DISCRIMINATION OF BRIGHTNESS DIFFERENCES BY RATS WITH FOOD OR BRAIN-STIMULATION REINFORCEMENT¹

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Rats were trained to respond to the brighter of two keys. Four animals were trained with food pellets and four with electrical brain stimulation. Each discrimination sequence was initiated when the animal broke a light beam at the rear of the chamber, turning on the key lights and starting a 30-sec reinforcement period. An initial response on the brighter key was immediately reinforced, and further responses on the brighter key were then intermittently reinforced. Any time the dimmer key was pressed, a 30-sec timeout was introduced. During timeout, no response had any programmed consequence. When the reinforcement period or the timeout ended, a new discrimination sequence could be initiated. Daily 1-hr training sessions were conducted, and after seven or eight sessions, all animals were at or near errorless performance levels. The luminance of the brighter key was then systematically reduced, in seven steps, with two 30-min test sessions at each step. Orderly psychometric functions were generated for individual animals. Initial acquisition, once position preferences were broken, was equally rapid for food and for brain-stimulation animals, and the two reinforcement procedures yielded comparable levels of brightness discriminability.

Intracranial self-stimulation (ICS) has been increasingly applied to standard problems in operant conditioning. This technique provides several advantages over traditional food reinforcement procedures. For example, the temporal and intensive parameters of the reinforcing stimulus can be varied with precision and convenience, and thousands of stimulations can be delivered in a daily session, greatly exceeding the feasible number of food reinforcements.

There is, however, relatively little direct evidence on the effects of various reinforcers on the acquisition and maintenance of stimulus control. For the most part, experimenters select reinforcers for convenience, assuming that one is more or less as good as any other, as long as adequate response rates can be sustained. This assumption should be cautiously accepted, especially where ICS is concerned. For example, there is considerable evidence that, in some loci, subcortical stimulation following a discriminative response can

produce deficits in retention (Glickman, 1961). Moreover, the degree of interference in such cases is greater with more difficult discriminations (Mahut, 1964). That such interference might be found in typical ICS situations is suggested by a recent report that reinforcing brain stimulation can inhibit sensory evoked potentials (Ball, 1967). From such observations, one might predict that ICS should produce inferior stimulus control, especially where small differences between stimuli are involved.

On the other hand, in a direct comparison of food reinforcement and ICS, Kling and Matsumiya (1962) found no differences in the initial acquisition of a light-dark discrimination. Similarly, in a study of auditory discrimination and generalization, Kling and Berkley (in press) obtained highly comparable acquisition and generalization data with food or brain-stimulation reinforcement.

This apparent discrepancy between the implications of the physiological studies and actual behavioral results may stem from the relatively gross stimulus differences, and the resulting easy discriminations, used in the behavioral experiments. Mahut's (1964) data suggest that a more sensitive comparison of ICS and other reinforcers probably would be possible if stimulus control were examined

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under conditions of minimal stimulus difference. ICS and other reinforcers have not been directly compared under such conditions, although this information would appear to be a necessary prelude to any application of ICS procedures in studies of stimulus control. To this end, food and ICS animals were trained in a two-value brightness discrimination. When consistently accurate responding was attained, the luminance difference of the discriminative stimuli was reduced in discrete steps in order to assess the degree of stimulus control under the two reinforcement procedures.

METHOD

Subjects

Eight male albino rats of the Charles River CD strain were reduced to 80% of free-feeding weight after electrodes were implanted.

Apparatus

The experimental compartment was constructed of clear Plexiglas side and rear walls, with an aluminum front wall, and measured 12.5 in. by 9.5 in. by 19.0 in. Two Gerbrands pigeon keys were mounted symmetrically on the front (9.5 in.) wall, 1.5 in. from the floor and 1.5 in. from each side wall. Incandescent lamps were mounted in aluminum cases behind the keys. The intensity of the stimulus lights was varied by adjusting the dc voltage to each lamp. Luminance levels were calibrated using an SEI exposure photometer (Salford Electrical Instruments, Ltd.).

A third light with a 1-in. diameter white lens was mounted at the center of the front wall, 3.25 in. from the floor, and a brass food cup was inserted below it. A photocell was mounted on one side wall 2 in. above the grid floor and 2 in. from the rear wall, and a light source with a red gelatin filter was focussed on the photocell from the other side of the box.

The compartment was placed inside a ventilated, sound-attenuating chamber, with a pulley-swivel system (Berkley and Kling, 1967) attached to the ceiling to prevent twisting of the flexible electrode leads when the animal turned or made sudden movements. Brain stimulations consisted of 0.5-sec trains of 60 cps sine waves, taken from an isolation transformer, stepped down by a variable trans-

former and adjusted by a potentiometer. A cathode-ray oscilloscope was used to monitor stimulus current by measuring the voltage drop across a fixed resistor in series with the animal.

Procedure

Electrode implantation. Electrodes were implanted with sodium pentobarbital anesthesia. Bipolar stainless steel electrodes, similar to those described by Valenstein, Hodos, and Stein (1961), were aimed at the region of the posterior hypothalamus with the aid of a stereotaxic instrument. The electrodes were secured to the skull by stainless steel screws and dental cement.

Rate-intensity testing. All animals were given rate-intensity tests approximately one week after surgery. These tests consisted of attempts to shape bar-pressing in a single-bar box, followed by determination of response rates on continuous reinforcement for a wide range of stimulus intensities. Animals were characterized as "positive" if shaping was successful and disruptive motor activity was not induced by brain stimulation. Four animals were thus chosen to serve in the ICS group, and thereafter received stimulation at the intensities which supported the most rapid responding. (One animal, E8, required an increase in current level to maintain responding during pretraining.) The four remaining animals were assigned to the food group; two did self-stimulate in preliminary testing, but exhibited disruptive motor effects. In all later procedures, both food and ICS animals always performed with the electrode leads attached.

Pretraining. After rate-intensity testing, each animal was given daily 1-hr pretraining sessions in the experimental compartment. For the food group, this initially involved a period of magazine training. Half of the animals were trained to press the right key and half to press the left key. The luminance of the training key was set at 9.94 millilamberts (mL) and that of the second key at 0.20 mL. Food animals received one 45-mg Noyes pellet per reinforcement, and ICS animals received one 0.5-sec stimulus train. Sessions were continued until each animal responded without long pauses on a 30-sec variable-interval (VI 30-sec) schedule of reinforcement. In this phase of training, pressing the dimmer key produced a 30-sec timeout, during which the

lights behind both keys were turned off and no reinforcement was scheduled.

Discrimination training. After three or four 1-hr pretraining sessions, the discrimination training procedure was introduced. (Rat E8 required an additional four pretraining sessions to determine its final ICS current level.) In the otherwise dark box, the center panel light was turned on and remained on until the animal interrupted the photocell beam; the center panel light then went out and the key lights came on. From this moment, reinforcement was available for 30 sec: if the animal pressed the brighter key (9.94 mL), the first response was reinforced and the VI 30-sec reinforcement programmer then came into operation; if the dimmer key was pressed, both key lights went out and a 30-sec timeout period followed. Switching from the brighter to the dimmer key during the 30-sec reinforcement period also produced a 30-sec timeout. When the 30-sec reinforcement period or the timeout ended, the center light signaled the start of the next discrimination sequence. The brighter key (S+) was varied from left to right

according to a Gellermann series, which allowed up to three successive presentations of S+ on a given key, and which insured that S+ appeared on each side exactly five times in each block of 10 discriminations. Progression through the Gellermann series occurred without regard for the outcome of the previous discrimination (a "noncorrection" procedure). The photocell beam response served the dual function of allowing the animal to set up the stimuli freely, and of bringing it to the rear of the compartment from where both keys could be viewed. Seven or eight daily 1-hr discrimination training sessions were given each animal.

Discriminability Test. After discrimination training the animals were given two consecutive 30-min sessions each day. The luminance of the brighter key (S+) was reduced for the second session in the following sequence: 9.94, 5.43, 2.99, 1.69, 0.90, 0.49, 0.27 and 0.17 mL. Thus, each S+ test value was presented for a total of 1 hr. The dimmer key (S-) was held constant at 0.20 mL during all sessions. (The lowest S+ luminance proved to be 0.03 mL

Fig. 1. Photomicrographs of frontal sections for the four rats in the ICS group. White marker denotes locus of electrode tip for Rat G3.

less than S—, and sessions at this value thus technically constituted a discrimination reversal. However, this difference was imperceptible to several human observers.) In two final 30-min sessions, the brighter key was returned to 9.94 mL. The original discrimination procedure was maintained in this phase of the experiment.

Histology. After the experiment, the four ICS animals were sacrificed and perfused with saline and formalin solutions. The brains were frozen, sectioned, and stained. Photomicrographs of frontal sections are shown for each ICS animal in Fig. 1. Electrode tips were localized in the following areas for individual animals, with the aid of König and Klippel's (1963) stereotaxic atlas: E8, Forel's field H2; G2, dorsomedial nucleus of the hypothalamus; G3, fornix; G5, lateral nucleus of the hypothalamus.

RESULTS

Discrimination Training

By the fourth session all animals were setting up the visual stimuli approximately 100 times per hour, and exceeding scores of 90% correct choice. As shown in Fig. 2, once a high level of differential responding appeared it

Fig. 2. Per cent correct choice as a function of daily 1-hr discrimination training sessions, for each animal in the food and ICS groups.

was maintained throughout the remaining acquisition sessions.

The animals almost always chose the pre-training key when it was brighter, from the very start of acquisition. However, they initially chose this key when it was dimmer, too, exhibiting "position preferences". Subsequent improvement in discriminative performance was solely a function of increased responding on the nonpreferred key, when it was brighter. Figure 3 shows cumulative records of correct choices of the brighter light on the nonpreferred key, for each animal. The data are plotted to an arbitrary criterion of 10 successive correct responses, though several hundred further discriminations were made. This analysis is restricted to the initial response made in the presence of each stimulus (the "choice"), without regard to the subsequent responding during the half-minute when the VI 30-sec reinforcement schedule was in effect. The four food animals all exhibited "absolute" position

Fig. 3. Cumulative correct choices of the brighter light on the nonpreferred key for each animal in the ICS and food groups, plotted to an arbitrary criterion of 10 consecutive correct choices. The data span 2 to 4 sessions for individual animals. The curves are arbitrarily displaced on the ordinate.

preferences, in that they failed to respond on the nonpreferred key when it was brighter for 8 to 107 consecutive stimulus presentations. Two of the ICS animals (G5, E8) also exhibited absolute position preferences, both within the range of the food animals. The remaining two ICS animals (G2, G3) did press the nonpreferred key the first time it was brighter, although both subsequently made errors. Thus, each animal showed some preference for its pretraining key in the early stages of discrimination training.

Several animals responded correctly (but intermittently) on the nonpreferred key as many as 30 times before attaining the discrimination criterion. Two animals (E9 and E7) showed a gradual positive acceleration while two others (G3 and E5) showed an intermediate decrement in accuracy before approaching criterion. It should be emphasized that responding at the preferred key, when it was brighter, was consistently at or near 100% accuracy for all animals throughout discrimination training.

The total number of stimulus presentations required by each animal to achieve 10 successive correct responses on the nonpreferred key appeared to be greater for the food animals, though there was considerable overlap in the distributions. The ICS animals clearly formed a more homogenous group, requiring 38 to 53 stimulus presentations, compared to 48 to 125 presentations for the food animals. If the initial period of absolute position preference is discounted for each animal, no difference in rate of improvement is apparent.

In both groups, the animal showing the strongest absolute position preference (E8, ICS; G4, food) made the fewest errors after the first response on the nonpreferred key, with very rapid approaches to errorless re-

sponding. For these animals, discrimination latencies preceding errors increased toward the end of the absolute position preference period, in comparison to latencies preceding correct responses. This trend is illustrated for Rat G4 in Fig. 4, where both latency and choice data (as cumulative correct responses) are plotted in analogous positions on the abscissa. The mean latencies for discriminations with S+ on the nonpreferred key increased from approximately 1.9 sec to 3.5 sec in the period directly preceding the first correct response on the nonpreferred key, while the mean latencies for discriminations with S+ on the preferred key remained fairly stable at approximately 2 sec. The latencies thus seem to show evidence of stimulus control before accurate choice behavior appeared.

After the absolute position preference was broken, choice latencies for discriminations with S+ on the nonpreferred key continued to exceed latencies for discriminations with S+ on the preferred key, even after errors were almost totally eliminated. This reflects a response topography observed in many animals: upon breaking the photocell beam in the rear of the chamber, the rat would first approach its preferred key, regardless of the brightness; if the key were brighter the rat would immediately press it (resulting typically in choice latencies of less than 2 sec), but if the key were dimmer the rat would pause and then approach and press its nonpreferred key (resulting in longer choice latencies, often greater than 3.5 sec).

Discriminability Test

Table 1 lists the per cent correct choice for each animal in the discriminability test series, reflecting performance on both keys. The data for 9.94 mL (maximum S+ luminance) are

Table 1
Per Cent Correct Choice as a Function of S+ Luminance

LUMINANCE OF S+ (mL)	FOOD ANIMALS					ICS ANIMALS		
	E5	E7	E9	G4	G2	G5	G3	E8
9.94	100	100	97	96	100	99	100	99
5.43	100	100	100	95	100	100	97	100
2.99	99	96	99	94	99	100	99	99
1.69	99	90	96	93	98	100	98	100
0.90	93	95	90	84	93	94	93	94
0.49	74	68	88	69	78	70	76	77
0.27	58	55	57	53	52	56	62	61
0.17	45	47	45	52	49	49	40	51

Fig. 4. A comparison of choice accuracy (cumulative correct responses) and choice latency during discrimination training, for Rat G4. Data are from the period immediately before and after the break of absolute position preference. Latencies are presented as means of blocks of 10 stimulus presentations, with the zero reference point denoting the break of absolute position preference. The first block of data represents the means for 60 stimulus presentations. The latencies have been dichotomized to reflect S+ presentations on the two keys separately. In every block of 10 S+ presentations half are on the preferred key and half on the nonpreferred key.

from the final 1-hr discrimination training session; values for the lower luminance levels are means from the two 30-min sessions. All animals maintained high levels of differential behavior as the brighter key was reduced in three steps from 9.94 to 1.69 mL. However, further decreases in luminance (from 0.90 to 0.17 mL) produced a general concomitant decrease in discriminative performance. The decreases were gradual, with ultimate levels at approximately 50% correct choice, where the luminance of the two keys was nearly equal.

A semi-log plot of these data suggests the form of the psychophysical ogive often obtained from humans by the method of constant stimuli (see Woodworth and Schlosberg, 1954, pp. 200-213, for a discussion of data

treatment). The analysis of the discriminability of luminance differences is based on the sessions where stimulus control decreased with decreases in S+ luminance (0.90 mL and below). These data were transformed to normal probabilities in order to derive a comparable measure of discriminability for all animals. This transformation converts probability values of correct response (estimated by the per cent correct choice measure) into standard deviation units (z-scores). Thus, chance responding at 50% correct yields $z = 0$, while responding at about 84% correct yields $z = +1$. In Fig. 5 straight lines were fitted to the transformed data by the method of least squares. The r^2 measure of goodness of fit (Lewis, 1960) ranges from 0.85 to 0.98 for individual ani-

Fig. 5. Normal probability plot of discriminative accuracy as a function of the relative luminance of the brighter key (log scale), for each animal in the food and ICS groups. The per cent correct scores (as shown in Table 1) are transformed here into standard deviation units. The steeper the slope of the least-squares line, the finer the brightness discriminability. The curves are arbitrarily displaced on the abscissa.

mals, supporting the applicability of this analysis to the data. With the exception of one food animal (G4, which had also shown the most persistent absolute position preference in discrimination training), these curves are quite similar.

An index of the difference threshold (D.L.) may be defined as the change in luminance required to produce a change of one standard deviation from the mean ($z = 0$) of the least-squares function. The D.L. is inversely proportional to the slope. Such an index is more refined than others (e.g., the value derived by linear interpolation between the two data points surrounding 75% correct choice) for it gives equal representation to all the data in the region of decreasing stimulus control. The resulting difference thresholds range from 0.334 to 0.419 mL for the seven animals that provided uniform sets of data (mean D.L. = 0.391 mL). The aberrant food animal (G4) yielded a D.L. of 0.886 mL, indicating poorer discriminability. Discrimination of minimal brightness differences does not appear to be a function of the particular reinforcer.

As a final test of stimulus control, the brighter key was increased again to 9.94 mL

after the discriminability test series. All animals showed immediate increases in discriminative accuracy. Seven of eight attained levels of 96 to 100% correct choice in single 30-min sessions, with one food animal (E5) attaining 90% correct.

Response Rate Measures

In addition to the reinforcement given for the initial correct choice, further responses were reinforced on a VI 30-sec schedule, during the remainder of the 30-sec stimulus presentation. If the discrimination procedure is viewed as a free-operant chain, the reinforcement period may be considered the S^D component for key-pressing, since responding on the keys was reinforced only when they were illuminated. In the remaining segments of the chain (periods of timeout following errors, and the time prior to breaking the photocell beam), key-pressing was never reinforced: this may be considered the S^A component of the chain. Figure 6 shows mean response rates for the food and ICS animals for the first six sessions of discrimination training and for the subsequent discriminability test. S^D response rates increased gradually throughout the experiment for both groups, with the ICS group

Fig. 6. Mean response rate on the two keys during the first six discrimination training sessions and the discriminability test, for the food and ICS groups. Responding in each session is divided into two categories: S^D rates are from the reinforcement period, during which the keys were lit; S^A rates are from the 30-sec timeout period and the segment before each reinforcement period.

showing consistently higher rates than the food group. This difference is almost certainly attributable to the considerable amount of time spent by the food animals at the food cup, even in the absence of pellets. S^A response rates showed a general decrease in the course of discrimination training, with the ICS group emitting consistently fewer responses than the food group. This is an illustration of the lower resistance to extinction often observed with ICS animals in simple free-operant procedures (e.g., Culbertson, Kling, and Berkley, 1966). In the discriminability test, the S^A rates appeared to increase for both groups as the luminance difference was reduced. The cumulative records of key-pressing suggest that this increase is attributable to bursts of responding during timeout periods. It should be noted that the number of timeout periods also systematically increased as the luminance difference was reduced.

DISCUSSION

Acquisition of a two-value brightness discrimination was accomplished in the context of a free-operant chain. By all indications, the discrimination was "easy". All animals achieved levels of 99% or 100% correct choice, most often within the first few sessions. Further, the psychometric functions provide evidence that the original stimulus values well exceeded the region of the rat's brightness difference threshold. Discrimination acquisition involved an orderly increase in responding on the nonpreferred key, when it was brighter, in contrast to a stable high probability that the animal would respond on the preferred key, when it was brighter. For most animals, improved responding on the nonpreferred key was preceded by a period of absolute position preference, during which the pretraining key was chosen regardless of its luminance.

Once absolute position preferences were broken (as shown in Fig. 3), the approach to criterion required as few as four presentations of S+ on the nonpreferred key (Rat E8) to as many as 64 presentations (Rat E7), with food and brain stimulation appearing to be equally effective reinforcers. In a pretraining procedure designed to minimize absolute position preferences in discrimination acquisition, Kling and Matsumiya (1962) also found equivalent rates of improvement for food and ICS

animals. These data do not support the suggestion (Olds, 1956) that discrimination acquisition by rats with brain stimulation reinforcement may be retarded in comparison to food controls. Any retroactive physiological consequences of brain stimulation (*cf.* Glickman, 1961; Mahut, 1964) or sensory inhibition (*cf.* Ball, 1967) apparently had no adverse effect on the behavior of our ICS animals. It is conceivable that an ICS-produced deficit might still appear in the initial acquisition of a difficult discrimination; however, decreasing the difference between S+ and S- after acquisition of an easy discrimination resulted in equally fine discriminative performance by the food and ICS animals. The more persistent absolute position preferences shown by food animals E7 and G4 in acquisition may possibly reflect the adventitious reinforcement of spatially oriented response chains during VI 30-sec pretraining, when approach to the food cup and the pretraining key was initially shaped.

It is unlikely that the lack of a differential reinforcer-quality effect on discrimination acquisition merely reflects the particular choice of brain stimulation intensities or food deprivation level used in the present experiment. Keesey (1966) and Sadowsky (1967) systematically varied ICS current amplitude in discrimination situations, and found no effect on acquisition. Miles (1959) and Hegge (1966) varied both food deprivation level and discrimination difficulty, and found no effect of deprivation level on acquisition.

That latency changes may antedate choice changes (as shown for Rat G4 in Fig. 4) raises interesting questions about the relation between these two measures of stimulus control. Mahut (1954) reported similar findings based on group data from a jumping-stand experiment, and Mackintosh (1965) observed a similar effect. It appears that this relation between latency and choice has been observed only on a baseline of absolute position preference. It may be that procedures which result in slower acquisition of stimulus control (e.g., by decreasing the difference between S+ and S-) would magnify the latency effect. The existence of an absolute position preference, however, is certainly not a sufficient condition for the emergence of a latency difference: several animals with absolute position preferences did not show the latency effect.

The decrease in correct discriminations as the luminance of the brighter key was reduced, and the immediate improvement when it was returned to its maximum level, is strong evidence that the behavior was under the control of the visual stimuli, an effect similar to that reported by Moskowitz and Kitzes (1966). It is interesting that this decrease may be described as an orderly psychometric function, showing evidence of reliable differential behavior, even at luminance differences barely detectable by human observers. This behavior contrasts with Mentzer's (1966) data on the pigeon, where rapid reversion to position preference was obtained when the S+ luminance was reduced.

The lack of differences between animals with food or brain-stimulation reinforcement suggests that discriminability of sensory stimuli may not be influenced by the type of reinforcer used to shape and maintain the correct responses.

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