

Changes in elicited behavior as a function of experience with stimulation and available goal objects

P. J. WATSON

The University of Texas at Arlington, Arlington, Texas 76019

Behavior elicited from the lateral hypothalamus of rats became stronger as a function of experience with stimulation and available goal objects, and changes in latency and duration were the most sensitive measures of this response emergence. The strength of an elicited behavior was not diminished by a period of time-off from stimulation, indicating that the changes were relatively permanent; and the performance of an already established behavior remained stable during the emergence of a new behavior. Animals with extensive deprivation experience also displayed response emergence. These findings are consistent with the argument that learning variables influence the development of elicited behavior. However, experience with the stimulation apparently was not the primary determinant of response dominance in situations where different goal objects were made available simultaneously.

In response to electrical stimulation of certain areas of the brain, animals often engage in such consummatory activities as eating, drinking, and gnawing (Valenstein, Cox, & Kakolewski, 1970). This elicited behavior (EB) usually appears gradually, and repeated stimulation of the subject while in the presence of appropriate goal objects is necessary for the behavior to reach asymptotic strength (Valenstein, 1973). Documentation of this emergence of EB comes from data which demonstrate that the probability of obtaining a behavior from a single electrode site (Valenstein, 1971) and from different sites in the same brain (Bowden, Galkin, & Rosvold, 1975) increases as a function of continued experience with the stimulation. Systematic declines in the threshold intensity needed to evoke EB (Wise, 1968, 1971) further suggest that the behaviors take some time to stabilize.

One prominent interpretation of behavior elicited from the lateral hypothalamus is that the stimulation excites neurons mediating normal motivation states; thus, elicited eating theoretically reflects a response to the artificial activation of a central hunger system (Devor, Wise, Milgram, & Hoebel, 1970). On the other hand, the failure of animals to display EB during initial stimulation experience presents the possibility that the hypothalamically generated stimuli

may differ in some aspect from the internal cues associated with normal motivation states (Wise, 1974). For the normal motivation position, the conceptual difficulty lies in explaining why an elicited eater does not eat immediately in response to the stimulation state if that state is like the one produced during food deprivation. Since effective hypothalamic electrodes often evoke more than one behavior and since no apparent correlations exist between the anatomical site of an electrode and the type of behavior it supports, Valenstein et al. (1970) have argued that the stimulation may activate a single functional mechanism which contributes to the execution of a number of consummatory responses. Hypothetically, emergence progresses as an animal learns to channel his behavior into one of the consummatory activities normally affected by a relatively nonspecific motivational system situated in the lateral hypothalamus (Valenstein, 1971). Advocates of the normal motivation point of view have counterclaimed that several motivationally specific systems are organized within the locus of the effective stimulation (Roberts, 1969); and in regard to the emergence data, they have suggested that the stimulation may produce progressive alterations in tissue excitability (Caggiula, 1969; Wise, 1968) or that the stimulation may create an emotionality which competes with the immediate expression of the elicited response (Wise & Erdmann, 1973).

Wise (1974) has emphasized that a detailed examination of the emergence of stimulation-induced responding may be valuable in attempts to understand the mechanisms underlying EB. The purpose of this series of studies was to begin such an analysis by examining the emergence of consummatory behavior elicited from the lateral hypothalamus of rats. Particular

Support for this series of studies was supplied by the Organized Research Fund of The University of Texas at Arlington. The assistance of Dr. Verne C. Cox and M. A. Short is gratefully acknowledged. Portions of this study were presented at the Psychonomic Society convention in Boston, 1974. Reprint requests should be sent to P. J. Watson, who is now at the Psychology Department, University of Tennessee Chattanooga, Chattanooga, Tennessee 37401.

attention was directed to the possibilities that learning variables, emotionality, and/or alterations in tissue excitability might play a role in strengthening stimulation-induced behavior.

EXPERIMENT 1

As Wise (1974) points out, only two measures of EB emergence, response probability (Valenstein, 1971) and stimulation threshold (Wise, 1968), have been reported. The purpose of this first experiment was to investigate the development of EB by noting changes in the latency and duration of the elicited response in addition to alterations in its probability of occurrence.

Method

Subjects. The six male rats utilized in this study were selected out of a larger pool of animals on the basis of their display of some consummatory activity in response to lateral hypothalamic stimulation.

Apparatus. Behavioral testing was conducted in a clear Plexiglas observation chamber. The $11\frac{1}{2} \times 10\frac{1}{2} \times 16$ in. enclosure was open at the top so that electrode attachment wires could enter from above. Holes on opposite walls of the apparatus, approximately 2 in. above the wire mesh floor, allowed for the insertion of drinking tubes. Other goal objects were placed directly on the floor. During screening, Purina Lab Chow pellets were placed in diagonally opposite corners; however, it was noticed that stimulated animals often gagged while trying to eat this food. Since this gagging could have introduced an unwanted source of variance into the duration data, an attempt to eliminate the problem was made during subsequent sessions by using a more palatable diet, Kenl Ration Regular Flavor dog food. This dog food was contained in two glass furniture coasters and was located in the two corners where the food pellets had been. Finally, white pine wood blocks $\frac{3}{4} \times \frac{3}{4} \times 4$ in., were positioned in the remaining two corners during screening. A sine wave stimulator was used to administer the brain stimulation, and solid state programming equipment was used to control experimental events and to record latency and duration data to within 0.1 sec.

Procedure. The procedure included three basic stages: surgery, screening, and experimental testing. In the initial stage, bipolar stimulating electrodes (Plastic Products .018-312-.010) were implanted in the lateral hypothalamic area of rats. The animals were anesthetized with Equithesin and were placed in a stereotaxic instrument. With the head of the subject level between lambda and bregma, the uninsulated tip of an electrode was positioned 3.5 mm posterior to bregma, 1.6 mm lateral to the midline, and 8.6 mm below surface of the skull. At least 1 week intervened between the operation and the beginning of any experimental observation, and some of the subjects were used in an intracranial self-stimulation procedure before they were examined for EB.

Next, the animals were screened for the appearance of stimulation-induced responding. On each of the 3 days preceding the first screening session, the subjects were adapted to the testing environment by being placed in the apparatus for 15 min; and all three goal objects, food, wood, and water, were made available. With the beginning of screening, stimulation was scheduled to occur automatically in 30 sec on/30 sec off trials. The current intensity was raised gradually until the subject responded to the stimulation with short-latency locomotor-exploratory activity. The animals then were observed for the display of eating, drinking, and gnawing. Throughout the experiment, eating was defined as the biting, chewing, and swallowing of food while the rat was oriented towards the food; thus, mastication during locomotor

activity did not qualify as eating behavior. Gnawing was designated as the biting and chewing of wood while the subject remained stationary, and drinking was defined as occurring when the animal licked at the spout of a drinking tube.

A "standard session" of 20 stimulation-on and stimulation-off intervals was conducted during each daily screening session in which no consistent elicited behavior appeared. Any time an animal engaged in a goal-directed response during three consecutive stimulation-on intervals, the subject immediately was given a "qualifying" standard session, again consisting of 20 on and off trials. A rat qualified for further testing if it displayed EB during at least 30% of the stimulation-on intervals of the qualifying standard session. Subjects were screened on 3 consecutive days; therefore, the animals utilized in this study were those that began to respond within this time limit.

On the day following qualification, each subject was placed in the chamber; and the goal object that the animal had responded to most frequently during the qualifying standard session was the only one made available. A standard session was conducted that day and at the same time each subsequent day for at least 6 consecutive days. Subjects which continued to exhibit response trends at the end of this interval were monitored over a number of additional days until the behavior reached maximal values or until responding stabilized according to two of the three dependent variables within a 20% band for 3 consecutive days. Thirty minutes before these testing sessions, all subjects were given a fresh supply of dog food, which supplemented the usual Purina Lab Chow pellets. This procedure helped insure that animals given access to more dog food in the chamber were satiated during experimental observation. The current intensity administered to each subject remained unchanged from that used in the qualifying standard session. An observer recorded the latency and duration of EB during each stimulation-on interval; and when a rat failed to respond within this interval, it was arbitrarily assigned a latency of 30 sec and a duration of 0 sec for that particular trial. Since stimulation trials were scheduled to last for a fixed interval of time, the duration measure was inversely related to response latency to a large degree.

Results and Discussion

All six animals that qualified for further testing did so during the initial screening session. Three rats (32F, 48F, and 2G) proved to be elicited eaters, while two (11F and 15F) were drinkers and one (37F) was a gnawer.

In the experimental sessions, only 37F failed to display clearly some strengthening of the elicited response. During the first testing session, 37F gnawed with a 100% probability. Such consistency was never reached again in the next 2½ weeks, and the percent trials/session in which this animal gnawed declined to as low as 35%. In addition, the mean latency value for 37F on the initial day was 10.9 sec with a mean duration of 11.4 sec. Thereafter, the latencies generally became slightly longer while the durations remained fairly stable. Two other unusual response characteristics of 37F were apparent. First, this subject was unlike the others in exhibiting a high level of behavior during the stimulation-off intervals, often gnawing during as many as 35% or 40% of these intervals. Secondly, 37F engaged in a number of stimulation-induced behaviors that came to compete with gnawing. One common response was grooming; and another, which at times seemed to be the strongest of all,

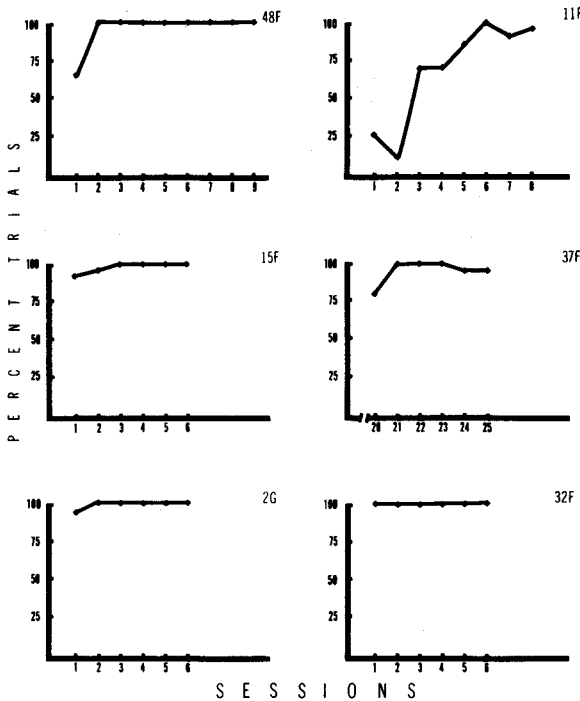


Figure 1. Percentage trials/session in which elicited responding was displayed by each subject.

was a vigorous licking along the chamber floor and walls. In summary, if any response emergence did occur with 37F, it did not do so with the target response, gnawing, but may have done so with other behaviors such as grooming and licking.

The erratic nature of 37F's stimulation and inter-stimulation behavior suggested that perhaps the electrode was not yielding stimulation-bound behavior. To test this possibility, 37F was given access to water rather than to wood during the next six sessions. Figure 1 illustrates the changes in the probability of response for all animals, including 37F after the switch to water. That 37F's electrode was capable of supporting stimulation-induced responding was demonstrated by the rapid appearance of drinking, which reached 100% consistency as early as the second water session. The data of four other animals (11F, 15F, 48F, and 2G) were supportive of Valenstein's (1971) finding that the probability of obtaining EB increases as a function of experience. Subject 11F presents the most dramatic demonstration of the effect. This animal drank only on 25% of the first session trials and only during 10% of the trials on the next day; however, drinking climbed to 100% on Day 6. Only rat 32F exhibited maximal responding from the outset according to this dependent variable.

Figure 2 shows that the changes in the latency and duration of EB were even more striking than the changes in response probability. In the final stages of the experiment, each animal responded to the stim-

ulation with shorter latencies and longer response durations than at the beginning. This emergence of EB was fairly rapid in some cases, with the process essentially being completed in two or three sessions. In other cases (11F and 48F), the emergence took considerably longer. The behavior of 48F was particularly noteworthy because the elicited eating of this subject appeared during every stimulation interval of Sessions 2-9; thus, while the probability of responding reached asymptotic levels quite early, the latency and duration measures continued to change gradually over a much longer interval.

Group analyses of the data revealed that the observed changes were statistically reliable. Since the animals received different amounts of stimulation experience, an analysis of variance for each dependent variable was conducted using the data from the first three and the last three sessions only. In addition, all the data were analyzed once with 37F's gnawing data and once with its drinking data. Finally, an arcsin transformation of the percentage measures was utilized as recommended by Myers (1972). With 37F's gnawing data, the changes in response probability did not reach significance ($F = .93, df = 5/25, p > .20$). However, both the latency ($F = 2.75, df = 5/25, p < .05$) and the duration ($F = 5.10, df = 5/25, p < .005$) measures yielded changes indicative of response strengthening. Figure 3 presents the group raw data and percent change data of all the animals, including 37F's drinking performance.

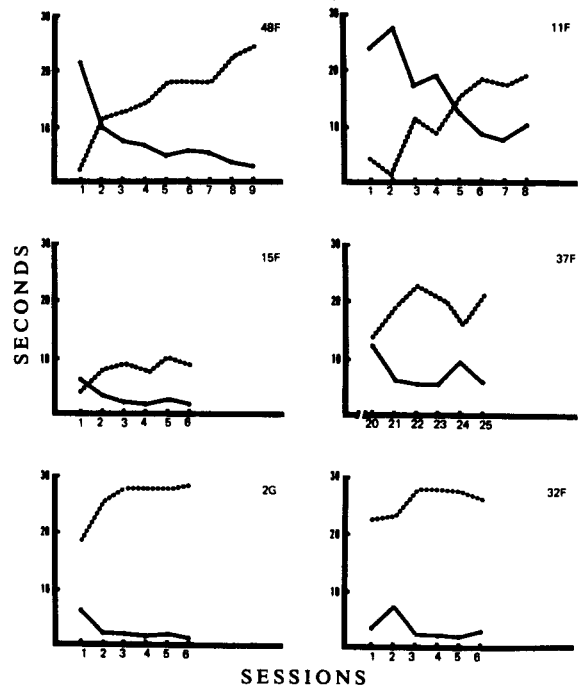


Figure 2. Mean trial latency (solid lines) and duration (dotted lines) of EB during each session for each subject.

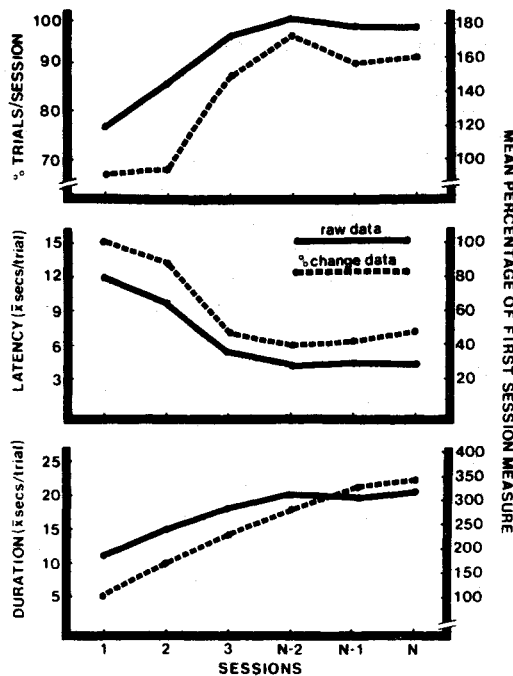


Figure 3. Average raw and percentage change data for the group of subjects during the first three and last three sessions. The averages include 37F's drinking performance.

Analyses of the raw data revealed significant results on all three measures. Response probabilities increased ($F = 3.49$, $df = 5/25$, $p < .025$), latencies became shorter ($F = 4.80$, $df = 5/25$, $p < .005$), and durations became longer ($F = 6.69$, $df = 5/25$, $p < .001$). The percent change figures give an indication of how much, on the average, an elicited response varied across sessions. They were obtained by dividing each subject's daily value of each dependent variable by the value of that variable recorded on the first testing day. By the last session, the response probabilities had increased to 162% of the first session performance while latencies had declined to 45% and durations had increased to 334% of initial values.

The findings of this experiment replicate and extend Valenstein's (1971) observations. In addition to increments in response probability, the period in which stimulation-induced behavior became stronger was characterized by reductions in response latency and by increases in response duration. Further, latency and duration seemed to be the more sensitive measures of EB emergence, because they often continued to change after the response probabilities had reached asymptotic levels. In some cases, the latency and duration did stabilize rapidly; however, two animals in particular displayed long-term changes that seemed incompatible with the idea suggested by Roberts (1969) that these variables improve only briefly during an interval in which subjects learn to locate and to approach the goal objects. The data imply that if

learning is at all involved in the emergence process, then it must be of a more substantial nature.

One factor that must be discussed is the possibility that changing from food pellets during screening to dog food during testing was a critical variable in producing emergence. While it cannot be ruled out that adaptation to a novel diet contributed in some portion to the response strengthening, it seems unlikely that it was a prime determinant, because those subjects given water, a familiar goal object, displayed the same emergence as those given food. The elicited gnawing of 37F perhaps should be given special consideration, because it did not strengthen, but rather seemed to weaken according to two of the three dependent variables. It is impossible to form any conclusions on the basis of a single subject, but one possibility is that elicited gnawing is fundamentally different in some important way from elicited eating and drinking. Consistent with this suggestion is the report of Cain, Skriver, and Carlson (1971) that stimulation-induced gnawing in the prairie dog "habituates" rather than emerges. In addition, Powley and Opsahl (1976) have reported that vagotomy may completely eliminate elicited eating while having no effect on elicited gnawing. This further suggests possible differences in the physiological foundations of the two behaviors. Finally, it should be emphasized that for all animals some response emergence undoubtedly occurred during the initial screening session and that the data therefore probably do not describe the response emergence phenomenon from its outset.

EXPERIMENT 2

The purpose of this experiment was to determine if the changes in stimulation-induced behavior are relatively permanent. One possible explanation of the growth of EB is that the electrical stimulation sensitizes the tissue underlying the elicited response and that the entire strengthening process reflects this sensitization (Cox & Kakolewski, 1971; Wise, 1968). Such an interpretation would gain strong support if the emergence were reversed by a period of no stimulation. Valenstein (1971) reported that EB remained fairly stable after 2 weeks without testing; however, he only monitored response probability, which the first experiment revealed to be a comparatively less sensitive measure of emergence. Specifically, this second experiment asked whether or not the latency and duration data remain stable after an intermediate period of time without any stimulation experience.

Method

The same six animals served as subjects in this experiment. Following the last day of observation during the first study, each rat was given a 10-day period of rest from stimulation. On Day 11, the subjects were administered another standard test using the same procedures as before. The performances during the last day be-

fore the rest (Phase I) and the first day after the rest (Phase II) were compared with a *t* test for related measures.

Results and Discussion

As depicted in Figure 4, there were virtually no changes from Phase I to Phase II in any response measure. Behaviors which occurred with a mean frequency of 98.3% of the time in Phase I climbed to 100% in Phase II [$t(5) = 1.59, p > .10$]. Both the durations [$t(5) = 1.21, p > .10$] and the latencies [$t(5) = 2.08, p > .05$] declined slightly, but nonsignificantly.

In short, even as measured by the more sensitive latency and duration values, EB was little effected by time-off from stimulation. This finding is in accord with the probability of response data presented by Valenstein (1971), and it indicates that the emergence process cannot reflect a short-term sensitization of some critical neural substrate. However, it does not eliminate the possibility that more permanent neuronal alterations unrelated to learning could be of causal importance. That repeated electrical brain stimulation can cause long-term physiological changes is suggested by work on the kindling effect (Gaito, 1974).

EXPERIMENT 3

The purpose of this experiment was twofold. First, an attempt was made to determine what factors, if any, predict which behavior dominates when an animal has access to a number of goal objects. Secondly, this experiment sought to determine if a new elicited response goes through an emergence process similar to the first one. Valenstein (1971) demonstrated that the display of a new response becomes more probable with repeated stimulation; and because that study was a first effort at demonstrating the phenomenon itself, no precautions were taken to insure that the

first behavior was at asymptote before the switch was made to another response. This procedural consideration raises the possibility that these data reflected systematic changes in tissue excitability or in emotionality that had not been completed when the new goal object was introduced. In the present experiment, this potential problem was controlled for in two ways. First, animals were at asymptote before they were switched; and secondly, the performance of the first elicited response was monitored throughout the testing sequence to guarantee that no changes were occurring in the first behavior while the new response was given the opportunity to emerge.

Method

The experiment was conducted in three phases, and the same six subjects were utilized. In the first phase, each rat was given a standard session with both food and water available; and the percent trials in which eating and drinking occurred and the duration of each response were recorded. The procedure for examining the emergence of a new behavior began after this initial competition session. At approximately the same time every day for 12 consecutive days, each subject was given access to food only or to water only during a standard session. Each goal object was presented on alternate days, with half the subjects getting the new goal object during the initial session and with the other half receiving the old one. Thus, each animal had six standard sessions with the old goal object and six with the new. At the completion of this phase, three more competition sessions followed; and, as in the first one, both food and water were presented to the animals.

Following this study, some of the rats were examined in another experiment (Watson & Cox, 1976). After that study, each subject was given an overdose of anesthetic and intracardially perfused with 0.9% saline and 10% Formalin solutions. The brain of each animal was removed and stored in Formalin. Then coronal sections of brain tissues were mounted and stained with cresylecht violet, and the König and Klippel (1963) atlas was used in locating the position of the electrode tip. It was not possible to find the electrode placement in subject 11F. Data from the other five animals were combined with that obtained from subjects used in the fourth experiment, increasing the sample size available for analysis purposes.

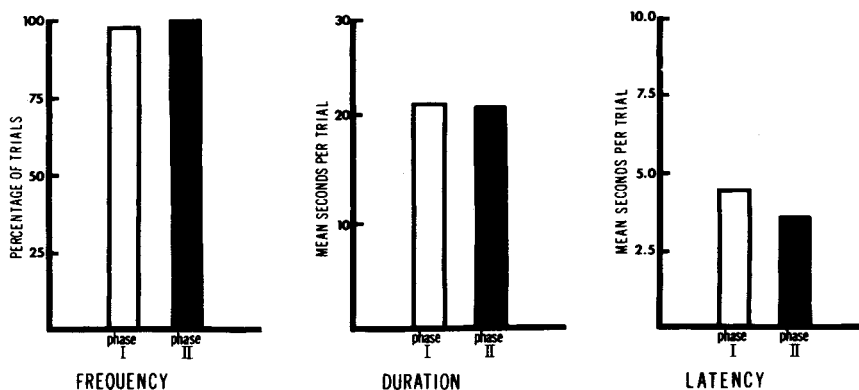


Figure 4. Group means of each dependent variable on the day before (Phase I) and the day after (Phase II) 10 days of no stimulation experience.

Results and Discussion

Initial competition session. If learning were the sole determinant of response dominance during competition sessions, the old, already acquired behavior should have been relatively stronger than the new, unpracticed one. On a group level, this prediction was upheld. According to a one-tailed *t* test for related measures, the old behavior occurred during a greater percentage of the trials ($\bar{X} = 83\%$ compared to 18%) than did the new [$t(5) = 3.00, p < .025$]; and the mean duration/trial (16.7 sec for the old and 3.0 sec for the new) also was significantly longer [$t(5) = 2.50, p < .05$].

Examining the data of each subject individually revealed a notable exception to this prediction of old behavior dominance. Animal 11F ate during 60% of the trials for an average of 8.3 sec/trial; and this new response was more prevalent than the already established drinking, which occurred during 40% of the trials for an average of 5.9 sec/trial. A high incidence of eating during the interstimulation interval suggested the possibility that the subject was not satiated while being examined; therefore, 1 more day of competition testing was run before changing to the single goal object procedure. Once again, the new response dominated in terms of the percentage of trials (75% to 35%) and in terms of the mean duration/trial (13.0 sec to 4.3 sec). A reexamination of 11F's record during the very first screening procedures of the initial experiment eliminated the possibility that 11F "learned" to eat food then. Although some wood gnawing had occurred, no food intake at all was elicited during early stimulation experience. Another possibility was that 11F learned to eat so rapidly during the competition testing that the new response had emerged enough to be dominant by the end of the session. The behavior of 37F suggested that this could happen. This animal exhibited elicited drinking, the old response, during nine of the first 10 stimulation trials, while eating appeared only once. However, drinking was elicited three times during the last half of the session, while eating occurred seven times. No such within-session emergence was discernible in 11F's data. In summary, the initial competition data indicated that, as a group, the old behavior was stronger than the new; but the fact that 11F most often engaged in a behavior it had never displayed during previous stimulation experience suggests that learning cannot be the sole determinant of response dominance.

New response emergence. Five of the six animals exhibited the new elicited response. For these subjects, an analysis of variance of the raw data indicated that there were no significant day-to-day changes in the old behavior according to any of the dependent variables: percent trials/session ($F = .77, df = 5/20, p > .10$), latency ($F = 1.55, df = 5/20, p > .10$),

and duration ($F = 1.02, df = 5/20, p > .10$). In contrast, the appearance of the new response grew more probable with experience ($F = 4.50, df = 5/20, p < .01$); and its latency decreased ($F = 4.55, df = 5/20, p < .01$) and duration increased ($F = 4.71, df = 5/20, p < .01$). The duration results presented in Figure 5A as raw data and in Figure 5B as percent change data demonstrate the stability of the old behavior and the growth of the new.

Also, the data were examined for the possibility that differences in the strengths of the old and new behaviors during initial and asymptotic performance could supply evidence as to why the stimulation elicited one behavior over the other during screening procedures. For example, it would seem logical to expect the old behavior to be stronger, since it was more potent at the beginning of these experiments. As measures of initial and asymptotic performance, the medians of each of the three dependent variables during the first three and the last three single goal object sessions, respectively, were determined for both responses. No significant differences between these measures of old and new behavior were detected.

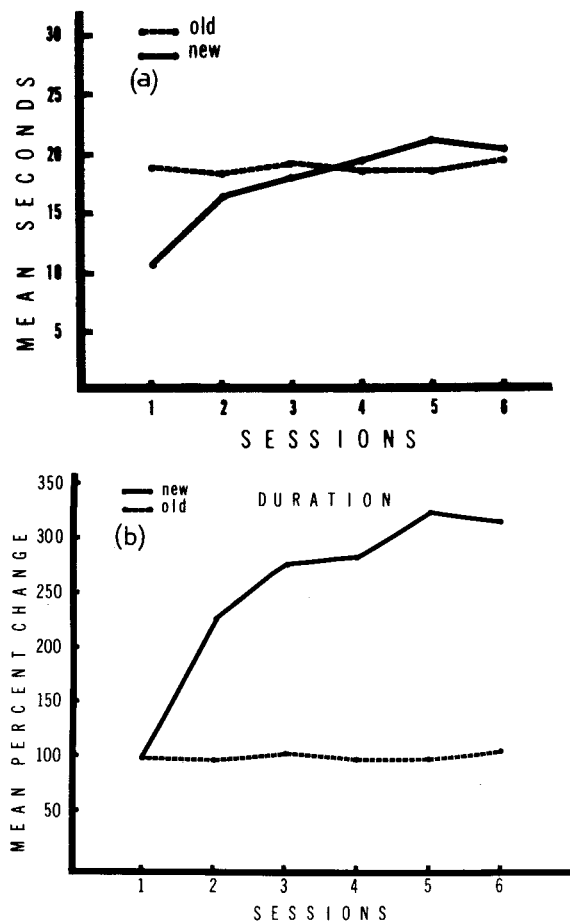


Figure 5. Average raw and percent change duration data for the new and old responses.

The generality of this result was uncertain for several reasons. First, the data came from a small sample containing the five subjects that displayed both responses. Secondly, unlike the procedure with the old response, the new behavior was not observed until it reached asymptote; rather, testing was conducted for an arbitrary number of sessions. Finally, and perhaps most critically, the food available during initial screening, Lab Chow pellets, was not the same diet presented during the subsequent sessions. When the initial and asymptotic data were organized in terms of the type of behavior elicited, eating vs. drinking, the initial duration of food intake was longer than that for water intake [$t(4) = 3.246$, $p < .05$], but no other comparisons were significant.

Only 48F, an elicited eater in the first experiment, failed to engage in the new target response with any degree of regularity; however, stimulation-bound responding was still apparent, because the stimulation evoked vigorous licking of the floor and walls. It should be emphasized that extreme care was taken to guarantee that the chamber was clean during these sessions, because it was thought that 48F might be licking at minute bits of food left on the wire floor from other procedures. Despite the precaution of washing and drying the entire chamber several times before testing, 48F's licking behavior persisted.

This experiment documents new response emergence following stabilization of the first behavior. As pointed out by Wise (1974), any hypothesis that tissue alterations underlie emergence appears to be challenged by this type of finding. The tissue at the electrode tip already had been bombarded by the stimulation for as many as 500-plus trials, and the first behavior had fully emerged before an attempt was made to switch to the new behavior. In addition, the strength of the first response remained constant during new behavior emergence. All these points argue for the stabilization of neuronal processes before second behavior emergence. A remaining possibility is that the stimulation sensitized neuronal systems away from the electrode tip. If this were the case, these distant systems would have to be different for different behaviors because any argument against sensitization at the electrode tip also applies to a hypothesis of sensitization at a single substrate efferent to the stimulated tissue. Even more precisely, the data would seem to necessitate the assumption that any presumed sensitization at different substrates would be possible only under specific environmental conditions. For example, to explain why the substrate of the second behavior was not sensitized while that of the first behavior was, it would seem necessary to claim that tissue mediating the second response could be sensitized only after appropriate goal objects had been made available. Other alternatives might be formulated. The point is that new

behavior emergence may not absolutely disprove the tissue sensitization hypothesis; however, as Wise (1974) suggests, it places severe constraints on the concept and in the process makes it seem implausible.

These data also may serve to put limits on the idea that a stimulation-induced emotionality interferes with the expression of behaviors appropriate to elicited hunger and thirst states. Such a hypothesis also must explain why EB eventually does emerge. One possibility is that the subject habituates to or learns to cope with the arousing properties of the stimulation; however, the emergence of a new behavior suggests that this cannot be the case. Hypothetically, the subject would have adapted to the emotionality during first behavior emergence; and therefore, nothing would remain to block the immediate appearance of the second response. Other possibilities compatible with the emotionality-normal motivation argument were considered in Experiment 4.

Final competition sessions. If changes in response strength had taken place during the preceding single goal object procedures, the expectation probably would be that the magnitudes of the old and new behaviors during final competition sessions would have changed from what they were during initial competition. The logical outcome would be a relative strengthening of the new response. To examine this hypothesis, the initial competition data and the data from the first session of the final competition sequence were compared with one-tailed *t* tests for related measures; and two results were consistent with the idea that emergence had occurred. First, the probability of obtaining the new response increased significantly in the later session [$t(5) = 2.33$, $p < .05$]; and secondly, the duration of the older behavior declined [$t(5) = 4.55$, $p < .05$]. This latter finding suggests that the new response had grown enough in potency to compete more effectively with the old response.

Overall, during the last three sessions, half the subjects displayed the new response to a greater extent than the old when given simultaneous access to both appropriate goal objects; and, of course, the opposite was true of the other three animals. Figure 6 presents the group competition data organized along new-old and food-intake/water-intake classifications, and it illustrates the relative unimportance of the new-old dimension in determining response dominance. The differences in percentage trials/session and in durations did not approach significance (both $F_s < 1.0$). Quite clear differences appeared when the data were organized according to the type of behavior displayed. All six animals ate more often than they drank according to the percentage trials/session ($F = 17.09$, $df = 1/5$, $p < .001$) and the duration ($F = 48.51$, $df = 1/5$, $p < .001$) variables.

In conclusion, data obtained in this final competi-

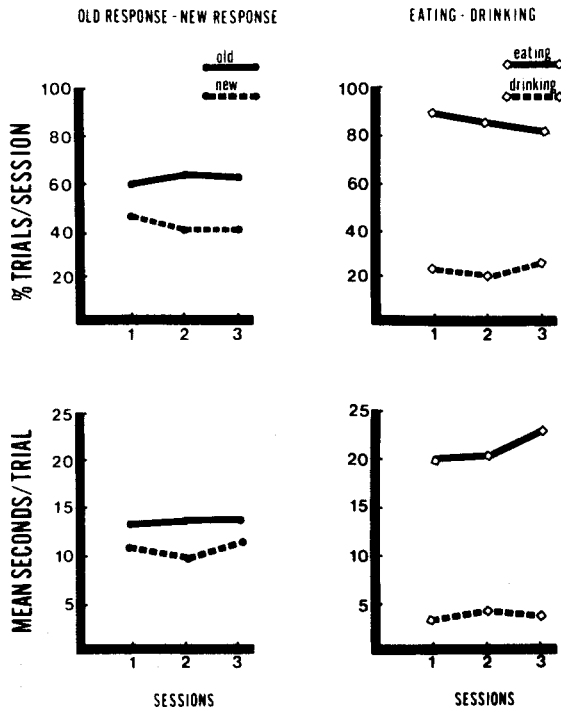


Figure 6. Group competition percentage trials/session and duration data organized according to the new-response/old-response and food-intake/water-intake classifications.

tion sequence tend to support points made previously. First, the increase in new and the decrease in old response strength during the first session of this sequence relative to the initial competition session further illustrates the response strengthening process. Secondly, the failure of the old response to dominate significantly during competition argues against experience with the stimulation and goal objects as being the sole determinant of response dominance. The subjects were given at least twice as much experience with the old goal object as with the new. If learning were the only variable determining response strength, it would seem reasonable to expect the more "practiced" behavior to be the stronger. The fact that eating dominated over drinking in every case argues for the contribution of nonexperiential, neuronal determinants.

EXPERIMENT 4

From the vantage point of a normal motivation view of EB, the conceptual difficulties presented by emergence exist only if it is assumed that subjects enter experimental testing with the ability to respond optimally to the physiological stimuli associated with need states. Ghent (1951, 1957) has demonstrated that the eating and the drinking performances of rats improve with increased experience with deprivation. Therefore, previously undeprived animals apparently

learn to respond to normal motivation states; and the emergence paradox may be based on a faulty assumption concerning the role of experience in normally motivated behavior. This experiment sought to determine if experience with need states would eliminate the emergence process.

Method

Eight male rats that displayed EB served as subjects in this experiment. The basic procedures remained unchanged from those of the preceding experiments with a few important exceptions. First, the animals were well adapted to the dog food diet before screening. For at least 1 week before receiving stimulation in the chamber, a fresh supply of this food was presented daily in the animal's home cage.

Secondly, testing for the emergence of the first response did not begin immediately after screening. Instead, animals that had qualified as elicited eaters were placed on a food-deprivation schedule, while animals that displayed elicited drinking were water-deprived. At the same time every day for 10 consecutive days, the subjects were placed in the chamber and were given 30-min access to the goal object appropriate to their deprivation state; and the experimental chamber was the only location where this goal object was made available. Immediately after the last session of this 10-day interval, the subjects were taken off the deprivation regimen. Testing for first behavior emergence began the next day and continued until the subject's elicited responding had stabilized.

Next, an attempt was made to switch the animals to a new response; but before stimulation sessions were conducted, the rats were deprived of the new goal object for a period of 10 days. In other words, elicited eaters were water-deprived and elicited drinkers were food-deprived. Access to this goal object once again was limited to 30-min sessions in the experimental chamber. Testing for second behavior emergence followed until stable performance was reached. In the final phase of the experiment, three competition tests were conducted. Histological procedures followed completion of another study (Watson & Cox, 1976).

Results and Discussion

Response emergence. Five of the animals (65G, 21H, 29HB, 5U, and 14U) qualified for further testing during the first screening session, and two others (4U and 11U) met criterion in the second session. Subject 8U did not qualify within three sessions. However, its aroused behavioral response to the stimulation suggested that EB would appear with a minimal amount of additional experience; and this subject began eating during the fifth screening session. All animals except 21H ate more than they drank during the qualifying standard session, and all subjects except 29HB switched to the target response during the second response emergence procedure.

Figure 7 illustrates the first and second response data for the seven subjects that displayed two responses. Two characteristics are immediately apparent in these graphs. First, some response strengthening was observed, although it was more apparent with the second behavior. Secondly, the first response was stronger than the second. The data of 29HB was not included in this figure or in the analyses because its performance would have exaggerated the contrasts between the first and second responses, and it was of interest to determine if significant differences between

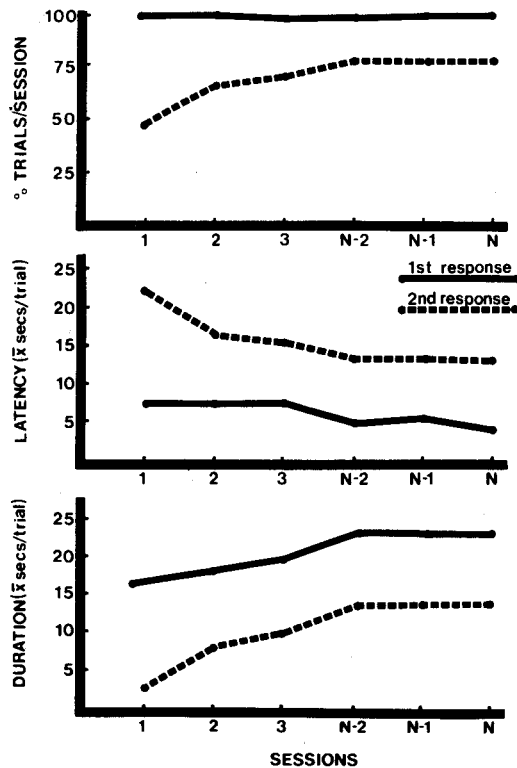


Figure 7. Average group measures of each dependent variable during the first 3 and last 3 days of single goal object testing.

responses did appear in those subjects displaying both behaviors. Nevertheless, 29HB's first elicited response did go through a period of emergence; but the only noticed behavior of this animal during the second response procedure was locomotor-exploratory activity.

For the seven rats exhibiting both behaviors, the first response occurred with a higher probability in single goal object sessions than did the new response (Response effect, $F = 8.73$, $df = 1/6$, $p < .05$); and the increases in response probability over days (Days effect, $F = 4.39$, $df = 5/30$, $p < .005$) were more marked for the second response (Response by Days effect, $F = 5.92$, $df = 5/30$, $p < .001$). In fact, the probability of the first response on the first day was not significantly different from its final day probability [$t(6) = 1.00$, $p > .10$]. In terms of the latency data, EB appeared significantly more rapidly as a function of experience (Days effect, $F = 8.25$, $df = 5/30$, $p < .001$), and the improvement over time was greater for the second response (Response by Days effect, $F = 3.32$, $df = 5/30$, $p < .05$). Again, changes in latency performance of the first behavior from the first to the last session were not statistically significant [$t(6) = 1.79$, $p > .10$]. The latencies of the first response were significantly shorter than those of the second (Response effect, $F = 12.36$, $df = 1/6$, $p < .025$). Also, the first

response occurred with a greater mean duration than did the second (Response effect, $F = 28.45$, $df = 1/6$, $p < .005$), and these durations became longer with experience (Days effect, $F = 30.14$, $df = 5/30$, $p < .001$). The response and days duration effects did not reliably interact (Response by Days effect, $F = .58$, $df = 5/30$, $p > .20$), reflecting the observation of significant duration increases in the first response [$t(6) = 5.08$, $p < .01$] as well as in the second. As in the first experiment, latency and duration values continued to change after the percentage trials/session measure had reached asymptotic levels. While some animals displayed stable latencies and durations within 2 or 3 days, this was not always the case. Most notably, 65G did not show maximal duration responding until Session 10, and 4U did not reach this value until Session 12.

This portion of the experiment demonstrated that prior experience with deprivation states does not eliminate response emergence. With the first response, some evidence was obtained that deprivation experience may have attenuated emergence because changes in percentage trials/session and in latency were not statistically significant. Nevertheless, the duration of the first response and all three second response dependent variables revealed significant strengthening. The emergence paradox therefore remains essentially intact, because animals who had "learned" to engage in behavior appropriate to normal motivation states did not immediately respond to hypothalamic stimulation at asymptotic levels. These data also seem to eliminate the possibility that switching from food pellets to dog food in the first experiment was the sole determinant of emergence in that study. At the same time, the data do suggest that this change in food form may have been an important factor in determining the relative strengths of the old and new responses. All the subjects in this study first displayed the response that subsequently proved to be significantly stronger in single goal object procedures. The failure of rats in Experiment 1 to perform similarly suggests that alterations in the palatability of the available food goal objects may have shifted the initial response from one motivational category to another. Findings consistent with this idea have been reported by Valenstein, Cox, and Kakolewski (1968).

Response emergence following deprivation experience further indicates that changes in latency and duration probably do not reflect learning to locate and approach goal objects in the apparatus. Animals had already learned these simple approach habits in the 10-day deprivation periods. The emergence of EB under these procedures also presents interpretative difficulties for an emotionality explanation of the response strengthening phenomenon. First, it might be argued that first-behavior emergence represents a gradual adaptation to the arousing aspects of the

stimulation and that the emergence of the second behavior occurred because the response tendencies of the first behavior competed with the immediate display of the second. This alternative seems unlikely because deprivation experience with the second response goal object should have already established the second response tendency within the experimental stimulus context before the initiation of stimulation experience procedures with this goal object. Secondly, it also might be argued that the emotionality of subjects never adapts and that what the animals habituate to is the novelty of experimental events (Wise, 1974). Wild and presumably hyperemotional rats display a neophobic response to a familiar food placed in a novel container (Barnett, 1958), and their eating emerges as their fear response to the change in their environment attenuates. Similarly, stimulated animals could remain emotional, and emergence could proceed as they become less fearful of changes in the experimental environment. The only problem with such an explanation is that the stimulated subjects in this experiment had already habituated to the change in goal objects during the 10 days of deprivation experience.

Competition sessions. Figure 8 presents the data from the final competition sequence in terms of the old vs. new and the eating vs. drinking categories. The old behavior was significantly stronger than the new according to both the duration ($F = 25.86$, $df = 1/7$, $p < .005$) and the percentage trials/session ($F = 22.75$, $df = 1/7$, $p < .005$) measures. No significant Days or Response by Days effects were obtained, with all Fs approximately equal to 1.0. In all animals, eating was the prepotent response. This was reflected in longer durations ($F = 50.93$, $df = 1/7$, $p < .001$) and greater probabilities of occurrence ($F = 38.37$, $df = 1/7$, $p < .001$). Again, no reliable Days or Response by Days effects were observed.

With one exception, orderly individual data were obtained across the screening, emergence, and competition sessions of this fourth experiment. The prepotent behavior during screening eventually proved to be the stronger response in sessions with goal objects available both singly and simultaneously. The one exception was subject 21H. This animal drank during screening, and water intake was the stronger response in single goal object sessions according to median initial and asymptotic performance values. However, eating was the stronger elicited response during competition sessions. One characteristic of 21H's record was that drinking was always the first behavior to appear and was relatively stronger during the first half of a competition session. Even during the single goal object tests, eating had been relatively weak during the first half of the sessions. For example, on the last 3 days in which food alone had been

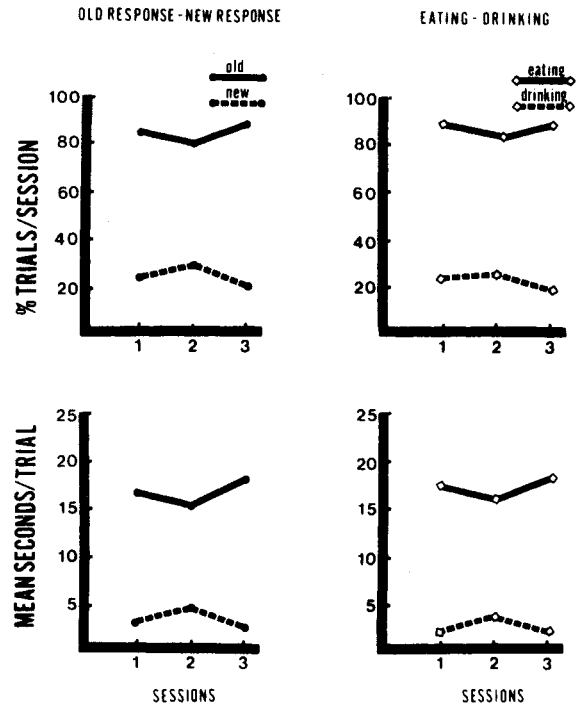


Figure 8. Group competition percentage trials/session and duration data for the second group of animals organized according to the first-response/second-response and eating-drinking categories.

made available, the mean duration of eating was 5.9 sec during the first 10 stimulation-on trials and 15.1 sec during the last 10. In contrast, elicited drinking remained stable in both halves of the single goal object sessions, averaging almost 15.0 sec. Therefore, drinking may have appeared first during screening because of its relative dominance over eating during the initial stimulation trials; and once water ingestion began, it may have blocked the appearance of eating, which had not yet emerged. The performance of 21H suggests that the behavioral influences of stimulation sometimes may depend upon how much stimulation the subject already has received within a session, and the average session performance may or may not be representative of the behavior elicited throughout a test.

Anatomical evidence. The electrodes of the five animals from the first three experiments and of the eight from the final study were located within the boundaries of the lateral hypothalamic area and medial forebrain bundle. Correlation coefficients between electrode coordinates and the behavioral data generally proved to be statistically nonsignificant. Two correlations indicated that eating in competition sessions was stronger from more anterior placements; however, the reliability of this finding is questionable due to the probability of obtaining some significant results by chance.

GENERAL DISCUSSION

Data from these experiments relate to three issues concerning the nature of lateral hypothalamic EB. First, they have implications for the argument that learning is a determinant of elicited responding. The emergence phenomenon is itself consistent with this contention; and those animals that displayed gradual increases in duration and decreases in latency presented especially strong evidence that acquisition-type data can be obtained. A learning argument also would have predicted the stable responding observed following a period of no stimulation experience and also the enhanced relative strength of a new response in competition sessions after that response had been given the opportunity to emerge. Thus, at least three findings are consistent with the idea that learning contributes to the display of the EB.

At the same time, a number of findings indicate that learning alone does not determine which behavior will be dominant; and this relates to the second major issue—the specificity or nonspecificity of the mechanism or mechanisms excited by the stimulation. The results of these experiments generally suggest that the properties of the neuronal substrate rather than the properties of the subject's experience are the principal determinants of dominance and asymptotic response magnitude during stimulation. In all 14 animals, eating was the prepotent response in competition sessions ($p < .001$, according to binomial probability). Further, one animal (11F) displayed eating rather than drinking as the dominant competition behavior, even though food ingestion had never appeared during any previous stimulation trial; and in the third experiment, the failure of the most "practiced" response to dominate after both behaviors had emerged suggests a secondary role for learning. The fairly orderly relationships observed in Experiment 4 across the screening, emergence, and competition sessions would support the idea that specificity at some functional level may determine the sequence of emergence, the asymptotic magnitude, and the dominant response during stimulation.

The final issue which these data may help elucidate is the degree of similarity between normal and stimulation-induced motivation states. If the tissue sensitization and hyperemotionality hypotheses are laid aside for the moment, these data seem to indicate that the two states are not isomorphic. As mentioned previously, the existence of the emergence phenomenon suggests differences between the two. The protracted changes in latency and duration demonstrate that response strengthening probably is not a trivial process reflecting the learning of simple approach habits. This conclusion is further strengthened by the evidence obtained following 10 days of deprivation experience, because animals familiar with the location of relevant goal objects and with the internal stimuli

associated with normal motivation states displayed improvement in elicited responding.

In summary, the evidence from these experiments is consistent with the hypothesis that the stimulation may activate relatively specific systems and that learning may play an important role in the development of the behavior. Further, EB may be displayed in response to internal cues which differ somewhat from those accompanying normal motivation states. The coexistence of specificity and learning may seem contradictory because the specificity concept implies an unmalleable process, while learning suggests pliability. This viewpoint, however, receives little support from research indicating that learning may be "constrained" (Shettleworth, 1972) and that supposedly specific behavioral systems are somewhat pliable. As an example of this latter point, traditional descriptions of imprinting in precocial birds emphasize its rapidity, irreversibility, confinement to a critical period, and acquisition in the absence of reinforcement (Fabricius, 1962). All these characteristics indicate that experience has little influence on the process and suggest that the development of filial behavior is almost totally under the control of predetermined neural events. However, Jaynes (1956, 1958a) reported that filial behavior improves as a function of practice and argued that young birds learn to associate stimuli with "innate responses." Jaynes (1958b) called this process "emergent discrimination." Hoffman and Ratner (1973) recently reviewed laboratory research which contradicts the idea that imprinting is insensitive to environmental events, and they suggest that reinforcement principles can be applied to the phenomenon. Perhaps the best behavioral description of EB is that it, like imprinting, arises from an internal state which makes certain dimensions of sensory input reinforcing. Elicited responding is specific in the sense that the internal state delimits boundaries of what is and what is not reinforcing; however, within those boundaries, experiential factors become an important determinant.

Finally, these experiments suggest that any tissue sensitization hypothesis capable of accommodating the data might be too refined to remain tenable. The hyperemotionality position (Wise, 1974) is supported by the findings that emotional, deprived rats display some of the characteristics of stimulated animals (Wise & Erdmann, 1973) and that the tranquilizer diazepam apparently removes a tonic block on elicited eating (Soper & Wise, 1971). Therefore, it remains a viable alternative which deserves further experimental consideration.

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(Received for publication December 13, 1976;
accepted January 9, 1977.)