reaction of the intact monkey to figures of equal area which differ in luminance. The discrepancy, however, may be more apparent than real, since in the latter experiments a brightness discrimination may have been established in their B-F type problem. This was not the case in our testing situation, and differences in conditions may account for the variance in results. The photometric levels used do not appear to be a crucial variable in view of the similarity of performance between our two groups. Other possible differences may exist, namely, the use of movable instead of stationary targets, or of light reflected from figures in place of transilluminated stimuli.

The present results have a striking qualitative resemblance to those which Klüver (*8*) obtained for the monkey following exclusion of the geniculostriate system. In a testing situation with stimulus parameters similar to those used in four of our animals (B-F problem with low photometric values), monkeys with bilateral occipital lobectomies, trained to respond to the brighter of two equally large areas (Klüver's condition 12), when confronted with stimuli differing in area but identical in brightness (our A-F type trials) reacted as our normal monkeys did by selecting the position of the larger stimulus. Moreover, in that study chance reactions occurred when the two stimuli were equated in luminous flux so that brightness and area were inversely proportional (a B/A type of situation presented as "critical trials"). Our normal monkeys also responded at a chance level when first presented with the B/A situation, although they could eventually be trained to master this problem. These similarities do not imply that visual behavior is not affected by bilateral occipital lobectomy. There are obvious gross behavior alterations after such ablation and we have previously reported a fivefold increase in postoperative error scores on a B-F type of discrimination as compared to preoperative levels (*9*).



B-F Problem

| | | | |
|---|---|---|---|
| A | 2.10 | 2.10 | $cm^2$ |
| B | 72.29 | 1.005 | foot-lambert |
| F | 0.1636 | 0.0023 | lumen |

B/A Problem

| | | | |
|---|---|---|---|
| A | 2.10 | 141.60 | $cm^2$ |
| B | 72.29 | 1.005 | foot-lambert |
| F | 0.1636 | 0.1532 | lumen |

A-F Trials

| | | | |
|---|---|---|---|
| A | 2.10 | 141.60 | $cm^2$ |
| B | 72.29 | 72.29 | foot-lambert |
| F | 0.1636 | 11.0191 | lumen |

Fig. 2. Stimuli used in each problem and "critical trials" with values given for luminance (B), area (A), and total luminous flux (F) in each situation. Each target is identified by a pair of letters indicating large (*A*) or small (*a*) area and high (*B*) or low (*b*) luminance. Note that target *aB* was present in all three conditions. This target determined the reward position in the two problems. In the "critical trials" both food-wells were baited. While nine of the monkeys were tested with the values as illustrated, the photometric parameters for the other four were reduced to 3.5 percent of the original values.

It is tempting to explain the qualitative similarity of behavior between our normal monkeys and Klüver's operated animals in terms of constancy phenomena. Klüver has suggested that exclusion of the geniculostriate system eliminates perceptual constancies of brightness, size, distance, shape, and so forth. Studies on humans have shown that constancies may be considerably decreased when background cues are reduced (*10*), and it might be argued that our normal animals tend to ignore the luminance of the stimuli in our situation where brightness constancy may be reduced (transilluminated figures with little background). However, experimental data to substantiate this interpretation are lacking at present.

Since this study was primarily designed to delineate the response determinants in the B-F problem, no clear conclusions can be drawn concerning the stimulus parameters used to solve the B/A task. The significant difference between the two sets of A-F trials indicate that the animals do not discriminate the same parameters on the B-F and B/A problems. In fact, the results on the A-F trials following this latter test suggest that various animals may solve the B/A problem in different ways.

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### References and Notes

1. F (lumens) = B (ft-lam) × 0.001076 A (where A is in square centimeters).
2. Brightness is the psychological correlate of retinal illumination, which in turn depends on the target's luminance as the psychophysical determinant. Intensity as a psychophysical dimension applies only to point sources (amount of light per unit solid angle) and consequently the use of this term is inappropriate for the kind of test under consideration [Optical Society of America, *J. Opt. Soc. Amer.* **34**, 244 (1944)].
3. M. P. Crawford, *Genet. Psychol. Monogr.* **17**, 77 (1935); H. Klüver, *Biol. Symposia* **7**, 253 (1942).
4. Report in preparation.
5. H. Klüver, *Behavior Mechanisms in Monkeys* (Univ. of Chicago Press, Chicago, 1933), pp. 19–25.
6. The B values were obtained by averaging 20 readings made with a Macbeth Illuminometer.
7. There is some indication that normal cats may exhibit this same type of behavior: P. Schilder, *J. Neurophysiol.* **29**, 888 (1966).
8. H. Klüver, *J. Psychol.* **11**, 23 (1941).
9. P. Pasik and T. Pasik, *Disturbances of the Occipital Lobe*, (Proc. 8th Intern. Congr. Neurol., Vienna, 1965), vol. 3, pp. 127–130.
10. R. H. Thouless, *Brit. J. Psychol.* **21**, 339 (1931).
11. We thank Victor Rodriguez for assistance in training the monkeys. Supported by PHS grants MH-02261 and K3 NB-16,865.

29 June 1967

## Behavioral Thermoregulation in the Desert Iguana

McGinnis and Dickson (*1*) have stated that there is a close similarity between the mean body temperatures of desert iguanas (*Dipsosaurus dorsalis*) in experimental thermal gradients (39.0°C) and those of active desert iguanas in nature, as studied by Norris (42.1°C) (*2*). However, there is a considerable difference, amounting to abou 3°C, between these means, and to overlook this fact obscures an important feature of thermoregulatory behavior in this species. That this difference between laboratory and field records can be significant is demonstrated by statistical analysis of similar data (*3*), for which standard deviations are available, which show a similar difference of about 3°C and demonstrate (*4*) a highly significant difference [$P <$ .001 that the two means ($\mu_1$, $\mu_2$) are equal ($H_0 : \mu_1 = \mu_2$)]. Such a significant difference is frequently observed between laboratory records and records made under the extremely hot conditions which prevail especially during summer (*5*). Under more moderate thermal conditions, as are those prevalent during spring and fall, significant differences between field and laboratory animals often do not exist; this fact is demonstrated by McGinnis and Dickson in their statistical comparison of their field records of late spring and their laboratory records, both of which have means in the preferred level of 38° to 39°C.

The higher mean body temperatures of desert iguanas under hot environmental conditions of summer are due to the fact that they abandon regulation at the preferred level under these conditions. Under such conditions there are no areas available within their territories, exclusive of burrows, cool enough to permit attainment of body temperatures as low as the preferred level of 38° to 39°C. When these conditions prevail, desert iguanas do not immediately retreat to their burrows, but usually seek the coolest place in their territory, and, if these places gradually warm up, as is common during the earlier portion of the day, these lizards let their body temperatures rise as high as the temperature at which panting begins (43° to 44°C). Under severely hot conditions of summer, therefore, it is not unusual to record body temperatures whose mean may be 42° or even 43°C, a value which may be as much as 4°C above the preferred level of body temperature as determined in experimental thermal gradients (*3*, *5*). The coolest places in the territory, exclusive of burrows, frequently are located in the heights of bushes as a consequence of the usual thermal inversion. It also is not unusual during these hot conditions to find that, of those desert iguanas outside burrows, most or all are in these coolest locations, particularly toward the end of the activity period (*2*, *5*). But, as demonstrated by the observations reported by McGinnis and Dickson, desert iguanas under the more moderate thermal conditions of spring may not resort to climbing bushes since temperatures suitable for regulation near the preferred level are available elsewhere in the territory. When the threshold for panting is reached, desert iguanas usually do not pant, but retreat instead to burrows they have constructed to such depths that a temperature of 39°C or lower always is available (*3*, *5*).

This feature of thermoregulatory behavior which permits abandonment of the preferred body temperature and conformance to the coolest available environmental conditions is of real importance to the success of desert iguanas in severely hot environments since it serves to prolong the period during which their various necessary activities may be conducted. On extremely hot days, for example, the period during which desert iguanas have environmental thermal conditions available which permit regulation at or near the preferred level is very brief, sometimes only about 30 minutes, thus severely restricting activities outside of burrows. By permitting body temperatures to rise above the preferred level, however, desert iguanas may increase this period to as much as 3 hours under these same conditions. This feature, which apparently is not restricted to desert iguanas, may not only permit increased activity periods, but, as a consequence, may also permit colonization of habitats which otherwise might be too hot. This feature of behavioral thermoregulation may very well be a major contributing factor to the success of diurnal lizards in hot desert environments (*3*, *5*).

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