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OPERANT CONDITIONING AS A MEANS OF TESTING THE ABILITY OF WHITE-CROWNED SPARROWS TO DISCRIMINATE STAR PATTERNS

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Operant conditioning can be a valuable technique for investigating biological problems, as has been demonstrated with pigeons (e.g. Meyer, 1964; McDonald, 1968). If an appropriate operant is selected, such as perch-hopping, the technique can be extended to passerine birds. Stevenson (1967) used alighting on a perch as the conditioned response with first-year male chaffinches which lived in the experimental chamber. Bastian & Hothersall (1970) obtained high fixed-ratio responses (FR up to 40) with redwinged blackbirds, which again lived in the experimental cages.

This study has developed techniques whereby wild-caught white-crowned sparrows, both adults and juveniles, have been successfully conditioned using relatively short training sessions, and have adapted to the frequent handling requisite to the use of a separate experimental chamber. This was advantageous in that it standardized the experimental situation for each animal and eliminated duplication of equipment.

Subjects which had been successfully conditioned to perch-hop in order to gain access to food were presented with stimuli consisting of two distinct groups of simulated stars in an attempt to determine whether they can discriminate star patterns. Mewaldt, Morton & Brown (1964) have established that the race of white-crowned sparrow used in this study (*Zonotrichia leucophrys gambelii*, a night migrant) shows directional orientation under natural night skies, and that this directional orientation may be independent of night restlessness. Since this experiment was concerned with the animals' ability to distinguish between stimuli and not with their ability to orient within a caged space, it was assumed that testing each bird at a different point in time, and even testing during the day, would not affect results.

METHODS

Experimental animals

From a total of nineteen Gambel's white-crowned sparrows trapped on the campus of the University of California at Santa Barbara between 7 October 1970 and 20 March 1971, six completed operant training, and five of these were given two phases of discrimination training. The sixth (no. 16) was caught on 7 March, too late to complete discrimination training. Subjects which had to be dropped were inactive in the experimental chamber (seven birds) and/or were difficult to handle (six birds)

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primarily because they learned to fly around in the home cages when the light was turned off, making it time-consuming to catch them for daily training sessions. (I always caught the birds in the dark in the home cages.) In practice, one could determine within a few sessions whether a given bird would be adaptable to training, based on whether it was active in the experimental chamber and ate from the hopper, and on how easy it was to catch. Juveniles proved by far the easier to handle and train. Nos. 5, 8, 15, and 16 were the only juveniles caught, and they were all successfully conditioned, while only nos. 4 and 9 (of the fifteen adults trapped) were successfully conditioned.

The birds were initially housed two to a cage in 40 cm × 63·5 cm × 45 cm cages kept on separate shelves in a 1·52 m × 2·44 m windowless room, with the temperature maintained at approximately 20 °C. When aggressive behaviour and singing began in February, some were moved to individual finch cages approximately half as large as the original cages. There was periodic turnover of the captive birds, as individuals that quickly proved unsuitable for training were released to provide cage space for others trapped later. An automatic light timer in the light-locked cage room provided a cycle of 5·5 h light–18·5 h dark. Tests on earliest caught subjects indicated that a 5·5 h artificial day caused the birds to be food-deprived enough to be sufficiently motivated for conditioning.

Subjects were fed on a mixture of canary seed and Ralston Purina game bird meal, plus a few grains of Big Kernel (parakeet) Bird Gravel. The seeds, which the birds seemed to prefer and which were used as a reward during training, were covered with the meal in the feed cups. One drop of Geisler Drop-A-Day multi-vitamin solution was added to the water; food and water were changed daily. Three birds whose weight dropped below 21 g became lethargic and very obviously appeared to be in poor condition. Isolating the affected individual, removing it from the training schedule, and adding two drops of vitamins to both food and water restored its normal weight and normal behaviour.

Apparatus

Training took place in a 34·3 cm × 44·5 cm × 30·5 cm experimental chamber made of 6·3 mm hardware cloth, with a removable lid made of the same material (see Fig. 1). A frame of 1·3 cm × 10·3 cm wood was attached to the outside along the horizontal midline of the sides and ends. Two T-shaped perches (perches *A* and *B*), with an 8·9 cm dead perch located 3·8 cm above each, were mounted one at each end of the box. Perches *A* and *B* were attached to microswitches adjusted to require a discrete jump by the bird in order to produce closure, which resulted in an audible click. The dead perch prevented the birds from sidling along the perch and causing the microswitch to chatter. A small background light was mounted outside the frame at each end, out of direct line of sight from within the cage, since the birds remained inactive during darkness. A standard electromechanical grain hopper, equipped with a photo cell and light, was mounted on one side. A small L-shaped perch in front of the hopper opening enabled the bird to feed when the hopper was activated. A 19 cm dead perch was mounted opposite the feeding perch to reduce flying back and forth between perches *A* and *B* (Bastian & Hothersall, 1970). Water was available in an open container at all times.

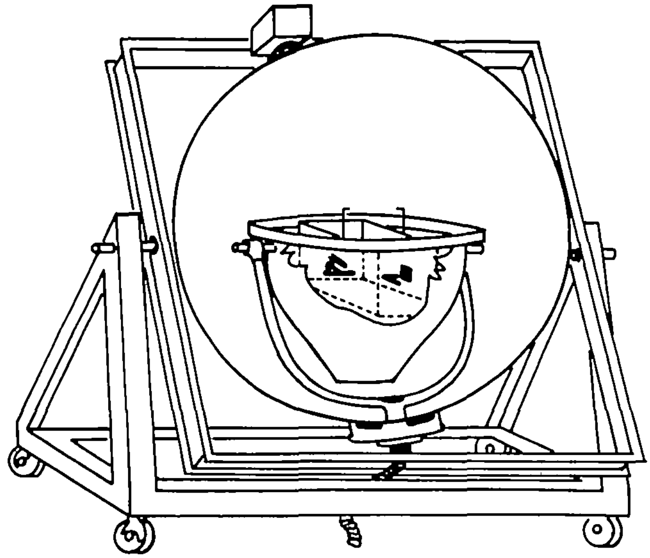

Fig. 1. Schematic representation of planetarium, with self-levelling basket cut away to reveal experimental chamber. Perch *A*, with dead perch above it, signal lights 1 and 2, hopper opening and feeding perch are also shown. Throughout the study the planetarium door faced toward the observer, opposite perch *A*.

The experimental chamber was placed inside an aluminium sphere of 1·52 m diameter, supported by its wood frame inside a self-levelling metal basket resting on a gimbal inserted through the bottom of the sphere. An electric blower circulated air through a hole in the bottom of the gimbal; part of the air hose can be seen in Fig. 1. The blower also provided masking noise. Cal-Glo Brite-Eye Micro-Miniature 5–6 V indicator lights glued into holes drilled through the aluminium sphere represented the 56 brightest stars in the major constellations of the northern hemisphere visible from inside the experimental chamber. The inside of the sphere and the surfaces of the lights were painted flat black, with a pinhole scratched in the paint covering each light. Individual potentiometers connected to the lights enabled the brightness of each to be adjusted to approximately the magnitude of the star it represented. This system placed the subject in the centre of the celestial dome, seeing the stars as emitted lights, whereas in a conventional planetarium with a central projector (e.g. Emlen, 1967) the experimental chamber must be placed off centre, and subjects are presented projected light images. The wire lid on the experimental chamber had been lightly sprayed with flat black paint, and the artificial stars were easily visible through it to a human observer. A light-tight, removable door in a relatively starless area of the southern hemisphere allowed access to the experimental chamber, which was oriented within the planetarium with perch *B* next to the door. All of the above apparatus except the experimental chamber was designed by W. J. Hamilton III.

Although the planetarium could be tilted and rotated, it was arbitrarily positioned throughout the discrimination training to show the sky as it would be seen in Santa Barbara at approximately 21·00 h on 25 December. The stars visible from inside the experimental chamber when the sphere was in this position were distributed randomly into two groups – I and II – containing an equal number of stars. As it happened, group I contained all of the stars in Ursa Major and most of Orion, while group II contained all of Cassiopeia; the two groups looked quite distinctly different to a human observer. As additional discriminative stimuli, two 14 V General Electric 1705-D Micro-Miniature lamps were mounted on Γ-shaped strips of 9·5 mm aluminium, with the lights positioned 10·3 cm above the top of the chamber and 3·8 cm in from the edge, at the mid-points of the chamber above the 19 cm dead perch and the hopper opening. These were called signal lights 1 and 2 and would be activated with group I stars and group II stars, respectively. A silent relay switch was used to ensure that an auditory stimulus was not presented at the moment the star pattern changed from one group to the other. In addition, all electrical equipment connected with the star lights was located outside the aluminium sphere.

Operant training

Food containers were removed daily from the home cages approximately 1 h before the lights came on. The birds were weighed and carried in a 15·2 cm length of core from a paper towel roll fitted with a lid at one end. When the tube was placed just under the removable cover of the experimental chamber, the bird inside would fly out into the chamber as soon as the lid was slipped off the tube. The training programme was turned on 1–2 min after the door to the planetarium was secured. This was ample time for the bird to calm down, as earlier observations of the home cages with closed-circuit television indicated that birds which were fluttering wildly about the cage resumed normal activity almost immediately after an observer left the room. After the training session the bird was caught with a small fish net, in semi-darkness. Food containers in each home cage were replaced as soon as both occupants had finished their training sessions. By the end of the operant training I had found that the total number of responses was higher if sessions were begun *before* the lights came on in the cage room – but only as much as 2 h earlier. Perhaps the birds were able to find spilled seeds in the sawdust beneath the grills covering the bottom of the cages and thus were not food-deprived enough for training, or perhaps they fed most actively when they were first awakened by light. The daily sessions were arranged during discrimination testing (see below) so that each subject was taken directly from the dark room and placed in the experimental chamber, with the lights in the cage room coming on while the last bird was in its training session.

Hopper training. Subjects were first trained to eat from a continuously lighted and continuously available hopper full of canary seed; the hopper opening was filled with additional seeds. The level of food was moved down on successive days until the subject was eating out of the bottom of the hopper. Electronic equipment recorded the number of times the bird landed on perches *A* and *B*, the number of times it entered the hopper opening, and the total number of seconds its head stayed in the opening. The length of daily sessions varied from 10 to 50 min, subjects being left in the experimental chamber until they had fed successfully.

During the second stage of hopper training the hopper stayed up, and the hopper light stayed on until the bird's head had remained in the opening for a total duration of 5 sec; then the light went off and the hopper moved down out of reach for 10 sec. After the subject was eating well during this stage, a fixed-interval schedule was introduced. Five-second periods of food availability alternated with 10 sec of unavaila-

Table 1. *Successfully conditioned subjects*

Subject	Age	Operant perch	Number of sessions before FR = 15 consistent	Highest FR	Positive discriminative stimulus (S+)
4	Adult	*A*	18	35	I
5	Juvenile	*B*	22	35	II
8	Juvenile	*B*	28	15	II
9	Adult	*B*	17*	37	II
15	Juvenile	*B*	13	15	I
16	Juvenile	*B*	6	15	—†

* No. 9 received seven reinforcements at FR = 15 on the third day of perch discrimination training, but its responses fell off within 2 days. After a total of seventeen sessions the bird was back to FR = 15.

† Not given discrimination training (see text).

bility. Background lights remained on throughout hopper training, and sessions after the initial stage were no more than 30 min long.

Perch discrimination training. During this phase food was no longer presented non-contingently; instead, the bird was required to land on the operant perch to gain access to the hopper for 5 sec. The perch least frequently landed on during hopper training was selected as the operant perch (see Table 1). All subjects except no. 9 (no significant preference) and no. 4 showed a preference for perch *A* – the farthest from the door of the planetarium. The fixed ratio (FR, i.e. the number of responses required for one reward) was initially one, but all subjects learned to jump on the perch several times in rapid succession, and the FR was increased to fifteen. The increase required from six to twenty-eight sessions (see Table 1). Background lights remained on during this and the following phase of operant training.

High FR phase. In order to gain some measure of how high an FR might be attained by white-crowned sparrows, three birds (nos. 4, 5, and 9) were subjected to increasing FRs, during an additional five to nine sessions before discrimination training began. Plans for further increments were abandoned when no. 9 began to show an alarming weight loss. All three subjects were then returned to FR = 15 before discrimination training. Of the two other subjects which were given discrimination training, no. 8 was held at FR = 15 for a time, and no. 15 was given discrimination training as soon as it reached FR = 15.

Discrimination training

One star group (I or II) was assigned, by flipping a coin, to each of five subjects as the positive discriminative stimulus (S+). When the contingency was in effect (see phase 1 below) hopping on the operant perch under S+ would earn access to the hopper, while hopping on the operant perch under the other group of stars – the negative discriminative stimulus (S–) – would not produce reinforcement. The number of responses on perches *A* and *B* during presentation of groups I and II was recorded, as was the number of rewards earned and the number taken (entries into the hopper opening as measured by the photocell). The background lights were turned off when food became available, and remained off until the availability ended. Hopper presentation was always accompanied by the hopper light. The stars, however, remained on during reinforcement.

Base phase. In order to determine the distribution of perching responses over time and as a function of star group, as well as the amount of individual variation, subjects were given a number of sessions during which fifteen responses on the operant perch earned a reward regardless of which star group was presented. Each group of stars was presented for 2 min, beginning with the group which was to become S+, and alternating with S− until each had been presented five times. Subjects were held at this level of training until I judged their responses stable. Nos. 4, 5, 8, and 9 received seven sessions each, and no. 15 received ten sessions.

Phase 1. During this phase reinforcement became contingent upon responding on the operant perch under S+. Initially the birds were given five 2 min presentations of each group of stars; as in the base phase, the stimuli alternated, with S+ presented first. The intention was to next present the stimuli in a random order if the birds showed, by reduced responses during S−, that they were making the discrimination between star groups I and II.

At the end of fifteen sessions it was apparent that three things were happening: (1) the number of responses was either higher during presentation of S− (i.e. the 'wrong' group of stars), or the responses were distributed at about the level one would expect by chance, (2) the total number of responses was falling off, so that the length of the sessions was increased in some cases in an attempt to prevent loss of perch training, and (3) the number of responses on the non-operant perch was increasing, indicating loss of perch training. Clearly, at this point the birds were not using S+ as a signal that only during its presentation would they be reinforced.

Phase 2. A crutch was introduced. During this phase signal light 1 accompanied star group I and signal light 2 accompanied group II. Subjects 4, 8, and 9 were given fifteen sessions, no. 5 received thirteen sessions, and no. 15 received ten sessions, all ending on 24 March. During this phase the length of the sessions was held at 16–20 min (four to five presentations of each discriminative stimulus, alternating, with S+ presented first).

RESULTS

The results of perch discrimination and high fixed-ratio training for subjects 4, 5 and 9 are shown in Fig. 2. Nos. 8 and 15 (not shown) produced similar functions. The values on the ordinate are the ratio of responses on perch *A* divided by the total responses; values above 0·5 mean that more than 50% of the responses were on perch *A*. Perch *A* was the operant perch for subject no. 4, and perch *B* was the operant for nos. 5 and 9. The mean number of responses ($\bar{X}_A$ and $\bar{X}_B$) on each perch are also shown for all three phases. It is quite clear that the birds learned the operant within the first two sessions. Evidence of learning is seen not only in the shift of the mean responses per session from *A* to *B* or vice versa, but also in the increasingly high mean levels of responses on the operant perch. Fig. 3 shows the highest number of responses achieved during single 15 min sessions during the high FR phase.

Figs. 4 to 8 inclusive show the results of discrimination training for subjects 4, 5, 8, 9 and 15, respectively. The data were plotted as the ratio of responses on the operant perch during presentation of S+ divided by the total number of responses on the

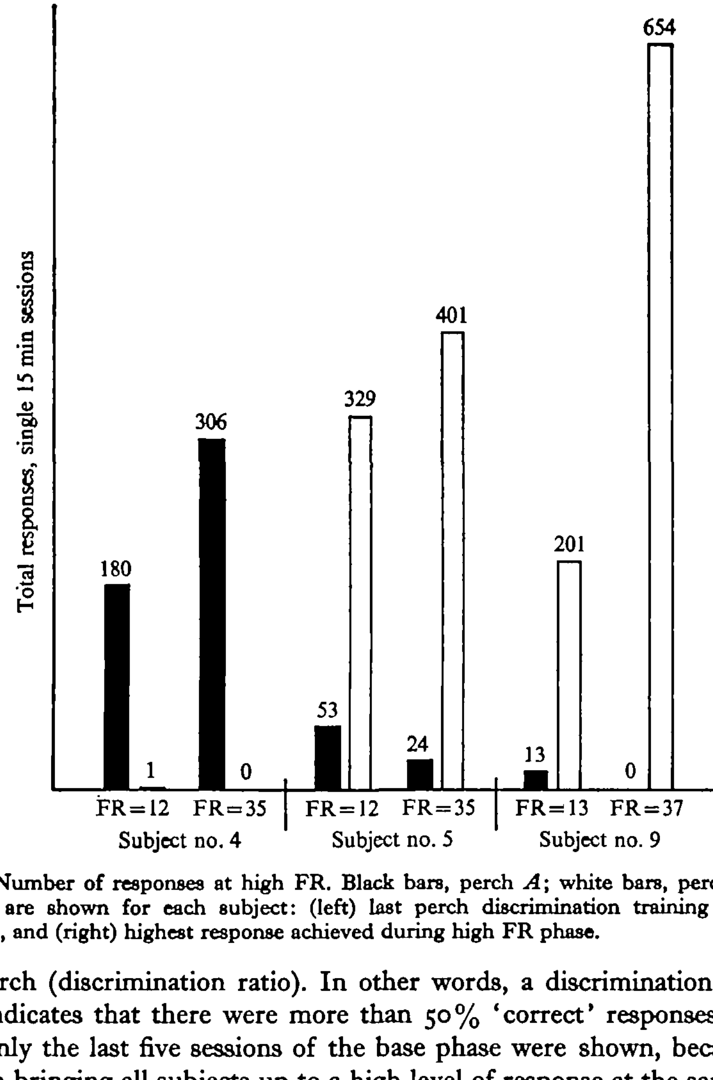

Fig. 2. Number of responses at high FR. Black bars, perch *A*; white bars, perch *B*. Two sessions are shown for each subject: (left) last perch discrimination training session at FR $\leqslant$ 15, and (right) highest response achieved during high FR phase.

operant perch (discrimination ratio). In other words, a discrimination ratio higher than 0·5 indicates that there were more than 50% 'correct' responses during that session. Only the last five sessions of the base phase were shown, because of some difficulty in bringing all subjects up to a high level of response at the same time (e.g. note session 2 for subject no. 15, below). $\bar{X}_I$ and $\bar{X}_{II}$ are the mean number of responses on the operant perch during presentation of group I stars and group II stars, respectively. That the response level was reasonably high throughout the study becomes more obvious when one realizes that the sessions were short – 16–20 min – and that each stimulus was only presented during half the session. (There were some longer sessions during phase 1, as noted above.) For example, $\bar{X}_I$ = 125 for subject no. 5 during phase 2 means that the bird jumped on the operant perch an average of 125 times in the 8–10 min that group I stars were presented – in addition to the number of responses on the operant perch during presentation of S– (group II stars).

There are no trends immediately obvious in the results of either phase 1 or phase 2 – nothing as dramatic as the results of the perch training, for instance. One may stipulate that in order to demonstrate that learning had taken place the ratio of responses during presentation of S+ in phases 1 and 2 would have to exceed the upper limit of

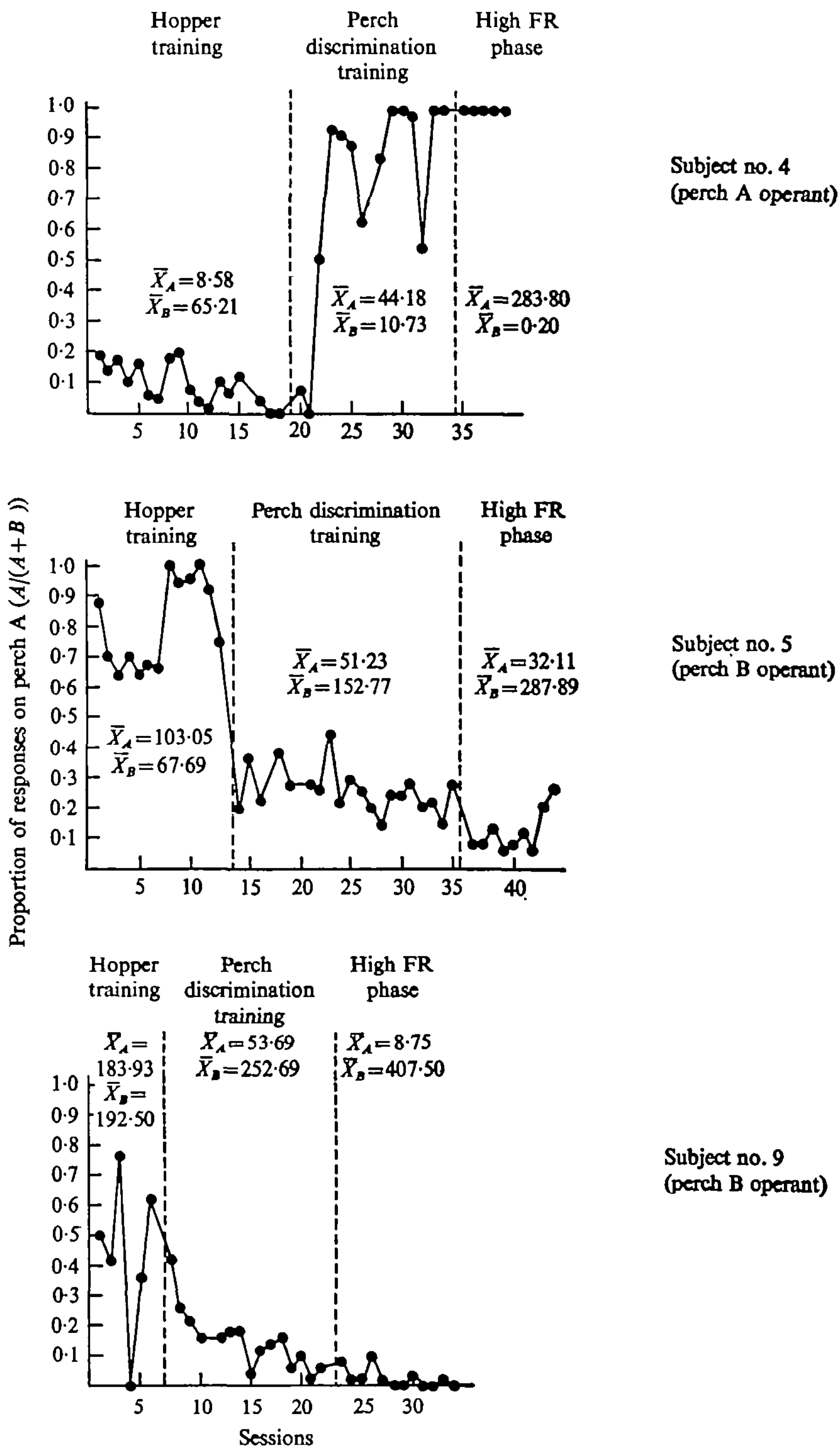

Fig. 3. Three phases of operant training. Mean number of responses per session during each phase is shown for both perches ($\bar{X}_A$ and $\bar{X}_B$).

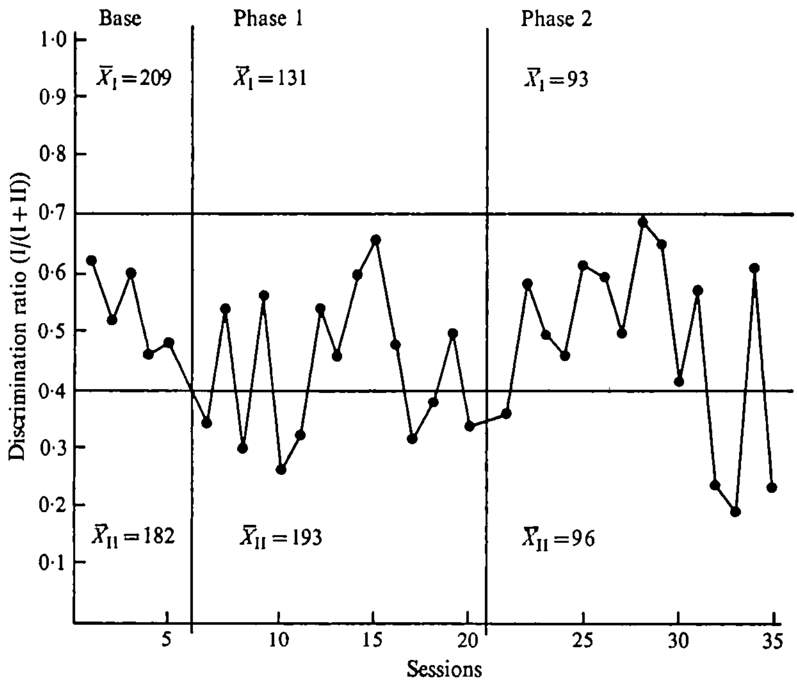

Fig. 4. Subject no. 4, discrimination training. Horizontal lines show range of responses for all subjects during base phase. See text for explanation of discrimination ratio.

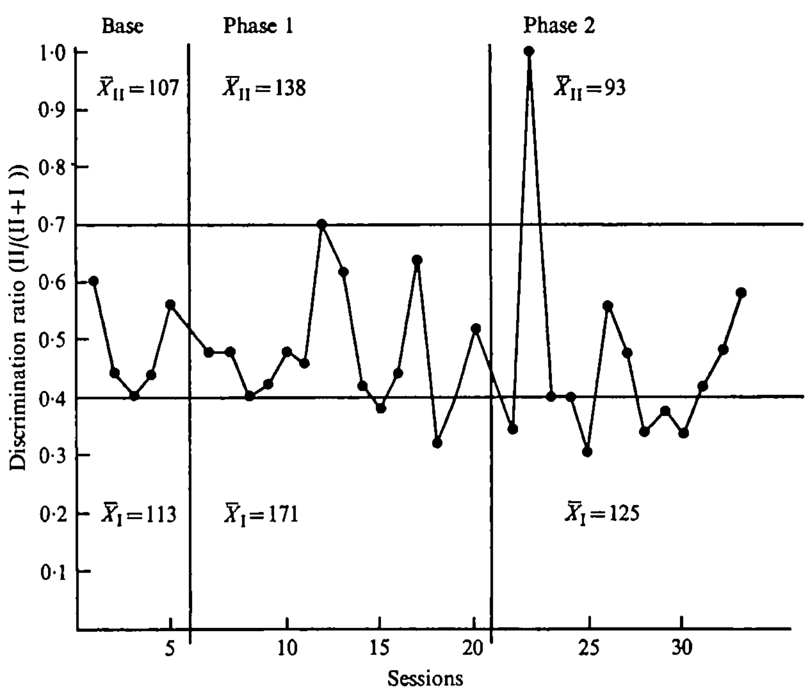

Fig. 5. Subject no. 5, discrimination training.

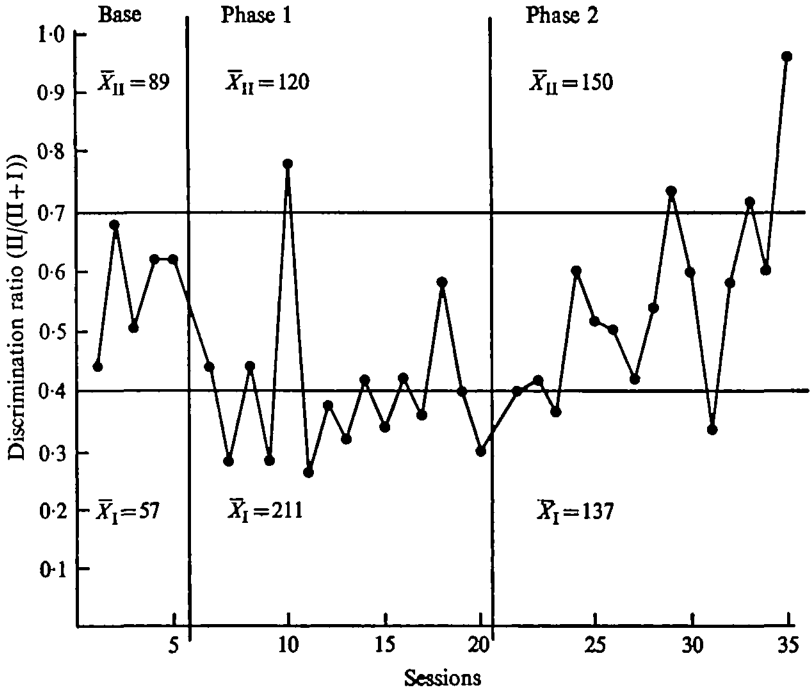

Fig. 6. Subject no. 8, discrimination training.

the range of responses in the base phase. Session 2 for subject 15 (Fig 8) should not be included because of the very low level of response during that session. The bird responded on the operant perch only sixteen times during presentation of S+ and once during S− (reinforcement during base was *not* contingent upon responding during presentation of S+). In other words, the subject earned only one reward during the session. The high peak must be regarded as an artifact due to the low level of response; the bird may well have earned the single reward at the beginning of the session and then stopped responding for the rest of the session. If this session is excluded, then, one can draw lines at 0·7 and at 0·4 to include the entire response range for the base phases of all subjects. The range is indicated by horizontal lines through these points on Figs. 4 to 8.

It is apparent that there were very few points on these graphs that lay above the range established during the base phase, while there were far more points below the base range – i.e. incorrect responses. No. 4 had no points above the line, and a total of eleven below the line during phases 1 and 2. No. 5 had seven points below 0·4, but only one point well above the 0·7 line (session 22). The latter can be dismissed as an artifact arising from a low level of responses (the subject earned two reinforcements when the session began, and then ceased responding). Subjects 9 and 15 had one and three points, respectively, above the base range of responses, but the fact that their responses did not continue at this level is strong evidence that learning did not take place. In addition, no. 9 had six and no. 15 had three points below the base range of responses.

Subject no. 8's single peak during phase 1 (session 10, Fig. 6) was probably an artifact also, since only two reinforcements were earned, and the number of correct

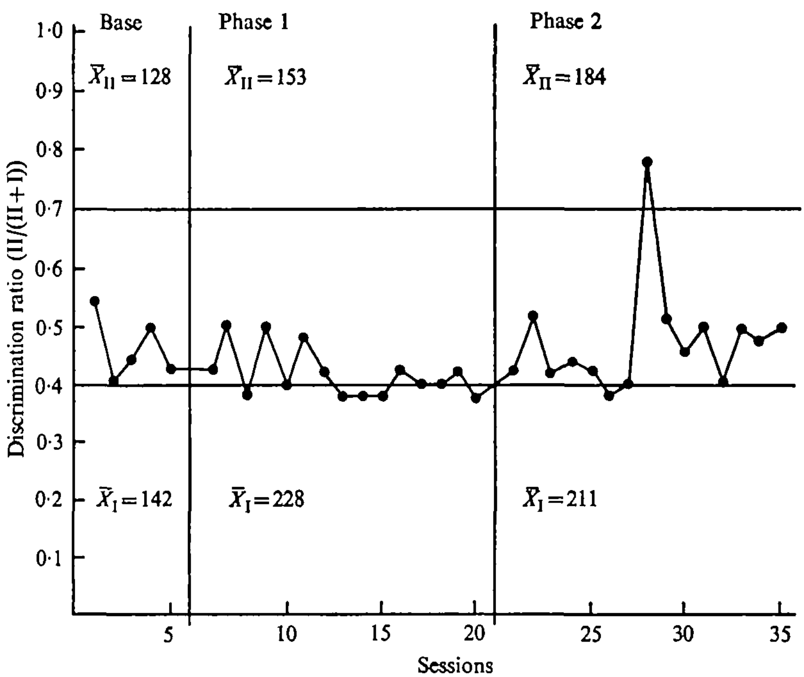

Fig. 7. Subject no. 9, discrimination training.

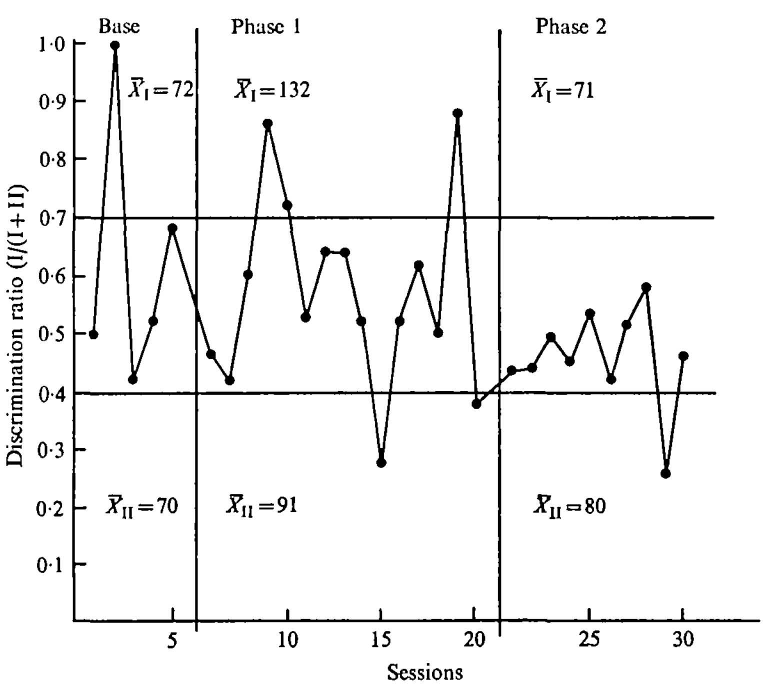

Fig. 8. Subject no. 15, discrimination training.

Table 2. *Subject no. 8: phase 2 of discrimination training*

Session	Responses on non-operant perch Star groups I	II	Responses on operant perch Star groups I	II	Number of reinforcements received
21	0	3	241	156	10
22	0	0	173	121	8
23	2	21	303	175	11
24	0	2	118	180	12
25	0	5	88	96	6
26	1	2	101	100	6
27	0	54	158	115	7
28	10	62	425	500	33
29	16	6	59	162	10
30*	0	0	64	94	6
31	1	6	122	64	4
32	11	4	68	93	6
33	5	0	85	227	15
34*	1	1	57	91	6
35	2	4	3	87	5

$\bar{X}_I = 211$, $\bar{X}_{II} = 184$

* 16-minute sessions. All others 20 min.

responses for this session (44) was well below $\bar{X}_{II}$ (120) for this phase. There was, again, no evidence such as a continued high discrimination ratio to indicate that learning took place during phase 1, and in addition there were eight sessions during phase 1 which fell below the base phase range. One can conclude, therefore, that no birds showed an increase in responses during presentation of S+ and extinction (a decrease in responses) during presentation of S−, which would have indicated an ability to discriminate the two groups of stars. Indeed, all subjects except no. 15 showed more sessions with higher total *incorrect* responses than correct responses (there were an equal number of sessions with correct and incorrect total responses for no. 15).

Subject no. 8 may have showed some ability to make a discrimination in phase 2, although there was certainly no striking difference in the response function as there was during perch discrimination (e.g. compare Fig. 2 with Fig. 6). However, in seven out of the last eight sessions the responses were higher during presentation of S+ than during S−, although only three of the points (sessions 29, 33 and 35) fell above the 0·7 line. That these values are not artifacts due to a low response level is apparent from Table 2, which presents the data for subject no. 8 during phase 2. Ideally, this subject should have been given another phase with random presentation of the stimuli, instead of alternating the stimuli beginning with S+, as had been done throughout phases 1 and 2. Unfortunately, the bird at this point suddenly dropped in weight and became extremely lethargic; further testing was abandoned after only one session with a random presentation of discriminative stimuli. During that one session there were no responses at all.

DISCUSSION

This study demonstrated that wild-caught white-crowned sparrows, both adults and juveniles, (1) can learn an operant, (2) can discriminate one perch from another, and (3) are capable of responding adequately to a relatively high fixed-ratio schedule of reinforcement. Furthermore, after simple initial selection by the experimenter for individuals that are easily handled, these birds can be given relatively short training sessions in an experimental chamber that is separate from the home cage. Operant conditioning in a separate experimental chamber has long been traditional with pigeons (e.g., Skinner, 1938). Hopping on a perch, rather than pecking a key, has been used as an operant response (Stevenson, 1967; Bastian & Hothersall, 1970), but the subjects were seldom handled. Bastian & Hothersall used redwinged blackbirds captured as 10-day-old nestlings; these would perhaps be more docile than birds caught either as adults or in the first juvenile plumage. Stevenson used sixteen first-year chaffinches with a single experimental chamber, but each bird lived in the experimental chamber during its 3 weeks of testing. The latter method has disadvantages if one needs to test a number of subjects in a short time, or during a particular season. It would also be difficult with the present method to run simultaneously a larger number of subjects than I used, since their response levels tended to drop off if they had either (1) to wait for their training sessions for more than an hour after the lights went on in the cage room or (2) to begin their training sessions more than 2 h before the lights in the cage room came on. However, one could conceivably get around this problem by having several cage rooms on staggered light schedules.

When presented with the task of discriminating two groups of stars, all subjects failed to show extinction during presentation of the negative discriminative stimulus; that is, they all failed to reduce their perch-hopping behaviour during the periods when food was no longer available. In addition, only one subject (no. 8) showed any indication that it was able to make a discrimination based on the larger signal lights (phase 2). Thus it remains in question whether white-crowned sparrows are capable of learning such a complicated discrimination task at all. How the discrimination task presented here compares in complexity with the task of orientation according to celestial cues (e.g. Sauer, 1957) is beyond the scope of this paper. It is worth noting, however, that Donner (1951) found the visual acuity of seven species of passerine birds to be poorer than that of humans. Adler (1963) concluded that theories of complete navigation (Type III of Griffin, 1952) require 'sense capacities far beyond those experimentally determined', although he supported the possibility of orientation according to celestial cues (Griffin's Type II), especially over short distances. On the other hand, radar observations of migrating birds (Bellrose & Graber, 1963; Bellrose, 1967) have shown that the birds were directionally oriented nearly as well under overcast skies as under clear skies. Direct observations of migrating birds from a small airplane (Bellrose, 1971) revealed them to be correctly oriented directionally, although a smaller number of birds was seen on completely overcast nights than on clear nights.

At any rate, the final word has not been spoken on the subject of orientation according to stellar cues. Operant conditioning, along with discrimination training, can provide yet another avenue of investigation. Presentation of the discriminative stimuli could well be arranged by projecting slides of real or simulated stars on a rear projection screen located at the top of an experimental chamber, thus making this method practicable in laboratories without planetariums. The trick, of course, will be to ask the birds a question they are capable of answering by making a discrimination.

SUMMARY

1. A method is presented for investigating the discriminative abilities which theories of stellar navigation assume small passerine birds to possess.

2. Six Gambel's white-crowned sparrows were operant conditioned to respond by hopping on one of two perches in order to gain access to food. Subjects were given short training sessions in an experimental chamber separate from their home cages.

3. Of the five subjects given discrimination training, in which reinforcement became contingent upon responding on the operant perch during presentation of one of two groups of star patterns, none showed evidence of learning the discrimination, although one subject may have learned to discriminate two larger signal lights.

I would like to thank Dr William J. Hamilton III for his planetarium, and Dr Barbara DeWolfe for traps, cages, and advice on handling white-crowned sparrows. Dr David Premack provided generous use of laboratory space and electronic equipment. Dr Mary Erickson gave me useful advice at several stages of my work and read the manuscript. Dr James Terhune provided invaluable technical assistance and critically read the paper. This work was supported in part by a grant from University of California Patent Funds.

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