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Variables affecting alternation behavior in the cockroach, *Blatta orientalis*

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To investigate alternation behavior in the cockroach as an invertebrate, three T-maze experiments were conducted assessing the effects of (a) intratrial (exposure) and intertrial (exposure to test) interval, (b) brightness similarity of the alternatives and response-direction factors, and (c) an initial free-choice vs. a varying number of forced-choice exposures. Alternation was enhanced with a long exposure on Trial 1, a short interval between Trial 1 and Trial 2 (test), greater dissimilarity (or discriminability) of the arm brightnesses and more frequent forced-choice exposures to an arm prior to test. These results highlight the role of intramaze brightness cues as controlling alternation in the cockroach and accord well with a response-to-change interpretation of the phenomenon. In addition, they suggest that the alternation paradigm can be used effectively to assay short-term memory storage in neurologically simple organisms.

Alternation behavior, the tendency of organisms to choose the unfamiliar or changed alternative in a two-choice situation, would appear to be a fairly ubiquitous phenomenon. It has been demonstrated in paramecia (e.g., Lepley & Rice, 1952), earthworms (e.g., Iwahara & Fujita, 1965; Wayner & Zellner, 1958), mealworms (e.g., Grosslight & Harrison, 1961), isopods (e.g., Iwata & Watanabe, 1957a, b), ferrets (e.g., Hughes, 1965), rats (see Dember & Fowler, 1958), children (e.g., Ellis & Arnoult, 1965), and adult humans (see Schultz, 1964). Apart from investigations employing rat and human subjects, however, the research with other organisms has served mainly to document the occurrence of alternation, for there has been little study of variables controlling the phenomenon.

The purpose of the present study was to extend investigation of the phenomenon in lower organisms by assessing factors affecting alternation in the cockroach as an invertebrate. Such an investigation is particularly important when it is considered that recent research with the rat (e.g., Bronstein, Dworkin, Bilder, & Wolkoff, 1974; Douglas, 1966; Eisenberger, Myers, Sanders, & Shanab, 1970) has contested the basis on which alternation occurs. Using the rat literature as a guide, the present study investigated six variables treated two at a time in three independent experiments which were ordered so as to facilitate parameter selection. In succession, the three experiments assessed the effects of: (1) intratrial (exposure) and intertrial (exposure to test) interval, (2) brightness similarity of the choice alternatives and response-direction factors, and (3) an initial free- vs. a varying number of forced-choice exposures.

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METHOD

Subjects

The subjects for all three experiments were naive, relatively intact, male and female adult cockroaches of the species *Blatta orientalis*. They were colony housed and maintained on a normal light-dark cycle, with training conducted between 2 and 5 p.m. Feeding of the subjects consisted of ad-lib water and Purina rat pellets.

Apparatus

The apparatus for all three experiments was an enclosed T-maze, with wooden walls, a transparent acrylic-plastic top, and a floor made of wire-mesh screening. The maze was uniformly 1.5 cm wide and 3.75 cm high, with the stem being 15.0 cm and each arm 7.5 cm. The entire maze was painted a mid gray, but wall inserts were available to effect different arm brightnesses ranging from black through dark, mid and light gray to white. A guillotine door was located at the choice point in each arm to prevent retracing and to permit forcing, i.e., by lowering the door to the inappropriate arm.

The maze was surrounded on three sides by a mid-gray screen (12.5 cm high × 22.5 cm wide on each side), with overhead fluorescent lighting providing a brightness of about 0.3 fc within the apparatus. The subjects were individually transported to and from the apparatus in an acrylic-plastic carrier (2.5 × 1.25 cm) which permitted exit through sliding doors at either end.

Procedure

Because of the similarity of the three experiments, the general procedure is first described, followed by the specific procedure for each experiment. One-half hour prior to testing, designated subjects were placed individually into 250-ml beakers which were then enclosed within a mid-gray surround (similar to that surrounding the maze but separate from it). Except in Experiment 3, where the effects of an initial free-choice vs. a varying number of forced-choice exposures were compared, the subject always received a forced choice on Trial 1 to either a black or white arm (counterbalanced for position and sex), where the subject was detained for a specified interval (*intra*trial interval). Between the end of Trial 1 and the beginning of Trial 2 (*inter*trial interval), the subject was returned to its 250-ml beaker located within the adjacent mid-gray surround. On Trial 2 (test), the subject was permitted a free choice, i.e., both arms were accessible.

Experiment 1. This experiment assessed the effects on alternation of varying intra- and intertrial intervals. One hundred and ninety-two naive subjects were randomly assigned to 12 groups of 16 subjects each, comprising a 3 by 4 factorial design of three intratrial intervals (0, 5, and 10 min) and four intertrial intervals (0, 15, 30, and 60 min).

Experiment 2. The second experiment assessed the effects of similarity of the stimulus alternatives and response-direction factors, e.g., specific turning response, "odor-trail" and "direction of movement" (see Douglas, 1966). Eighty naive subjects were randomly assigned to five groups of 16 subjects each. Following a 3-min intratrial interval on forced-choice Trial 1, the subjects of each group received a free choice on Trial 2 between their Trial 1 exposure brightness (black or white) and one of the following brightnesses: black, dark gray, mid gray, light gray, or white. In addition, to assess response-direction factors, the brightness-position experienced on Trial 1, e.g., black-right, was the same on Trial 2 for half of the subjects of each group, but was reversed to the other position, e.g., black-left, for the other half of each group. The intertrial interval was about 30 sec, the time required to adjust the apparatus.

Experiment 3. The third experiment assessed the effects on alternation of an initial free-choice vs. a varying number of forced-choice trials. Eighty naive subjects were randomly assigned to five groups of 16 subjects each. For one group, Trial 1 was a free choice between black and white arms, with brightness counterbalanced for position and sex. The subjects of the remaining four groups received 1, 2, 4, or 8 forced choices to a black or white arm, with brightness also counterbalanced for position and sex; however, for a particular subject, the brightness-position was the same over successive forced-choice trials. The test trial following either the single free-choice trial or the different number of forced-choice trials was a free choice, with brightness-position maintained from the initial trial(s) to the test trial. The intratrial interval on all trials was 0 min, i.e., the subject was removed immediately following choice. Similarly, the intertrial interval between successive forced-choice trials was 0 min, i.e., the subject received forced-choice trials in immediate succession. Prior to the test trial, however, the intertrial interval for each subject was 5 min.

RESULTS

The chi-square test was used throughout to assess deviations from chance, as well as differences among the groups. Because of the expectation of an alternation tendency, as opposed to repetition, and relatedly that such alternation would be influenced by the present variables in the same direction as indicated in the rat literature (see, e.g., Dember & Fowler, 1958), all chi-square values were interpreted on the basis of a one-tailed test. With few exceptions, however, all significant chi-square values satisfied a two-tailed test. Analysis of the free-choice (test-trial) data for all three experiments also included assessment of brightness and position preferences, as well as differences due to sex. Except in Experiment 3, however, these analyses yielded no significant effects.

Experiment 1: Intratrial and Intertrial Interval

Figure 1 presents percentage of alternation for the 0-, 5-, and 10-min intratrial groups as a function of intertrial interval. As shown, all groups were at or above an a priori (50%) chance level of alternation, so that, for the subjects collectively (N = 192), alternation was highly reliable ($\chi_1^2 = 17.52$, $p < .001$). Considered by groups (n = 16), however, only those with 75% alternation or more showed a significant deviation from chance ($\chi_1^2 = 4.00$, $p < .025$). Thus, reliable alternation obtained primarily under conditions of long intratrial and short intertrial intervals, specifically for the 5/0-, 10/0-, and 10/15-min groups (first and second numerals designating intra- and intertrial intervals, respectively). Basically the same results were obtained when alternation was evaluated by interval condition. Assessed by intratrial interval (i.e., collapsing intertrial subgroups), reliable alternation occurred for the 10-min condition ($\chi_1^2 = 10.56$, $p < .005$) and the 5-min condition ($\chi_1^2 = 6.24$, $p < .01$), but not for the 0-min condition ($\chi_1^2 = 2.24$, $p > .05$). Assessed by intertrial interval, reliable alternation was found for the 0-min ($\chi_1^2 = 10.08$, $p < .005$), for the 15- and 30-min conditions ($\chi_1^2 = 4.08$, $p < .025$ in each case), but not for the 60-min condition ($\chi_1^2 = 1.32$, $p > .10$).

Because of the gradual decline in percentage of alternation across conditions of shorter intra- and longer intertrial intervals, a χ^2 multiple contingency analysis of differences among the groups (Sutcliffe, 1957) showed no significant main effects or inter-

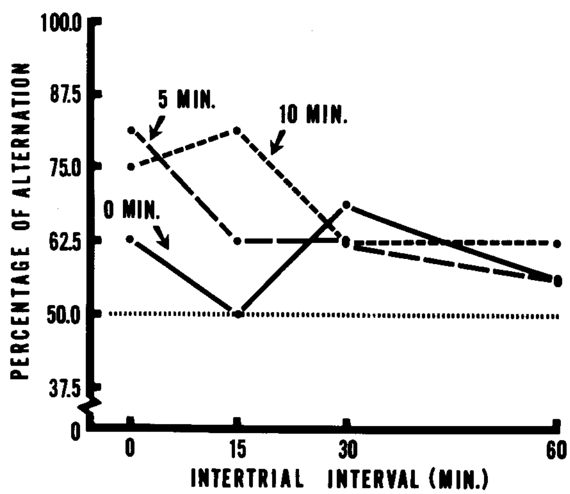

Figure 1. Percentage of alternation for the 0-, 5-, and 10-min intratrial groups as a function of intertrial interval.

action. However, when those interval conditions for which alternation would be expected to be pronounced, viz, the long (5- and 10-min) intratrial and the short (0- and 15-min) intertrial intervals, were contrasted with the remaining interval conditions, a significant difference was obtained ($\chi^2_1 = 4.10$, $p < .025$). A breakdown of this effect showed that the difference between the combined 5- and 10-min vs. 0-min intratrial condition was reliable when assessed over the 0- to 15-min intertrial conditions ($\chi^2_1 = 3.49$, $p < .05$) and that the difference between the 0- to 15-min vs. 30- to 60-min intertrial conditions was reliable when assessed over the 5- to 10-min intratrial conditions ($\chi^2_1 = 2.91$, $p < .05$). Collectively, these and the preceding results indicate that alternation was enhanced by the combination of a long intra- and a short intertrial interval.

Experiment 2: Arm Brightness and Response Direction

Figure 2 presents percentage of alternation for subjects of the "same" and "reversed" brightness-positions (i.e., from Trial 1 to Trial 2, test) as a function of dissimilarity of the arm brightnesses. (Degree of dissimilarity ranges from 0, no difference, e.g., black vs. black, through to 4, a maximal difference, i.e., black vs. white.) In this experiment, alternation was defined with reference to the subject's forced-choice brightness, so that for subjects of the "reversed" condition, a *repetition* of the forced-choice position response was scored as an alternation (of brightness), whereas for subjects of the "same" condition, alternation was scored as usual, i.e., as selection of the nonexperienced brightness position.

Excluding the 0-dissimilarity condition, in which same or reversed brightness position is meaningless (since the arm brightnesses are identical), the overall percentage of alternation for the "same" groups was 68.7 as opposed to 65.6 for the "reversed" groups, a nonsignificant difference ($\chi^2_1 = .07$, $p > .35$). (Inclusion of the 0 dissimilarity groups does not alter this outcome: $\chi^2_1 = .88$, $p > .15$.) Given that the "reversed" brightness condition opposed alternation of the forced-choice brightness and response-direction factors (e.g., specific turning response, odor trail, direction of movement), the absence of a difference between "reversed" and "same" groups indicates that the subjects were alternating predominantly on the basis of arm brightness.

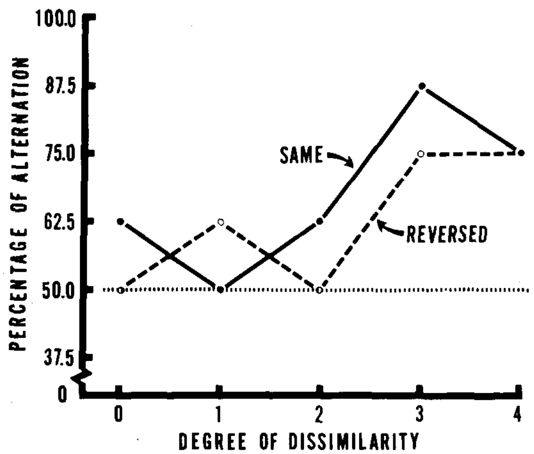

Figure 2. Percentage of alternation for groups (n = 8) receiving the same or reversed brightness-position on Trial 2, as a function of the degree of dissimilarity of the alternatives. (Degree of dissimilarity ranges from 0, no dissimilarity, e.g., black vs. black, to 4, maximal dissimilarity, i.e., black vs. white.)

As shown in Figure 2, percentage of alternation for each of the dissimilarity conditions (with respective "same" and "reversed" groups pooled) was above an a priori (50%) chance level, so that for the subjects collectively (N = 80) alternation was highly reliable ($\chi^2_1 = 7.20$, $p < .005$). Considered by dissimilarity condition (n = 16), however, only those with 75% alternation or more showed a significant deviation from chance ($\chi^2_1 = 4.00$, $p < .025$). Thus, reliable alternation occurred only for dissimilarity Conditions 3 and 4, i.e., where subjects were given a choice between highly dissimilar brightnesses (light gray vs. black or dark gray vs. white) and between completely dissimilar brightnesses (black vs. white). These two, high-dissimilarity groups did not differ from one another, but combined, they differed reliably from the remaining three groups ($\chi^2_1 = 4.04$, $p < .025$), which themselves did not differ. Consistent with the outcome of the "reversed" and "same" comparison, these data indicate that alternation was a positive (at least stepwise) function of the dissimilarity (or discriminability) of the arm brightnesses. (Note further that, under conditions of reduced or zero discriminability, there was no evidence of a tendency to alternate position as the overall percentage of position alternation for dissimilarity Conditions 0-2 was 52.1). The present findings are also important in supporting the conclusions of Experiment 1 regarding enhanced alternation with a long intra- and a short intertrial interval. Under similar interval conditions, specifically a 3-min intra- and a 30-sec intertrial interval, the high-dissimilarity groups of the present experiment showed an overall percentage of alternation (78.1) which was virtually the same as that (81.3) obtained for the 5-min intra- and 0-min intertrial-interval group of Experiment 1.

Experiment 3: Free- and Forced-Choice Exposures

In contrast to the results of Experiments 1 and 2, those of Experiment 3 showed a significant black preference on the free-choice test trial for subjects of the forced-choice groups ($\chi^2_1 = 19.60$, $p < .001$). Similarly, a significant black preference was exhibited on the initial trial for subjects of the free-choice group (χ^2_1 = 4.00, p < .025). Since these effects were not present in Experiments 1 and 2, they presumably related to sample selection. Accordingly, percentage of alternation for each group in Experiment 3 was adjusted for this bias following Douglas' (1966) formula.

Adjusted percentage of alternation for the groups (n = 16) receiving 1, 2, 4, and 8 successive forced-choice trials to one arm prior to the free-choice test trial was 75.9, 75.9, 96.0, and 92.0, respectively (as compared with actual values of 62.5, 62.5, 93.7, and 87.5, respectively); for the comparison group which received a single free-choice trial prior to the test trial, the adjusted percentage was 58.3 (as compared with an actual value of 43.7). Collectively, the forced-choice groups showed a highly reliable alternation effect (χ^2_1 = 31.08, p < .001); furthermore, each of these groups by itself deviated significantly from chance ($\chi^2_1 \geq 4.20$, p < .025). In contrast, alternation for the free-choice group was not reliable (χ^2_1 = .42, p > .25).

Analysis of the differences in percentage of alternation among the free-choice group and the several forced-choice groups showed a significant overall effect (χ^2_4 = 9.00, p < .05). Partitioning of this effect indicated that the difference between forced-choice Groups 1 and 2 and between forced-choice Groups 4 and 8 were not reliable, but that the difference between these two sets of groups was significant (χ^2_1 = 4.27, p < .025), as it was between the forced-choice groups and the free-choice group (χ^2_1 = 5.52, p < .025). However, the difference in alternation between the free-choice group and the single-trial forced-choice group was not reliable (χ^2_1 = 1.11, p > .10). These data indicate that, comparable to the effect of a long intratrial interval, a greater number of forced-choice exposures to one alternative prior to test also enhances alternation.

DISCUSSION

Collectively, the results of the three experiments indicate that alternation in the cockroach is facilitated by (a) a relatively long initial exposure (intratrial interval) to one alternative prior to choice, (b) a short intertrial interval between initial exposure and subsequent choice, (c) greater dissimilarity or discriminability of the alternative brightnesses, and (d) more frequent exposure to one alternative prior to choice. The comparisons of a free vs. a single forced-choice trial (Experiment 3) did not yield significance, but the direction of the difference favoring the forced-choice procedure is consistent with the reliable effect reported for the rat (e.g., Dember & Fowler, 1959). Such an effect is usually taken to indicate that an initial free-choice trial allows the subject to visually sample the nonchosen alternative from the choice point, with the result that the novelty or "stimulus change" provided by this alternative is reduced and hence alternation is as well. In the present study, it is not unlikely that a more optimal exposure condition (and a greater sample size) would have produced a significant difference between the two procedures; the conditions of Experiment 3 were specifically structured so as to minimize alternation with a single forced-choice exposure and thereby allow enhanced alternation with an increased number of forced-choice exposures.

The results of Experiment 2 on the effect of dissimilarity of brightness of the choice alternatives showed no difference in alternation when the stimulus brightness to which the subject was forced on the first trial was either retained in the same position or reversed to the other position for the free-choice test trial. This result is particularly important in view of Douglas' (1966) findings indicating that alternation for the rat is to some extent dependent upon odor-trail avoidance and particularly so on a tendency to reverse spatial direction. In that the reversed stimulus procedure of Experiment 2 placed these response-direction factors (as well as others relating to extra-maze stimuli, place cues, and specific turning responses) in opposition to the subject's exposure brightness and yet did not produce a significant decrement in alternation, the findings are clear in highlighting intramaze-brightness cues as a major determinant of alternation in the cockroach. This conclusion is bolstered by the related observations that alternation was enhanced with a long intratrial interval (Experiment 1) and with greater discriminability of the arm brightnesses (Experiment 2). Furthermore, under conditions of reduced or zero brightness discriminability, there was no evidence of a tendency to alternate on the basis of position cues alone.

A direct comparison of the present findings with Douglas' (1966) results is precluded by the different subjects employed and also by Douglas' use of an initial free-choice trial as compared with the forced-choice procedure of the present study (Experiment 2). However, recent research by Bronstein, Dworkin, Bilder, and Wolkoff (1974) has called into question the potency of response-direction factors as controlling alternation in the rat, and still other research (e.g., Eisenberger, Myers, Sanders, & Shanab, 1970), which has controlled for these factors in a free-choice situation, has indicated that rats will also alternate on the basis of intramaze visual cues. These comparable findings for the rat and the cockroach accord well with a response-to-change (novelty) interpretation of alternation behavior (e.g., Dember, 1956; Fowler, 1965) and also with other, both human- and animal-related, phenomena (see Cantor, 1969; Fowler, 1967) which have emphasized the role of prior exposure as a determinant of change. That is to say, a particular object, condition, or alternative can only provide a change relative to the antedating condition of stimulation to which the subject has recently been exposed. In illustration of this principle, the results of the present study indicate that the extent to which a change in stimulation is responded to, as in the alternation paradigm, is dependent not only upon the discriminability of the exposure and change (novel) alternatives, but also upon the duration and frequency of the antedating exposure and the temporal relation of such exposure (cf. intertrial interval) to the point of introduction of the change.

Apart from their significance for interpretations of exploratory phenomena, the present findings are also important in illustrating that the alternation paradigm can be used effectively to assay short-term memory mechanisms in neurologically simple organisms such as the cockroach. Evidently, increased "rehearsal" as provided by a long initial exposure or more frequent exposures which are relatively free of interfering input (cf. a free- vs. a forced-choice exposure) will facilitate storage, with the retention and display of such information being a function of the time to recall and the discriminability of the store from alternative features of the surround.

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