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COMPLEX RESPONSE PATTERNS DURING TEMPORALLY SPACED RESPONDING

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A series of experiments is reported in which two monkeys emitted complex response patterns, not specified by the experimental program, during the DRL component of a multiple schedule. Administration of sodium pentobarbital and *dl*-amphetamine, drugs which disrupted the DRL performance, were also observed to suppress these collateral responses. Sequences of these collateral responses appear to mediate, at least in part, the timing process required for reinforced performance on the DRL schedule.

The data to be described in this report were obtained during an investigation of the electroencephalographic correlates of timing and avoidance behavior in monkeys (Ross, Hodos, & Brady, 1962). The methodology consisted of recording the electroencephalogram (EEG) during each of the several components of a multiple schedule. However, during certain components of the schedule, the movements of the animal produced "artifacts" in the EEG that consistently hampered efforts to determine the presence or absence of EEG correlates. A frequency analysis of the "artifacts" indicated that the movements which had been obscuring the EEG had a consistent and well-defined temporal distribution. Furthermore, the movements seemed most regular during the differential reinforcement of low rates (DRL) component of the multiple schedule. These movements are similar to responses described by Wilson and Keller (1953) as occurring during DRL performance. Wilson and Keller referred to these movements as "collateral responses."

The plan of the present investigation was to determine whether the emission of these collateral responses was correlated with reinforced performance on the DRL schedule, and to what extent reinforced performance was dependent on the emission of collateral responses.

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METHOD

Subjects

The subjects were two adult rhesus monkeys. Each monkey had bipolar, stainless steel electrodes in a pedestal of the type described by Sheatz (1961) implanted in caudate nucleus, nuclei paraventricularis, reticularis and intralaminar of the thalamus, medial forebrain bundle, globus pallidus, amygdala and ventral tegmental nucleus. Histological sections of the brain are presented elsewhere (Ross, Hodos, & Brady, 1962). The monkeys were maintained in primate restraining chairs of the type described by Mason (1958), each of which was equipped with a lever, stimulus lights, connections for administering foot shock, and a food-pellet dispenser.

Training Procedure

Each monkey was trained in the following multiple schedule: (1) 15 min of DRL in the presence of a green stimulus light during which only lever presses preceded by 21 sec of no responding were reinforced with food pellets; (2) a 15-min time out (TO), with no stimulus light during which lever responses were not reinforced; (3) 15 min of avoidance (Sidman, 1953), in which the animals were required to press the lever at least every 20 sec in the presence of a red stimulus light in order to avoid painful electric shock to the feet; and (4) a second 15-min TO, with no stimuli or reinforcements. Each experimental session was 6 hr. Except for vitamin supplements, each animal's total daily ration of

food[2] was provided during the DRL components.

The EEG recordings were made during each component of the schedule on a six-channel Grass Model 5 polygraph equipped with interchangeable EEG preamplifiers. Correlations between the animals' behavior and the EEG "artifacts" were determined differently for each of the two animals. With Monkey M-49, the artifacts occurred simultaneously with a rapid jerking motion of the head, which was repeated with great regularity every 1.5 to 2.0 sec. These head movements were recorded on the polygraph by placing silver electrodes subcutaneously on the monkey's neck and then recording the electromyogram (EMG) through an EMG preamplifier. With Monkey A-73, the artifacts occurred when the animal licked the lucite holder of its water bottle. A metal strip was placed on this area and connected in series with the animal to the input of the EMG channel of the polygraph. Each time the animal licked the metal strip, the impedance of the circuit was changed and the polygraph pen was deflected.

Drug Studies

Several doses of *dl*-amphetamine and sodium pentobarbital were administered intraperitoneally to each animal to determine whether these drugs, which have been reported to alter lever-pressing performance (Sidman, 1955, 1956), would also affect the patterns of collateral responses.

RESULTS

Figure 1 shows a segment of the polygraph record from Monkey M-49. The uppermost channel indicates lever responses. A food-reinforced response appears at the extreme right of the record. The second channel records muscle potentials from the neck of the animal. The remaining channels depict brain electrical activity. In the middle EEG channel, prominent potentials appear which are larger than the background activity and which occur simultaneously with the potentials in the EMG channel above.[3] This record was obtained during the DRL component of the schedule. It was during this component that the collateral responses were consistently observed in M-49. Although potentials of equal amplitude were occasionally observed in other components of the schedule, they failed to present the orderly temporal distribution displayed during DRL.

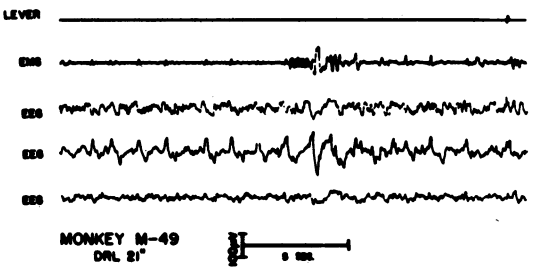

Fig. 1. A segment of a polygraph record of Monkey M-49. The uppermost channel indicates lever responses. The second channel records the electromyogram (EMG). The remaining three channels record the electroencephalogram (EEG). The large potentials in the middle EEG channel are artifacts produced by movements of the animal, and occur simultaneously with potentials in the EMG channel.

Figure 2 illustrates the distribution of interresponse times (IRT) of the head movements during a 5-min sample of each component. The data were obtained by compiling a frequency distribution of time intervals between EEG artifacts of 50 μV or more. The EMG record was not satisfactory for this purpose, since the amplitude of the potentials varied considerably from one session to the next. Nevertheless, the EMG was a valuable indicator of whether EEG potentials over 50 μV were produced by head movements or not.

During TO and avoidance, the distributions were essentially rectangular. During DRL, however, the distribution had a definite peak during the interval between 1.0 and 2.0 sec. A distribution of IRT's of the animal's lever presses during the DRL component is shown in the inset figure. The ordinate presents the relative frequency (*i.e.*, percentage of total) of responses in each class interval of time.

Figure 3 depicts the distribution of the head movements during a predrug control period and under the influence of 12.0 mg/kg of sodium pentobarbital. Because the distributions for TO and avoidance are nearly identical, only the distribution for TO is shown.

[2]D. & G. Special Monkey Food Tablets, Dietrich and Gambril, Inc., Frederick, Maryland.

[3]Because of a defective electrode, the recording in the middle EEG channel was monopolar, with the steel electrode pedestal in the skull as the "indifferent" electrode.

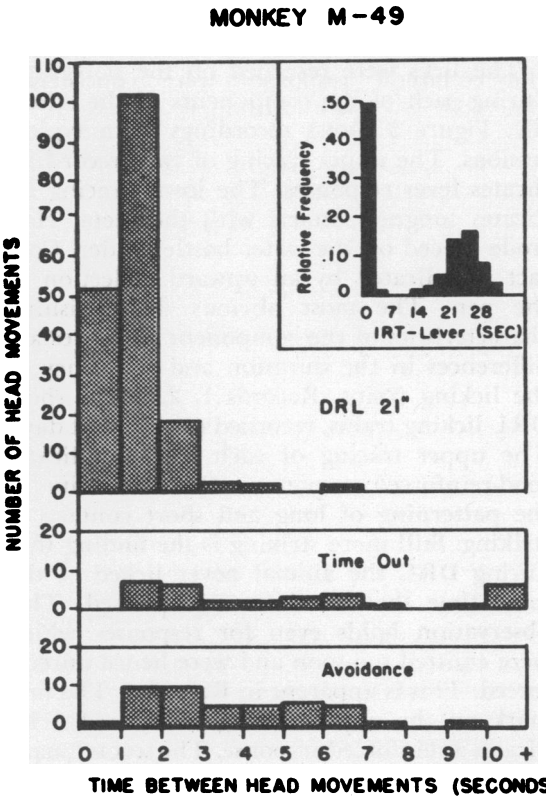

Fig. 2. The stippled graphs represent a distribution of inter-response times (IRT's) of the head-movement response during each component of the multiple schedule. The inset figure represents the IRT distribution of lever presses during the DRL component.

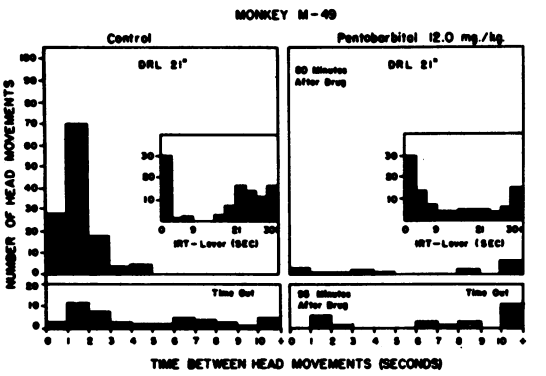

Fig. 3. The effects of administration of 12 mg/kg of sodium pentobarbital on the IRT distributions of head movements and lever presses. The data in the left half of the figure were obtained during a predrug control period. The data in the right half of the figure were obtained 80-95 min following administration of the drug.

An examination of the head movements during DRL, 80 min after the drug administration, indicates that the number of head-movement responses has diminished to nearly zero under the drug condition. In addition, the distribution now appears to have no peak, indicating that the head movements were no longer emitted at the predominant frequency.

Inset in each half of Fig. 3 are the IRT distributions of the lever responses during the control and drug DRL components. The IRT distribution of lever responses during the control condition shows that better than 50 per cent of the animal's responses were made following a nonresponse interval of 21 sec, and were thereby reinforced. Under the influence of pentobarbital, the distribution has become quite flat, and nearly three-quarters of the animal's responses are preceded by intervals of less than 21 sec and are not reinforced. The rate of lever pressing during avoidance dropped from approximately 100 per min during the predrug control to about 65 per min after administration of pentobarbital.

A comparison of the performance in the TO component under the control and pentobarbital conditions reveals that although the distribution of head movements remained essentially rectangular, the total number of such responses diminished following drug administration.

Figure 4 shows the effects of *dl*-amphetamine on the collateral responses. The left of the figure shows the IRT distributions of the head movements during DRL and TO components before administration of the drug. The right shows the effects of administration of 3.0 mg/kg of *dl*-amphetamine. Under the influence of the drug, the distribution of collateral responses during TO assumed a shape usually observed only during DRL. This characteristic distribution pattern of head movements was also observed during the avoidance component following drug administration, and persisted for approximately 3 hr. Throughout this period of *dl*-amphetamine activity, the distribution of head movements recorded during the avoidance and TO components could not be distinguished from the distribution of head movements recorded during the DRL component.

Inset in each half of Fig. 4 are the IRT distributions of the lever responses during the DRL components before and after the administration of *dl*-amphetamine. Following drug administration, the peak of the dis-

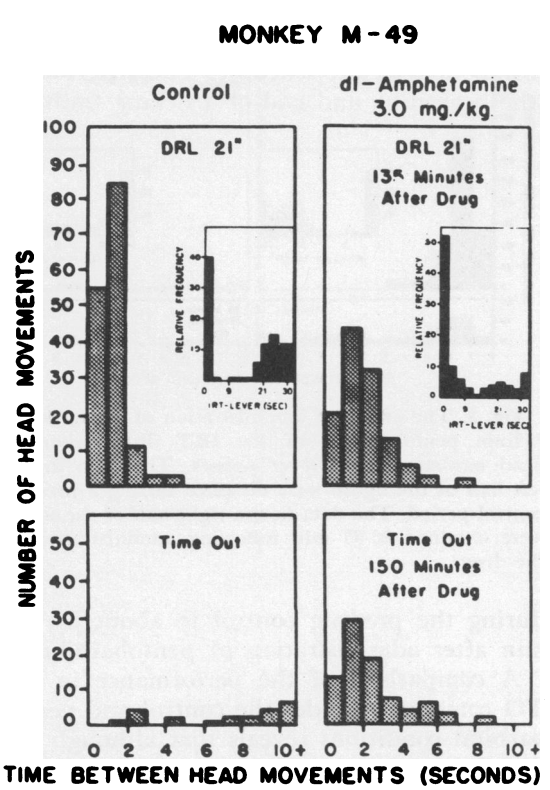

Fig. 4. The effects of administration of 3 mg/kg of *dl*-amphetamine on the IRT distributions of head movements and lever presses. The data in the left of the figure were obtained during a predrug control period. The data in the right half were obtained 135-150 min following administration of the drug.

tribution shifted toward the shorter time intervals, and more than three-quarters of the responses were unreinforced.

Administration of *dl*-amphetamine also produced a marked rise in the lever-pressing rate during the TO periods (approximately 30 resp/min), and some local elevations in the avoidance rate were also apparent under the influence of the drug. In addition, a striking elevation was observed in the amplitude of the EMG recorded from the neck muscles during the drug periods.

The collateral responses observed with the second monkey, A-73, consisted of its licking the lucite holder of the water bottle. Unlike Monkey M-49, Monkey A-73 emitted these collateral responses during all components. The temporal distribution of the trains and their temporal relationship to the lever response, however, renders the three components easily distinguishable from each other solely on the basis of differences in the licking pattern.

The licks were recorded on the polygraph during each of the components of the schedule. Figure 5 shows recordings from typical sessions. The upper tracing of each record indicates lever responses. The lower tracing indicates tongue contacts with the metal electrode placed on the water bottle holder. Contact is indicated by an upward deflection of the pen. The most obvious distinguishing characteristics of the component schedules are differences in the duration and frequency of the licking trains. Records 1, 2, and 3 show DRL licking trains, recorded on different days. The upper tracing of each record indicates food-reinforced responses. The similarity in the patterning of long and short contacts is striking. Still more striking is the finding that during DRL the animal never licked at the same time that the lever was pressed. This observation holds even for responses which were emitted too soon and were hence unreinforced. This is apparent in Record 4. The first mark on the upper tracing of Record 4 indicates a reinforced response. The second mark indicates an unreinforced response. Notice that in neither case was the tongue in contact with the electrode at the same time of the

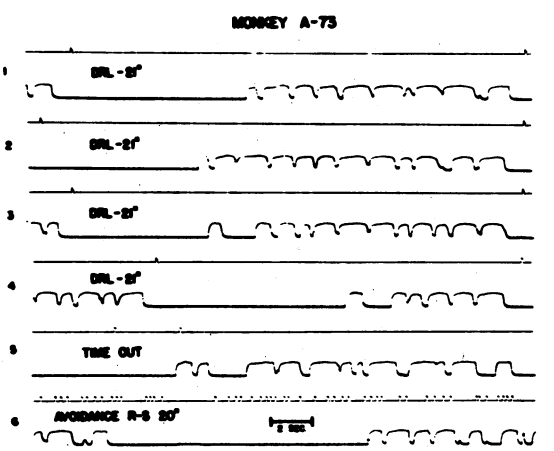

Fig. 5. Segments of polygraph records of Monkey A-73. The upper channel of each record indicates lever presses. The lower channel of each record indicates tongue contacts with the metal strip. Records 1-3 show the food-reinforced performance of the DRL. Record 4 illustrates the performance of a reinforced response followed by a nonreinforced response. Record 5 represents lever presses and tongue contacts during the TO component of the multiple schedule. Record 6 represents lever pressing and tongue contacts during the avoidance component.

lever-press response. This is in sharp contrast to the performances in Records 5 and 6. Record 5 shows the TO performance, in which the animal may or may not be licking while pressing the lever. Record 6 shows the avoidance performance, in which the only correlation between licking and lever pressing seems to be an increase in lever-pressing rate during a pause in licking.

Figure 6 illustrates IRT distributions of licking-train durations and lever responses. Lever-response IRT's during DRL are presented in the inset portion of the figure. The stippled bars represent frequency distributions of licking-train durations during each component of the schedule. The criterion for the beginning and end of a licking train was a pause in licking of 5 sec or longer. During the DRL component, the temporal distribution of the licking trains appears to be similar to the IRT distribution of lever responses. The TO licking appears to occur in a rather random temporal distribution, whereas the distribution of avoidance responses shows a clustering at the longer train durations.

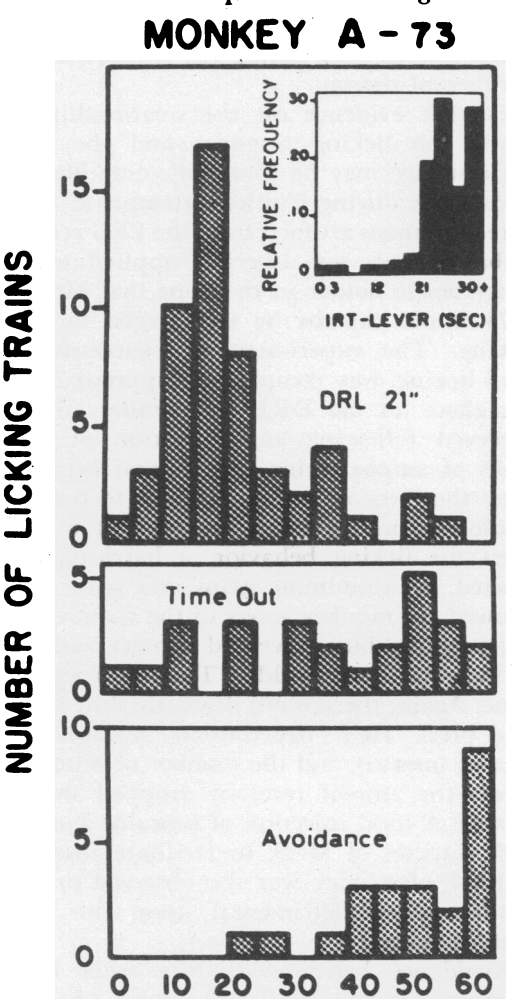

Fig. 6. The stippled graphs represent frequency distributions of licking-train durations during each component of the multiple schedule. The inset figure represents the IRT distribution of lever presses during the DRL component.

The same drugs studied in Monkey M-49 were also administered to Monkey A-73. Pentobarbital (10.0 mg/kg intraperitoneally) completely suppressed licking during all components. In addition, the drug also suppressed lever pressing in both DRL and TO. During the avoidance component, however, lever pressing continued at a slightly lowered rate, and the monkey successfully avoided all shocks during the drug period despite the complete absence of licking.

Nearly identical results were observed with *dl*-amphetamine. Following administration of 2.0 mg/kg of the drug, licking was suppressed during all components. Lever pressing was suppressed during DRL and TO, but it continued at approximately the same rate during avoidance. However, 2 hr after the drug had been administered, lever-pressing behavior recovered during DRL, but at a rate much too high to result in reinforcement. Licking behavior did not recover during the remainder of the experimental session.

DISCUSSION

Wilson and Keller (1953) have described "collateral responses" which their rats emitted during the interval between lever presses on the DRL schedule. They suggest that these collateral responses may operate to keep the lever responses spaced far enough apart to satisfy the temporal requirements of the schedule. Wilson and Keller also noted that because no particular collateral response is specified by the DRL schedule, it should not be surprising that each animal may acquire a unique pattern of collateral responding.

On the other hand, Anger (1956), who was unable to observe any evidence of collateral responding during DRL, suggested that "rats

have some internal variable that changes with the time since the last response. This variable may function like an external stimulus in that a difference in the reinforcement of responses at different values of this variable results in a high probability of response at the values reinforced more" (p. 159). Recently, Bruner and Revusky (1961) have presented records obtained from human subjects during DRL which show clearly that the subjects have imposed highly individual response patterns upon themselves which were not specified by the experimenters.

The complex response patterns observed in the present investigation seem to be of the type described by Wilson and Keller and later reported by Bruner and Revusky. With Monkey M-49, the characteristics of the collateral head movements were such that the animal appeared to be making a crude estimate of the number of head movements before pressing the lever. These highly periodic movements of the head occurred only during the DRL component, and at no other time. This observation was so reliable that one could easily determine whether or not the animal was in the DRL component by merely glancing at the polygraph record. This suggests the possibility that the head-movement response may have been an essential condition for the execution of reinforced DRL responding.

Further support comes from an analysis of Monkey M-49's performance after administration of pentobarbital and amphetamine. Pentobarbital eliminated all evidence of temporally spaced responding. Following administration of this drug, no particular class interval of time seemed to be predominant in the IRT distribution. The effect of this drug on the head-movement response was to all but eliminate it. With amphetamine, however, the distribution of lever-press IRT's is not flattened, but rather the peak of the distribution shifts toward the shorter intervals. Under the influence of this drug, the animal seemed unable to control the emission of head-movement responses. This is inferred from the observation that the distributions of head-movement IRT's during TO and avoidance have assumed the general appearance of the distribution during DRL. This argument is further substantiated by the large increases in EMG amplitude after amphetamine. The presence of these uncontrolled movements seemed to have resulted in the animal's incorrect estimation of the number of head responses. This may partly account for the shift in the peak of the distribution of lever presses under amphetamine.

An analysis of the licking behavior of Monkey A-73 may be made in a similar way. The picture is somewhat more complicated because the animal licked in all components of the multiple schedule. Nevertheless, the patterning of the licks was such that the various components could be distinguished with little difficulty. Moreover, several 24-hr recording sessions revealed that A-73 contacted the water bottle holder only during the 6 hr of the experimental session.

Further evidence on the relationship between the licking response and the DRL performance may be found in some observations made during fruitless attempts to eliminate movement artifacts from the EEG records. Tabasco sauce was liberally applied to the water bottle holder in the hope that Monkey A-73 would thereby be encouraged to cease licking. The experiment was successful in that licking was completely suppressed, but the effect on the DRL was similar to that observed following administration of large doses of amphetamine: the animal began to press the lever at a rate too high to produce reinforcement. In a similar attempt to suppress the licking behavior, a barricade was erected, of aluminum strips and wire. This allowed the monkey access to the spout of the water bottle, but prevented contact with the lucite water bottle holder. The result was the same. Again, there was a dramatic shift in the lever-press IRT distribution towards the shorter interval, and the number of reinforcements the animal received dropped sharply to zero. A local injection of procaine into the neck muscles of M-49, to facilitate insertion of EMG electrodes, was also observed to have similar effects detrimental upon the DRL performance.

Avoidance behavior, on the other hand, appeared far less dependent on the temporal patterning of the licking response as indicated by the drug experiments. Both amphetamine and pentobarbital completely suppressed the licking response and also severely disrupted the DRL performance. However, avoidance behavior was affected only slightly by the drug administration, despite the absence of licking.

Because no particular pattern of collateral responding is specified by the requirements of the DRL schedule, each animal is likely to acquire a unique pattern of responses, some more complex than others and some more overt than others. The topography of the collateral responding in Monkeys M-49 and A-73 was such that it could be both observed and recorded conveniently. There is, however, no reason to suppose that the collateral responses observed in these two animals represented anything more than a fraction of some more complex pattern. Such a pattern might be further composed of respiratory responses and small movements of skeletal musculature which could only be detectable by electromyographic analysis. Indeed, the critical process may be covert, as Anger has suggested.

The subjects of the present investigation emitted consistent patterns of collateral responses during DRL. The data suggest that the same processes which control these responses may also control the DRL performance. Variables which interfered with the execution of the collateral responses appeared to have a disruptive effect upon DRL performance. It does not seem unreasonable to conclude that the animals may have been estimating the passage of time by emitting chains of collateral responses which more or less pace the interval between lever presses. Such timing behavior would then appear to be partly based upon the discrimination of the number, pattern, or other aspects of these collateral response chains, some characteristic of which becomes associated with reinforcement.

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