JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR VOLUME 8, NUMBER 6 NOVEMBER, 1965

OPERANT DISCRIMINATION OF AN INTEROCEPTIVE STIMULUS IN RHESUS MONKEYS[1]

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Five rhesus macaques monkeys surgically prepared with Thiry small intestinal (jejunum) loops and implanted brain electrodes were restrained in primate chairs and kept on 23-hr deprivation-feeding cycle. After being trained to press a lever for sugar pills on an FR 25 schedule of reinforcement, a discrimination training procedure was established. Lever presses were reinforced during the S^D—a non-aversive mechanical stimulus applied to the internal walls of the Thiry loop by rhythmic inflation-deflation of a small latex balloon by air at the rate of one cycle per sec at 100 mm Hg pressure. The S^Δ was the absence of the visceral stimulation. The monkeys successfully discriminated between presence and absence of the internal stimulus. A discrimination reversal was attempted and completed on one monkey. The results clearly show operant discrimination based on an interoceptive stimulus. Cortical and subcortical EEG records reflected the onset but not termination of the visceral stimulation.

Stimulus control of behavior can be achieved by appropriate differential reinforcement contingencies; *i.e.*, emitted responses are reinforced only in the presence of a given stimulus and extinguished in its absence (Frick, 1948; Sidman, 1960; Skinner, 1937, 1938). Subsequently, the discriminative stimulus (S^D), by virtue of its association with reinforcement, sets the occasion for responding, while its absence (S^Δ) decreases responses. The analysis of operant discrimination has been based exclusively on exteroceptive stimuli (Skinner, 1938). There is full agreement that operant responses may be controlled by a visceral or interoceptive stimulus, although confirming data have not been available. The S^D, as experimentally manipulated, has been restricted to external energy sources due to methodological ease rather than to theoretical considerations (Skinner, 1953). At best, empirical findings point to internal events, such as pain, not under the control of an experimenter that come to function as discriminative stimuli for certain operants.

A direct approach to visceral afferents in intact animals has been developed by the Pavlovian workers studying respondent conditioning. Special surgical interventions have provided much information on interoceptive systems (Cook, Davidson, Davis, and Kelleher, 1960; Razran, 1961; Speranskaya, 1953). With few exceptions, these techniques have not been applied to operant conditioning studies.

Cook *et al.* (1960) conditioned a leg-flexion avoidance response to shock in dogs using drugs and internal stimulation as conditioned stimuli. Shapiro (1960, 1961*a*, 1961*b*, 1962), studying respondent conditioning, demonstrated a correlation between salivation and an operant response. Earlier, Konorski and Miller (1930, 1937, 1961) studied this correlation using a passive leg-lifting response and salivation. Razran (1961) cites Soviet studies by Krasnagorsky, Ayrapetyants, and Lichkus, and others using passive motor responses as conditioned stimuli for salivation. A study by Schuster and Brady (1964) dealt with the discriminative control of a food-reinforced op-

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[1] Supported in part by a grant from the National Institute of Neurological Diseases and Blindness (NB-00611). The authors are grateful to Mr. George Dillard for technical laboratory assistance, to Mr. Donald Oper for aid with the apparatus construction, to Mrs. Elizabeth Baum and Mr. Timothy Dodge for preparing the figures, to Mrs. Dorothy Springer for preparing the manuscript and to Dr. J. A. Gengerelli, Department of Psychology, University of California, Los Angeles, and Dr. S. A. Mudd, Department of Psychology, University of Southern California, for critical readings of the manuscript.

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erant by interoceptive stimulation, consisting of the intravenous infusion of (a) epinephrine and (b) saline-dextrose mixture directly into the superior vena cava of rhesus monkeys.

Bykov (1959), in discussing the interoceptive-exteroceptive research dichotomy, concluded "that the time for such parallel and distinctively separate lines of investigation should come to an end" (p. 251).

The present research was designed to study operant discrimination in rhesus monkeys surgically prepared to permit an interoceptive (visceral) stimulus to be experimentally manipulated. The object was to determine whether, with appropriate reinforcement contingencies, these visceral stimuli would take on discriminative functions, *i.e.*, set the occasion for operant responses.

METHOD

Subjects

Five experimentally naive adult rhesus monkeys (three females and two males: Eva, Zsazsa, Georgia, Charlie, and Adolph) whose body weights ranged from 5 to 7 kg were used. Each was seated in a modified Foringer Primate Chair in the vivarium and placed on a daily 23-hr deprivation-feeding cycle of a restricted diet of monkey crackers and fruits. This regimen was begun at least two weeks before the first experimental procedure and maintained throughout the study. The animals were fed 1 hr after daily experimental sessions ended. Bottles containing water and multivitamin drops were available at all times except during experimental sessions.

The following operations were performed under barbiturate anesthesia with sterile technic on each monkey several weeks before the experiment.

1. *Thiry small intestinal fistula.* A fully innervated and vascularized 6-in. segment of the small intestine (jejunum) was separated from the gastrointestinal tract. One end was closed off and the other sutured to the abdominal wall; thus, the segment remained internally situated while its lumen was externally available (Fig. 1). The continuity of the gastrointestinal tract was restored by a side-to-side anastomosis of the two cut ends.

2. *Chronic electrode implantation.* Approximately three weeks later, when the monkeys had fully recovered from the Thiry operation, nine chronic bipolar electrodes were stereotactically implanted in several brain structures: two cortical, two hypothalamic, two hippocampal, two tegmental plus one indifferent reference lead. The cortical electrodes were silver and the others were nichrome.

Apparatus

The subject's room was moderately sound-attenuated, illuminated, well ventilated, electrostatically shielded and had a one-way glass window for behavioral observation.

The Foringer Primate Chairs were slightly modified by removing the rear plate and adding a track on the inner surface of the two side plates slightly above the monkey's waistline. Two $\frac{3}{8}$-in. thick removable plastic plates were placed horizontally on these two tracks —one from the rear, the other from the front— around the animal, confining its arms above the waist away from the Thiry fistula. The plates were put in place several minutes before each experimental session (after a towel had been wrapped around the monkey to make

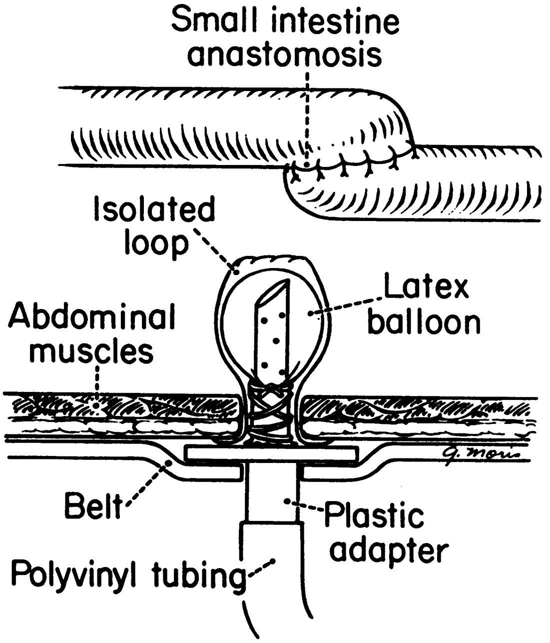

Fig. 1. Schematic diagram of a Thiry loop preparation. An isolated jejunal segment, closed on one end and sutured to the abdominal muscles and skin on the other, is shown with a fully inflated balloon held in place by a belt around the monkey's abdomen. The continuity of the gastrointestinal tract is restored by a side-to-side anastomosis. Not shown are the blood vessels and nerves for the small intestines and isolated loop.

a snug and painless fit) and removed after the daily run. This procedure assured complete experimental control while eliminating interferences with the visceral stimulation from manipulations by the monkeys.

The balloon unit, shown in Fig. 1, was assembled from the large, rigid female adapter and plastic tubing from an intravenous extension tube (K-50 Baxter) enveloped by a thin latex hood firmly secured to the tubing with thread to insure an airtight fit. The latex balloon was lubricated and placed into the Thiry intestinal fistula before each day's experiment. A perforated belt with Valcron fasteners held the assembly snugly to the abdomen.

The experimenter's room, immediately adjacent to the chamber, contained the EEG machine, the Foringer programming equipment, a Davis cumulative recorder and the syringe mechanism to inflate and deflate the balloon in the monkey. Electrostatically shielded cables and a PE 320 polyethylene tube through the wall connected the brain electrodes with the EEG machine, the lever and pellet dispenser with the programming equipment and the balloon in the monkey with the syringe mechanism.

Procedure

Visceral stimulation. Rhythmic inflation and deflation of the balloon in the Thiry small intestinal preparation served as the visceral stimulus. Air was delivered manually to the balloon at the rate of 1 cycle per sec by using a 50-cc metal syringe connected to a long polyethylene tube (PE 320). The pressure was read directly on a manometer dial and measured 100 mm Hg pressure on full inflation and zero on full deflation. The visceral stimulation was accomplished noiselessly with no exteroceptive feedback. Special care was taken to insure that the balloon stimulated only the visceral segment and did not initiate proprioceptive or tactile afferent impulses. This control was achieved by leaving a distance of 1-in. between the tied end of the balloon and the layers of abdominal muscles (Fig. 1), and by infiltrating the skin and muscle layers around the fistula with a solution of 5% Procaine before studying the effects of visceral stimulation on the EEG (Adam and Meszaros, 1962).

After the animals were fed, the EEG was recorded with the deflated balloon in the intestinal fistula. When the resting potentials (low-frequency, high-amplitude) were predominant, the oscillating visceral stimulation was applied for several seconds for each presentation. This procedure took place a day before the first operant conditioning session (see below) and on several consecutive days, 2-3 hr after the daily conditioning sessions.

Operant conditioning. Sugar pellets (Noyes; dextrose 44.6 mg, starch 2.2 mg) were delivered into a hopper near the monkey's chin when a Davis dispenser was activated. The animals quickly learned to eat the pellets on delivery. A lever was subsequently introduced and pressing was established on a continuous reinforcement schedule (CRF). Sugar pellets were made contingent on gradually increasing FR schedules and eventually reached FR 25 after a few sessions. After the response rate had stabilized, visceral stimulation was presented for intervals ranging from several seconds to 2 min (not contingent on lever pressing) to determine whether the stimulus produced any observable behavioral effects. Daily sessions varied from 30 to 190 min. The cumulative recorder was on continuously, and eating time is thus included on the records.

Operant discrimination. After the response rate had stabilized on FR 25 reinforcement, an operant discrimination paradigm was initiated, using the visceral stimulation as an S^D. Thus, only lever presses emitted in the presence of this rhythmic stimulus were reinforced on FR 25. Responses occurring in the absence of this stimulation were not reinforced. The S^D and S^Δ were alternately presented, the duration of each phase being varied to minimize the probability of temporal conditioning. Since it was not advisable to stimulate the viscera for more than 3 min due to physiological considerations, and, in order to devote a larger part of sessions to extinguish the S^Δ responses, the visceral stimulation was established as the discriminative stimulus. Thus, the S^D duration varied from 0.5 to 3.0 min, the S^Δ from 1.0 to 20.0 min.

Clicks and buzzes from the programming equipment were audible in the subject's room. A silent DPDT knife switch controlling the feeder circuit and two sets of response and reinforcement counters was manually shunted in correspondence with the S^D and S^Δ phases. Thus, the programming equipment functioned and emitted noises at all times but the

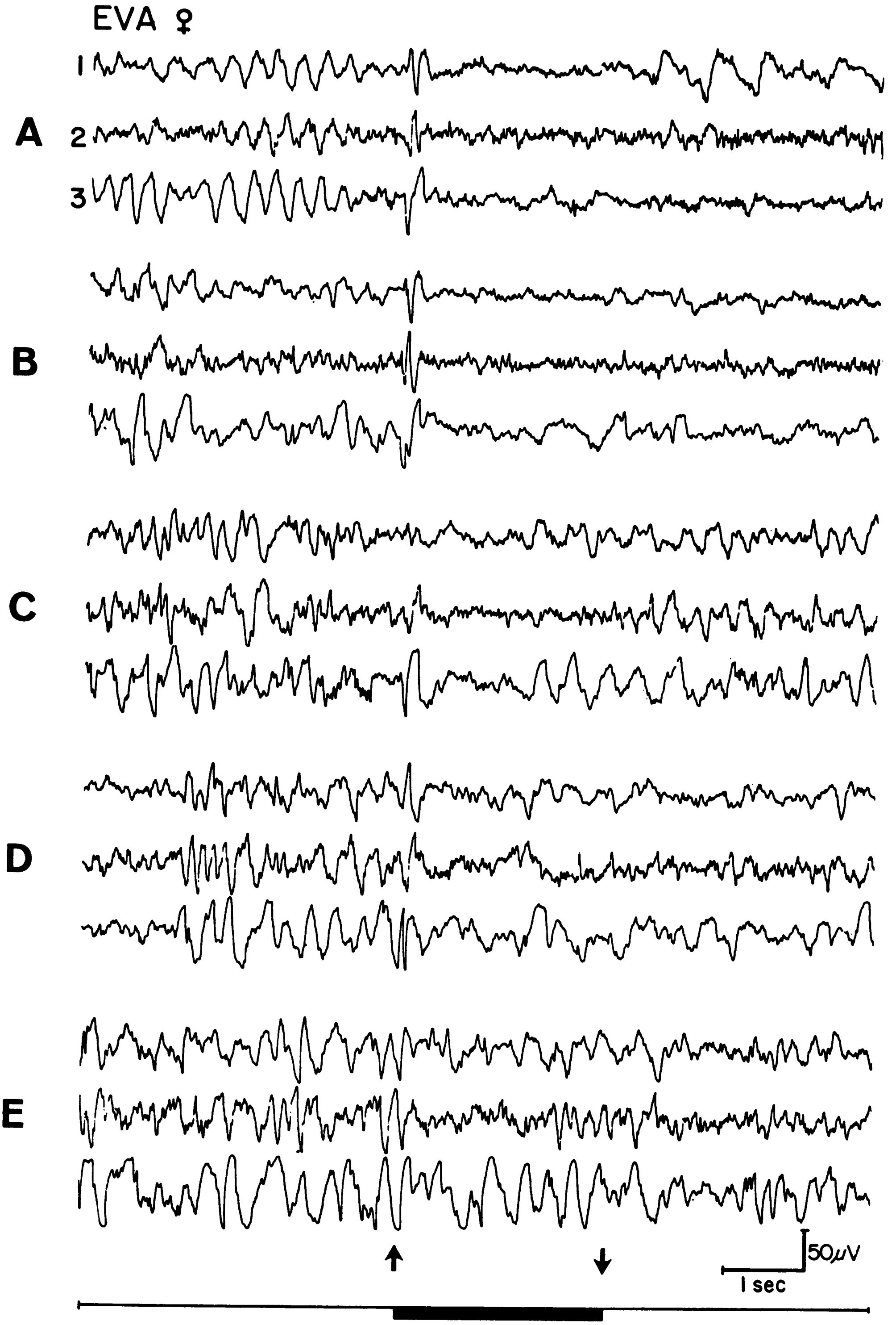

Fig. 2. Representative electroencephalographic tracings showing the effects of rhythmic visceral stimulation. The onset and offset of the interoceptive stimuli are indicated by an upward and downward arrow, respectively; the duration of repeated inflation-deflation cycles is represented by the heavy black strip between the arrows. A through E indicate the consecutive records taken on sequential stimulus presentations while number 1 of each group refers to the cortical, 2 to the hypothalamic and 3 to the reticular formation leads.

reinforcements and the corresponding pips on the cumulative records were presented only during the S^D phase. In this manner, every 25th response was followed by a buzz accompanying the resetting of the stepper. Data were also recorded on eight counters: four for total responses and "stepper resets" for S^D and S^Δ per session, and four for number of responses and "stepper resets" per S^D and S^Δ segments.

The stepper was not reset for each S^D or S^Δ phase. The first reinforcement could thus be delivered after fewer than 25 responses.

Discrimination reversal. After discrimination had been established, its reversal was undertaken to serve as an experimental control. Thus, the visceral stimulation became the S^Δ and varied from 1.0 to 3.0 min while its absence, the S^D, lasted from 0.5 to 3.0 min. Except for this change, the discrimination reversal phase was identical to the discrimination conditioning.

RESULTS

Effect of visceral stimulation on EEG. The effect of intestinal stimulation on the EEG is shown in Fig. 2. When the rhythmic distention began, a marked evoked potential and an immediate desynchronization of electrical activity occurred. Ending the stimulus had no apparent effect and the desynchronized pattern continued. Thus, the low-frequency high-amplitude EEG typical of a drowsy or resting animal was altered to a high-frequency low-amplitude pattern. After restoring synchronization, repeated 3-sec oscillating stimulation several minutes apart resulted in a typical habituation process which can be clearly followed on the graphs for five consecutive stimulus presentations (A through E in Fig. 2). The other animals yielded similar daily records. Recordings from the hippocampal electrodes were not available due to technical difficulties. Electrode placements were histologically verified in three animals. As the EEG observations were of a general nature and not localized, the remaining two animals were not sacrificed for this purpose.

Effects of visceral stimulation on operant responding. After stable rates of responding had been established, but before discrimination training began, the visceral stimulus was

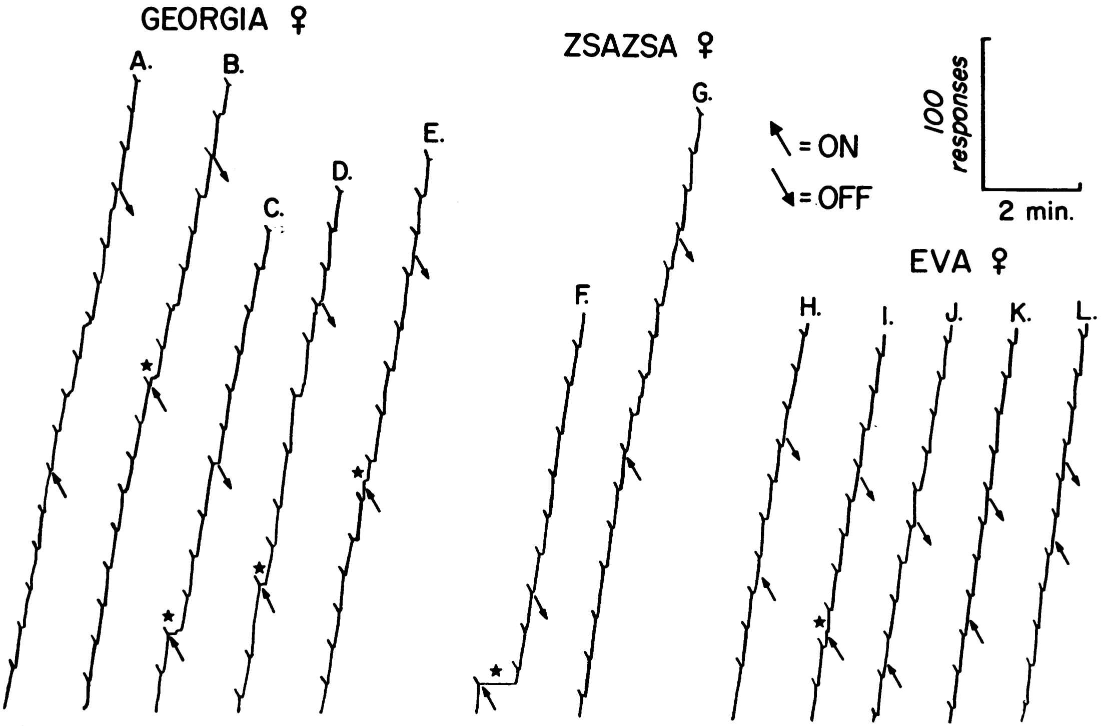

Fig. 3. Sample cumulative level-press response curves showing the effects of visceral stimulation on ongoing behavior. The interoceptive stimulus has had no differential reinforcement (discrimination training). The diagonal pips indicate reinforcement, presented on a fixed ratio 25:1 (FR 25) and the stars represent auxiliary head turning behavior observed by the experimenters.

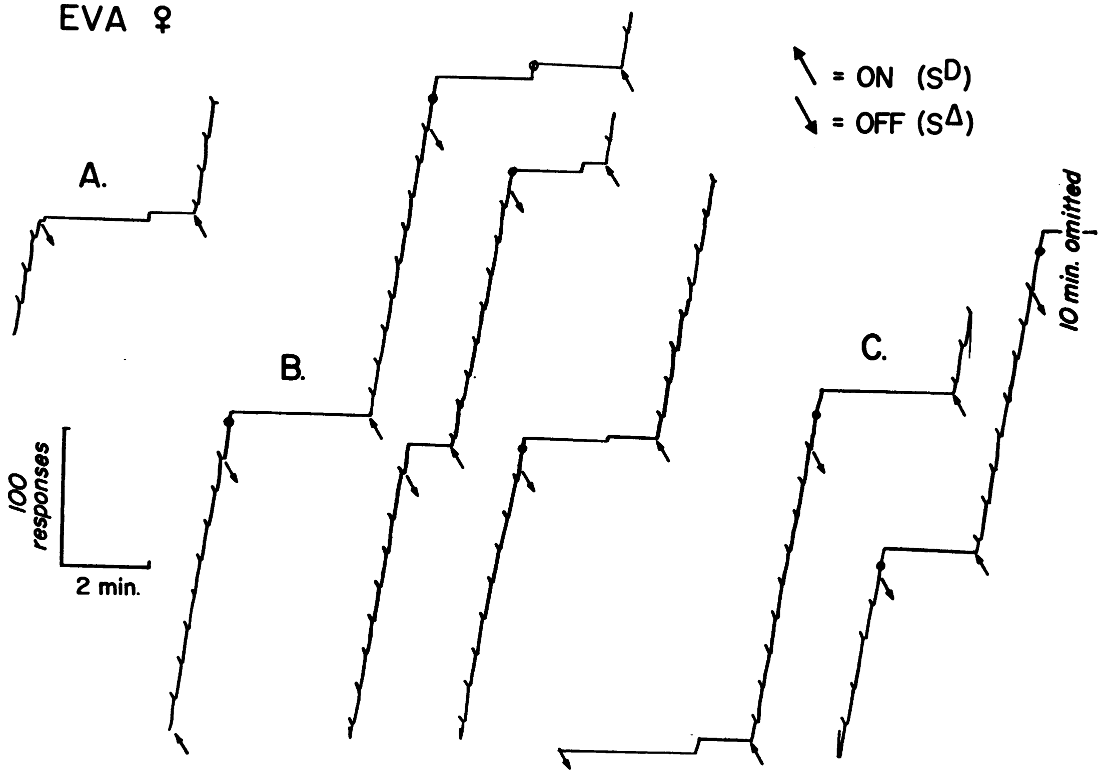

Fig. 4. Typical records of cumulative lever-press response curves upon the establishment of an interoceptive stimulus discrimination. Reinforcement is contingent on the emission of 25 responses (FR 25) during S^D (presence of visceral stimulation) and withheld during S^{Δ}. Pips indicate reinforcement while the circles (o) represent the reset of the stepper (with no reinforcement). Note the short latencies between onset of S^D and lever presses but longer latencies between offset of the visceral stimulus (S^{Δ}) and cessation of responding.

presented intermittently for varying periods to determine if it influenced behavior. Figure 3 includes segments of cumulative response curves at the time these first stimuli were presented. A through E are in chronological though not consecutive order for Georgia. Segments of cumulative curves were omitted between A and B, B and C, *etc.*, since responding was steady and no interoceptive stimulation was applied. The first stimulation had no effect on the lever-pressing response. Several minutes later, in B, responses ceased momentarily, accompanied by head turning behavior indicated by a star in Fig. 3. This pattern persisted over several presentations, but lever-pressing was always resumed and maintained during the rest of the stimulation. For Zsazsa, only the first stimulus presentation decreased behavior momentarily (curve F). Eva paused only briefly and looked around on the second stimulation on curve I. Both Charlie and Adolph showed the same pattern as Eva; *i.e.*, a very brief pause only on the first or second stimulus. At times, the stimulus presentation, as in curve G, slightly decreased overall rate, though the head turning pattern was lacking. However, the most prevalent finding was the absence of any sustained behavioral effect of the visceral stimulation.

Discrimination training. After extended training, visceral distention became established as the discriminative stimulus for lever pressing. The data in Fig. 4, based on terminal performance by Eva, illustrate the stimulus control. In A, upon stimulus termination, the responding ceases and, except for two very brief bursts of two and four responses respectively, does not resume until visceral stimulation begins. In B, the onset occurs at the upward arrow at the bottom of the first curve and the stimulus ends 1 min later at the downward arrow. However, the responding continues until the stepper is reset (indicated by the circled point on the curve) after which the responses cease until the S^D is again presented. The latency for resumption of pressing after the onset of the stimulus is less than 1 sec, while the responding sometimes overshoots stimulus termination by some 5-10 sec and then ceases abruptly. Often, as shown in the second curve of Fig. 4B, after the stimulus terminates, the responding ceases before the stepper reset and does not resume until after the S^D is re-introduced.

Figure 5 shows the mean number of responses during the S^D and S^Δ phases of a day's session representative of the terminal behavior of each animal. Charlie and Adolph were in the experiment for the early phases only of the discriminative training (3 and 4 hr of discriminative training, respectively). Georgia had about 6 hr of discriminative training while Eva and Zsazsa completed 18 and 16 hr, respectively.

The same chronological progression of the discrimination is shown for Eva in Fig. 6. In A, the first hour of discrimination training, there is little or no difference between the response rates in S^D and S^Δ. By the beginning of the ninth hour, B, a clear-cut difference is evident. The 18th hour for Eva is included in Fig. 5.

Discrimination reversal. The final phase, *i.e.*, discrimination reversal, was begun with Eva. As shown in the last curve in Fig. 4C, 10 min of no responding elapsed before the first S^Δ response occurred, clearly demonstrating the stimulus control. From this point on, the absence of the visceral stimulus signified the S^D and its presence the S^Δ.

In Fig. 7, curves A-D show the beginning of the discrimination reversal following curve C of Fig. 4. No stimulus discrimination effects are evident at this point. However, after 10 daily 1 hr sessions, the behavior changed, as is evident in curves E-H of Fig. 7. At the top of curve E, the second presentation of the visceral stimulus almost immediately halted lever-pressing not dependent on the stepper reset. Eventually, stimulus termination is followed more closely by responding (curve G and H).

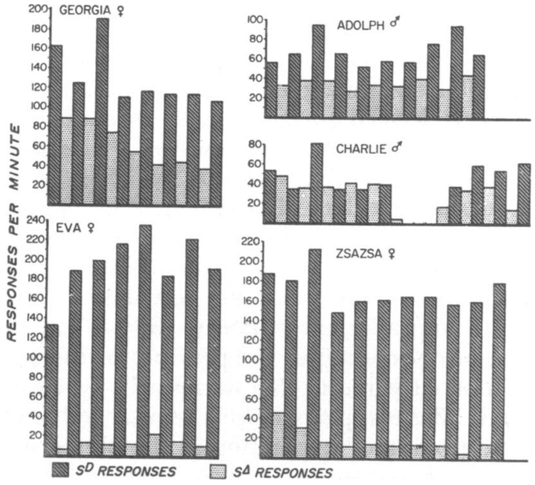

Fig. 5. Representative day for each of the five monkeys at different amounts of S^D-S^Δ training. Charlie and Adolph are at the early phase, Georgia at the intermediate and Eva and Zsazsa at the final phase of the discrimination.

DISCUSSION

The results clearly indicate that operant behavior may be brought under the control of interoceptive stimuli. Thus, a mechanical stimulus presented interoceptively may come to serve as an S^D for operants through differential reinforcement contingencies, *i.e.*, in the presence of a visceral stimulus an operant will be followed by reinforcement, while responses in the absence of the internal stimulation will be extinguished. It is noteworthy that the intensity of the interoceptive stimulus itself had little effect on behavior, even though its effects on the EEG were marked. These EEG observations were similar to those reported by Adam and Meszaros (1962). On the basis of these data, however, it is reasonable to conclude that the visceral stimulus employed does produce afferent impulses which reach structures such as the hypothalamus, reticular formation and cortex.

Bykov (1959) emphatically stated that ". . . changes in the state of the internal organs must produce cortical effects which cannot

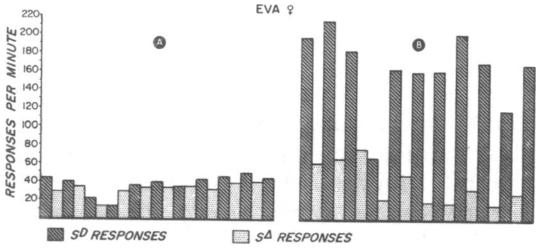

Fig. 6. Two phases of discrimination training for Eva: A, first hour; and B, ninth hour of differential reinforcement of lever presses in the presence and absence of interoceptive stimulation. The 18th hour for Eva is shown in Fig. 5.

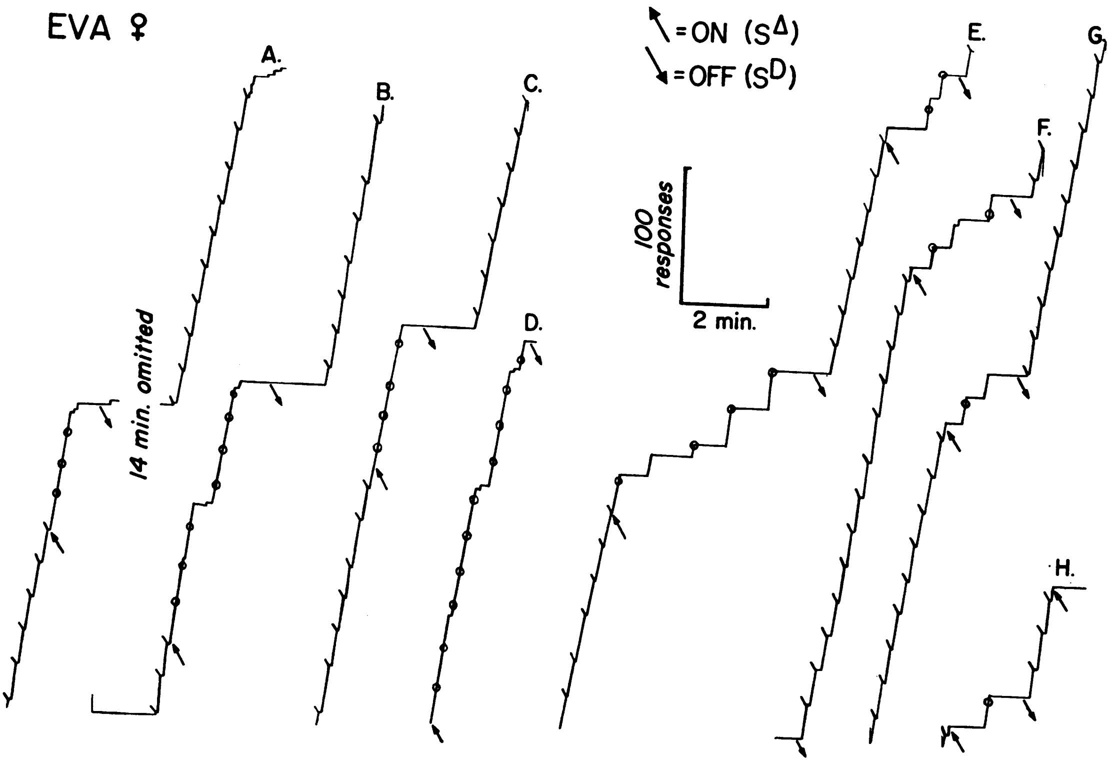

Fig. 7. Discrimination reversal. Curves A-D were recorded immediately following the last curve in Fig. 4. Reinforcement (indicated by pips) is contingent on 25 responses (FR 25) in the absence of visceral stimulation (S^D), while stepper resets without food (shown by circles) are presented following 25 responses in the presence of the visceral stimulation (S^{Δ}). Curves E-H were recorded after several days of reversal training. Note the changes in latency between onset and offset of stimuli and initiation and termination of responses. The latency following the onset of the visceral stimulation is shorter than following its offset.

help but be felt in the animal's reaction to its external environment" (p. 252). The present EEG data corroborate this, relating the interoceptive stimulus and the cortex, although the data do not necessarily support the latter part of Bykov's statement. Before discrimination training the cumulative curves were only minimally affected by the internal stimulation. On the basis of present findings, two preliminary conclusions may be formulated. The visceral stimulation was not aversive or painful, as demonstrated by the absence of a marked suppression of lever-pressing during the operant conditioning phase before discrimination training. Secondly, the presentation of a visceral stimulus which produces any EEG change may be insufficient to affect overt behavior consistently.

Furthermore, the discrimination phase data raise doubts that the visceral stimulation alone is sufficient to initiate a motor response (such as lever-pressing) greater than an orienting reflex. When behavior is differentially reinforced in the presence and absence of an interoceptive stimulus, it will set the occasion for responses. Only by including this last qualification can we agree completely with Bykov. Also, it seemed to take longer to master the task based on an interoceptive as compared to an exteroceptive stimulus, which is in accord with the data of Bykov (1959).

Present discrimination data agree with those of Frick (1948), who, using exteroceptive visual (dark-light) stimuli, concluded that: "with supraliminal stimulus differences, the rate of responding in the presence of the nonreinforced stimulus (S^{Δ}) decreased to a steady level. There appears to be a regular inductive conditioning of responding in the presence of S^{Δ} which shows no signs of breaking down even after extended training." During S^{Δ} some responses continued to be emitted.

It is most obvious that the stepper-reset noise, by being paired with food reinforcement, came to function as a conditioned reinforcer (S^r). The presentation of these S^r's on an FR 25 during the S^{Δ} phases probably retarded establishment of a discrimination. These technical difficulties have now been eliminated.

The data from the early phase of the discrimination reversal verify that termination of the visceral stimulation was the primary controlling agent for halting lever-pressing during the discrimination. In curves A through D, Fig. 7, the responses occur in the presence of the stimulation, even though the stepper resets and no primary reinforcement is delivered. Some decrements in response emission result. Furthermore, the late phase of the discrimination reversal (Fig. 7, E through H) reveals a pattern similar to that in the discrimination training, *i.e.*, the onset of stimulation is immediately discriminated but its termination is not so readily perceived. It is thus concluded that in the terminal phase of discrimination training (Fig. 4), the overshoot of the responses is most probably due to some after-effects of the stimulation.

Stimulus control was also clearly demonstrated in Fig. 7, curves A and B. After the discrimination reversal procedure had been initiated and 96 responses emitted in the presence of the visceral stimulation (now S^{Δ}), a few more responses occurred during the new S^D and then no response was emitted for the next 14.5 min (yet only one more lever-press was necessary for a reinforcement to occur). Again, pauses occurred at the upper segment of curve A and lower section of curve B despite the fact that lever-presses were being reinforced.

Neither the respondent conditioning (Adam, 1958) nor the EEG methods (Adam and Meszaros, 1962) provided for recording of effects of internal stimulus cessation. Operant techniques, as used here, reflect both initiation and termination of the visceral stimulation.

Observations of the monkey's behavior yielded noteworthy information. When S^D was terminated and S^{Δ} begun, upon cessation of lever-pressing, the monkey put its head back and to the side and would sometimes close its eyes. Periodically during the S^{Δ} interval, it would sit up straight, quickly look around and put its head back. Sometimes, on sitting up, it would also press the lever several times. This agrees with Shapiro (1962), who observed that a tail-wagging response very often would precede lever-pressing. Cook *et al.* (1960) observed similar results, *i.e.*, physiological responses would consistently occur before the avoidance response. In the present study it may be that the brief bursts of responses during the S^{Δ} phase in conditioning were initiated by a vigorous peristaltic movement in the small intestine.

Since behavior is a function of both internal and external stimuli, study of the viscera as a stimulus source for operant conditioning is essential.

In discussing the differences between interoceptive and exteroceptive stimuli, Skinner (1963) concluded that the events taking place within the organism's skin have the distinction of limited accessibility by the community. "So far as we know, the same process of differential reinforcement is required . . . to distinguish among events occurring with . . . [one's] own skin . . . The verbal community . . . cannot always arrange the contingencies required for subtle discriminations . . . it cannot be sure of the presence or absence of the private patterns of stimuli appropriate to reinforcement or lack of reinforcement" (p. 953). He was optimistic that techniques would be developed making these private stimuli experimentally available as independent variables to study their functional relation to the organism's behavior. This new avenue of research, combining operant, respondent and EEG techniques, should prove very promising to behavioral workers.

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Received January 18, 1965