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ANALYSIS OF THE MEDIATORY ROLE OF COLLATERAL BEHAVIOUR, USING A DIFFERENTIAL REINFORCEMENT OF RESPONSE DURATION (DRRD) SCHEDULE WITH EXTERNAL CUES, IN THE DOG

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Numerous authors assign a mediatory role in respect of temporal regulation to collateral behaviour. Several hypotheses are proposed to account for these stereotyped activities: proprioceptive feedback, superstition or motor activities chain. They could intervene as compensatory mechanisms for the inhibition which is brought into play when there is temporal regulation and might only play a secondary role in marking out the time elapsed. The object of the research reported here is to evaluate the mediatory role of collateral behaviour in the dog, using a DRRD schedule. The DRRD schedule conditions the subject to hold a response for a fixed period and therefore restricts the repertoire of possible collateral activities and limits them spatially, thus adding a supplementary inhibitory charge to the temporal contingencies. The addition to this schedule of positive and negative external cues allows the measurement in respect of their compensatory role for the inhibitory mechanisms inherent in the temporal regulation.

INTRODUCTION

Using schedules with temporal cues like the DRL (Differential Reinforcement of Low rates of response), numerous experimenters have been able to show that collateral stereotyped patterns of behaviour are present, which are quite different in nature from explicitly reinforced operant responding. (Anderson & Shettleworth, 1977; Fraisse et al., 1979; Hodos et al., 1962; Laties et al., 1969; Richelle & Lejeune, 1980; Wilson & Keller, 1953).

According to Holz et al. (1963) and Wilson and Keller (1953) these collateral activities could originate from superstition maintained through adventitious reinforcements. By another way, Anderson and Shettleworth (1977) note, in FI and FT procedures, anticipation of food in typical terminal activities. The temporal and spatial organization of those activities could be induced by the periodicity of food delivery.

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Several authors assign a mediatory role in respect of temporal regulation to this behaviour. According to the theory of the "motor chain activities", the animal would not really evaluate the time; instead, it would simply form a chain of motor activities corresponding to the time to be estimated, the last link in the chain consisting of the response that the experimenter has chosen to reinforce. (Anger, 1963; Dews, 1962). Collateral behaviour would consist of mediators exempting the individual from any real temporal assessment. Voluntary interference on the part of the experimenter in the normal course of the behavioural chain results in the temporal adjustment of the responses being disturbed and consequently to performance being impaired (Laties et al., 1969).

According to Schmidt and Christina (1969), the proprioceptive feedback coming from muscles, tendons and joints during the temporal interval would supply the necessary stimulus for the correct temporal positioning of responses. In this sense, collateral activities could provide proprioceptive cues useful for behavioral adjustment to time.

Other authors insist on the importance of the inhibitory processes which are brought into play when there is temporal regulation. In fact, the DRL schedules impose a total absence of operant responses during the time delay (Macar, 1980; Richelle & Lejeune, 1980; Staddon, 1977), and make a certain motor inhibition compulsory. Thereafter, the collateral activities could intervene as compensatory mechanisms for the inhibition induced into these experimental procedures and might only play a secondary role in marking out the time elapsed. Falk (1971), McFarland (1974) and Staddon (1977) establish an homology between this behaviour and the displacement activities developed when oriented behaviour is actively inhibited by the animal and in the same way collateral activity might appear when this same behaviour is sanctioned by the experimenter (McFarland, 1974).

It is acknowledged that the extent of active inhibition is limited by the maximal inhibitory charge that can be tolerated. This inhibitory charge would be offset by compensatory activities, namely collateral behaviour (Richelle & Lejeune, 1980). To define more fully the role of collateral behaviour, the experimenters have developed several techniques for intervening directly in this behaviour. Among these, the DRRD (Differential Reinforcement of Response Duration) conditions the subject to hold a given operant response for a fixed period beyond which withholding the response produces the reinforcement. This procedure, therefore, restricts the repertoire of possible collateral activities

and limits them spatially, thus adding a supplementary inhibitory charge to the contingencies. (Ferraro & Grilly, 1970; Kuch, 1974; Lachter, 1984; Lejeune & Jasselette, 1987; McMillan & Patton, 1965; Molliver, 1963; Platt & Kuch, 1973; Platt & Scott, 1981; Stevenson & Clayton, 1970). However, collateral behaviour does not disappear altogether, as is shown in Greenwood (1977). Using a two-lever DRRD schedule in the cat, she notes that certain of her subjects adopt rhythmical reaching movements in the direction of the milk cup, while at the same time keeping the paw on the lever. The performance of one of the subjects could be explained in proprioceptive terms while for the others all interpretations of collateral behaviour remain plausible.

The object of the research reported here is to evaluate the temporal, mediatory role of collateral behaviour in the dog, using a DRRD schedule. The addition to this schedule of positive and negative external cues should allow the measurement in respect of their compensatory role for the inhibitory mechanisms inherent in the temporal regulation.

METHOD

Subjects

These consisted of 5 male dogs (D1 to D5), all Beagle and five years of age. Their weight varied from 11 to 14 Kg. The animals were kept in an animal house, in separate cages (1,2 × 0,8 × 1,2 m). They were fed daily on Cervo Expan based food (250 g).

Experimental test-room (Figure 1)

At the entrance to the test-room (5,6 × 3,4 × 2 m), there was a board (60 × 50 × 2 cm) which was fastened to the ground. In the opposite corner was the food dispenser (50 × 76 × 52 cm). The height of the food dispenser meant that the animal must make a jump in order to receive reinforcement. The end wall had a full-width window, 80 cm from the ground and opening outwards. In the lower left corner of the room was an obervation post (1,55 × 1,4 × 2 m). Equipped with double two-way windows, it enabled the experimenter to remain isolated and to observe the subjects directly during the experiment. It contained all the material for observing, recording and collecting the data as well as the controls for giving the experimental auditory stimulus and for distributing reinforcements.

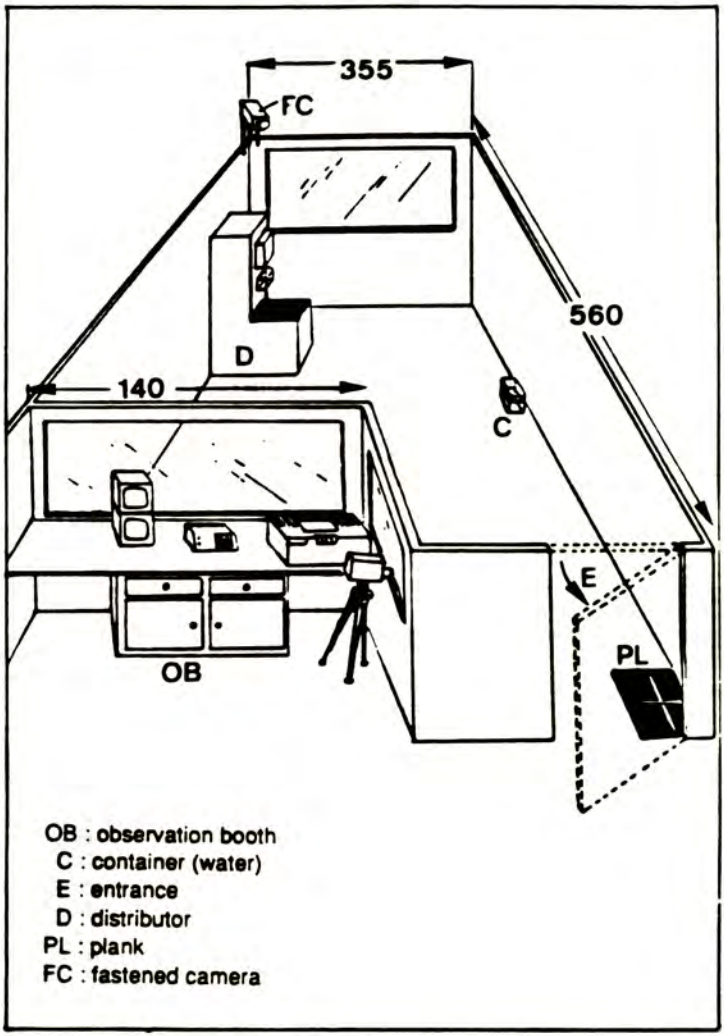

Figure 1. Test room.

Experimental procedure (Figure 2)

The conditioning schedule was composed of two types of trials (1st and 2nd) employed at random (Bruhwyler et al., 1988).

1) When the dog had taken up a position on the board and maintained it for 9 seconds, a positive auditory stimulus (S^+ = click) was given. If the dog left the board between 9 and 10.5 seconds (Limited Hold = 1.5 sec) and jumped on to the dispenser, it was positively reinforced (reinforcement = a piece of sausage weighing 5 g).

2) On the second type of trial, this same auditory stimulus, which was physically identical, was given at random between the 3rd and the 6th second of the delay, but if ever the dog left the board in response to this stimulus, there was never any reinforcement (S^-). If the dog had checked its move to leave the board, the signal was given at the 9th second, this time as S^+.

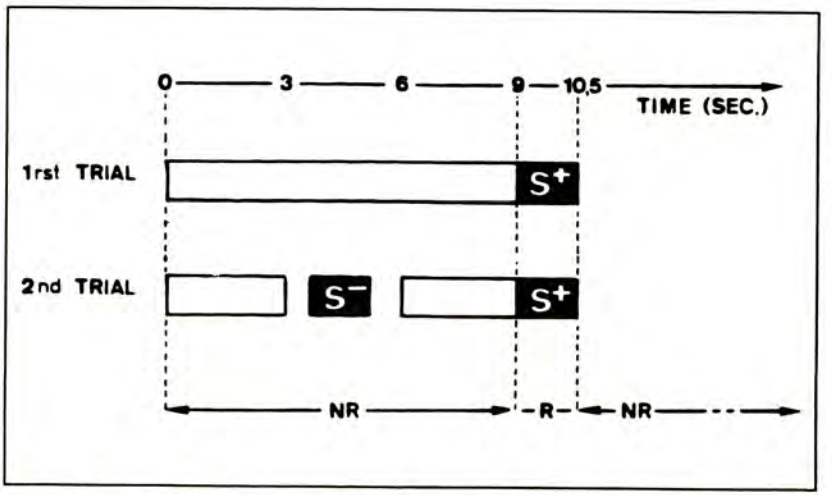

Figure 2. Description of the experimental procedure (Nr: Non-reinforced responses; R: Reinforced responses; S^+: Positive auditory stimulus; S^-: Negative auditory stimulus).

These two types of trial succeeded each other randomly in the course of the experimental sessions. Every response, correct or erroneous, reset the time and the trial. A complete session consisted in obtaining a maximum of 8 reinforcements within a maximum total period of 15 minutes. The experiments took place daily between 10 a.m. and 12 a.m.

This procedure corresponded to a DRRD 9 sec LH 1.5 sec with external cues. The unit of behaviour requiring reinforcement was twofold and consisted of a locomotor inhibition response lasting 9 sec

followed by a locomotor response and of a jump on to the dispenser, which terminated the operant sequence.

Holding the response triggered mechanisms of spatial discrimination (taking up position on the board) and discrimination of auditory cues solely on the basis of their temporal positioning in the fixed time period. Those auditory signals have a disinhibitory function. It's only in relation with their temporal context that they can induce or not the move of the subject toward the food dispenser. Between 3 and 6 seconds, the S^- accentuated the contribution of the inhibitory processes assuring the holding of the response.

Observation, recording and analysis of collateral behaviour

While the response was being held on the board, a series of collateral activities appeared and filled the waiting period. A marked inter-individual variability characterized them. They might very well consist of barkings, body and head rotations, swaying movements of the body and other stereotyped motor patterns. This behaviour was filmed during experimental sessions through the two-way window by means of a fixed camera (ITC Ikegami) and recorded on audio-visual tapes (Betamax). A digital timer (Qualec) with a 0.1 degree of accuracy, was added to the video tape. The tapes were then played at slow speed so that the collateral behaviour could be analyzed and set out on a separate sheet, divided into 18 squares (2 squares per sec) for each trial. For each half-second, the presence or absence of behaviour was indicated by the figure 1 or 0 respectively so that the data could eventually be entered into the computer (VAX 8600). All this study has been carried out on 14 sessions characterized, for each subject ($N = 5$), by a stabilized performance (75% of reinforced responses).

Statistical analysis

The statistical analysis of the results was obtained using Student's T test with observations coupled in pairs.

Results

Figure 3 shows the temporal distribution of response durations for the 5 dogs (D1 to D5) for a stabilized performance and reveals a bimodal pattern. The principal mode is centred on 9 secs (75%) and corresponds to correct responses. The second one is centred on the interval of 3 to 6 secs.

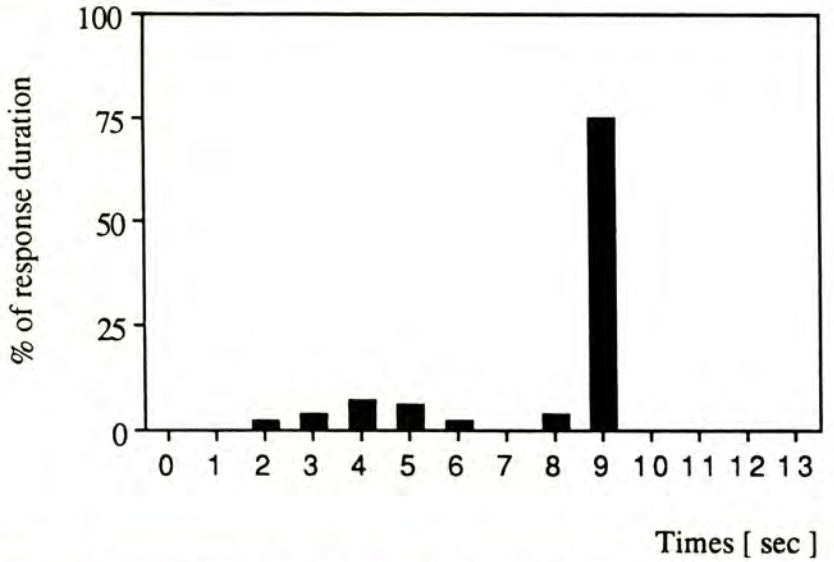

Figure 3. Temporal distribution of the operant behaviour for the group (D1 to D5) after stabilization of performance.

— Selection of collateral behaviour: For each subject, the collateral behaviour appearing with the highest frequency was included for analysis. Collateral activities appearing in less than 20% of responses (either reinforced or not) have not been analysed in a first time. For D1 and D4 this highest frequency behaviour was barking, for D3 and D5 head rotation and for D2 body swaying. Figure 4 shows that the presence of these types of behaviour is linked in a highly significant fashion to success in the trial for all the subjects. However, in the case of certain subjects (D3 and D5) a not altogether negligible percentage (19 and 6%) of trials were successful in the absence of such behaviour. The correlation between collateral behaviour and percentage of non reinforced responses has not been calculated because of heterogeneity in erroneous response durations (a response duration of 3 secs is not comparable to a response duration of 6 secs). However, it appears that the majority of errors are accompanied of the collateral behaviour.

— Temporal distribution of the frequency of collateral behaviour: Figure 5 (A to E) displays the evolution of the frequency of the collateral behaviour specific to each subject calculated on successful trials with the negative stimulus (N = 48) and without negative stimulus (N = 48). Inter-individual variability is revealed by the fact that D2 displays a progressive increase in the frequency of his behaviour

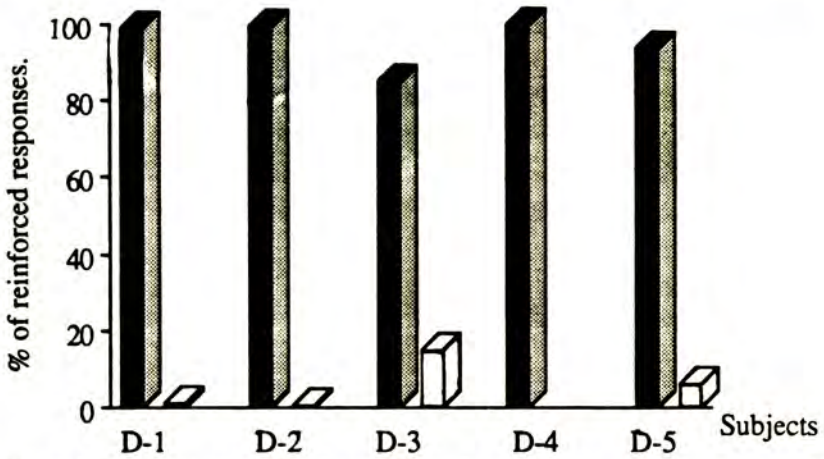

Figure 4. Percentage of reinforced responses in function of the presence or absence of collateral behaviour in the 5 dogs (D1-D4: barking, D2: swaying, D3-D5: head rotation). (■ = presence of collateral behaviour, □ = absence of collateral behaviour).

whereas the reverse is the case for D3. For D4, evolution is more heterogeneous. With 3 of the subjects (D2, D3, D4), the distribution of frequency of collateral activity reveals no marked inter-trial differences between 0 and 3 secs whereas subjects D1 and D5 show a more marked variability. The inter-trial differences become more marked for all the subjects between the 3rd and 9th sec. For the group, Figure 6 shows the evolution of the mean frequency of collateral activity throughout the delay for the two types of trial. Although this curve represents a summation of different collateral patterns, a significant difference emerges between the 2 types of trial, which is characterized by an increase in activity between 5 and 6.5 sec for the trials employing the negative stimulus. This significative difference between 5 and 6.5 secs is largely induced by the behaviour of three subjects: D1, D2 and D5 (Figure 5).

— Sequential analysis of collateral behaviour: Figure 7 shows the sequences of collateral behaviour for several successive trials, successful or unsuccessful, without the negative stimulus. The trials using a negative stimulus were intentionally set aside in order to avoid any supplementary behavioural variability linked to the reactions of the subjects to the presentation of this stimulus. For each subject, considerable intra-individual variability is observed in the sequences of their respective collateral behaviour throughout the time delay and this is as true for successful trials as for unsuccessful ones. Furthermore, an analogous sequence can just as well characterize failure as success.

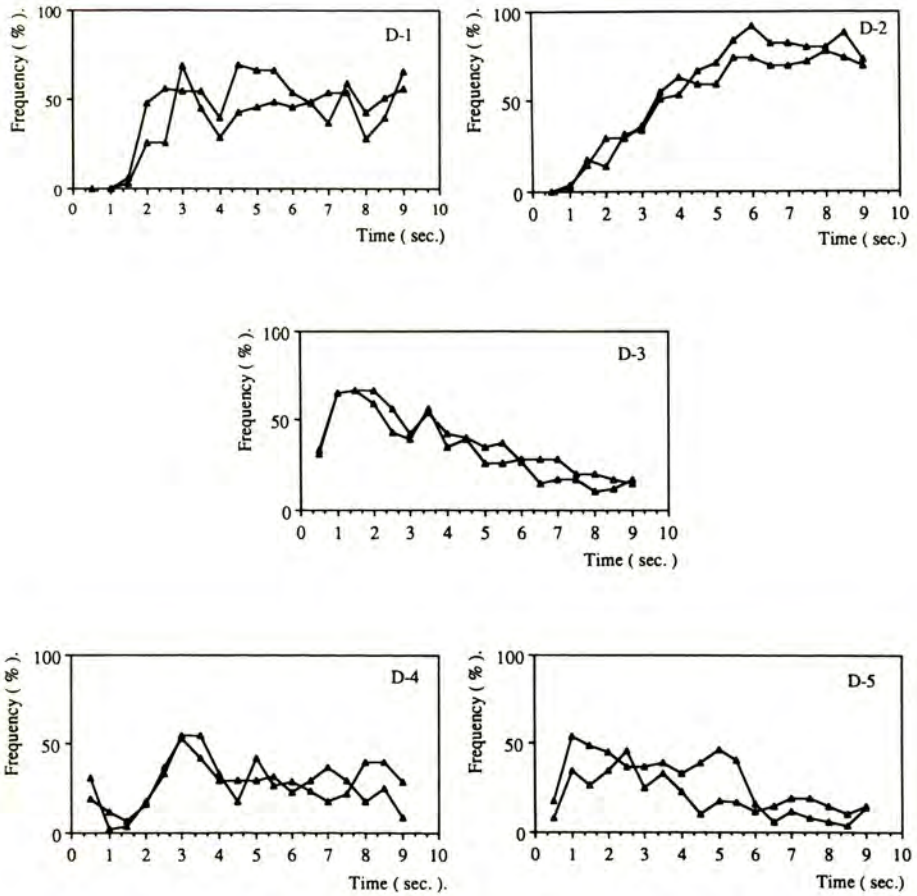

Figure 5. Temporal distribution of the frequency of collateral behaviour in the 5 subjects (D1 to D5) for the reinforced trials with S^- between 3 and 6 seconds (▲ : n = 48) and without S^- between 3 and 6 seconds (△ : n = 48).

Discussion and conclusion

The bimodality of the temporal distribution of response duration shows that positive and negative stimuli have an important controlling effect on the responses since the two modes, one between 3 and 6 secs, the other at 9 secs, correspond to the moments when the stimuli are presented. Duration also has a controlling effect on performance since

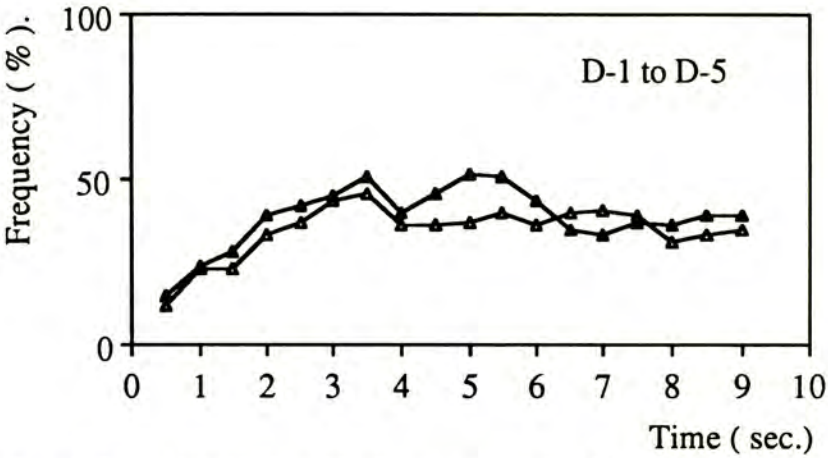

Figure 6. Temporal distribution of the frequency of collateral behaviour for the group (n = 5) for the reinforced trials with S^- between 3 and 6 seconds (▲ : n = 48) and without S^- between 3 and 6 seconds (△ : n = 48).

the principal mode (75%) is centred at 9 secs, the animal being able to discriminate the stimuli only on a temporal basis. This finding supports the position of Kuch (1974) for whom "an organism that terminates a response t sec after the response is initiated might be thought of as responding to a temporal stimulus correlated with response duration". The low rate of responses in the brief inter-response intervals (IRT) supports the observations made using the DRRD (Platt & Kuch, 1973; Platt & Scott, 1981).

Generally speaking, it seems that collateral behaviour plays an important mediatory role in schedules of temporal regulation. Our findings reveal an important correlation between the presence of such behaviour and the efficiency of the response, in agreement with the results of Blancheteau (1967), Laties et al. (1965), Lincé (1976), Schwartz and Williams (1971), Slonaker and Hothersall (1972). However, a low percentage of successful trials occurs without the necessity for collateral activity, It seems, therefore, that such behaviour is necessary but not indispensable. Moreover, Figure 7 shows that the collateral behaviour can accompany erroneous responses. This observation limits their role of first order in temporal regulation. Fraisse et al. (1979) showed that disturbing the chain of motor activities impairs temporal regulation but does not suppress it entirely. Considerable inter-individual variability is noted whether this be in the type of collateral motor pattern developed by our subjects or in the evolution

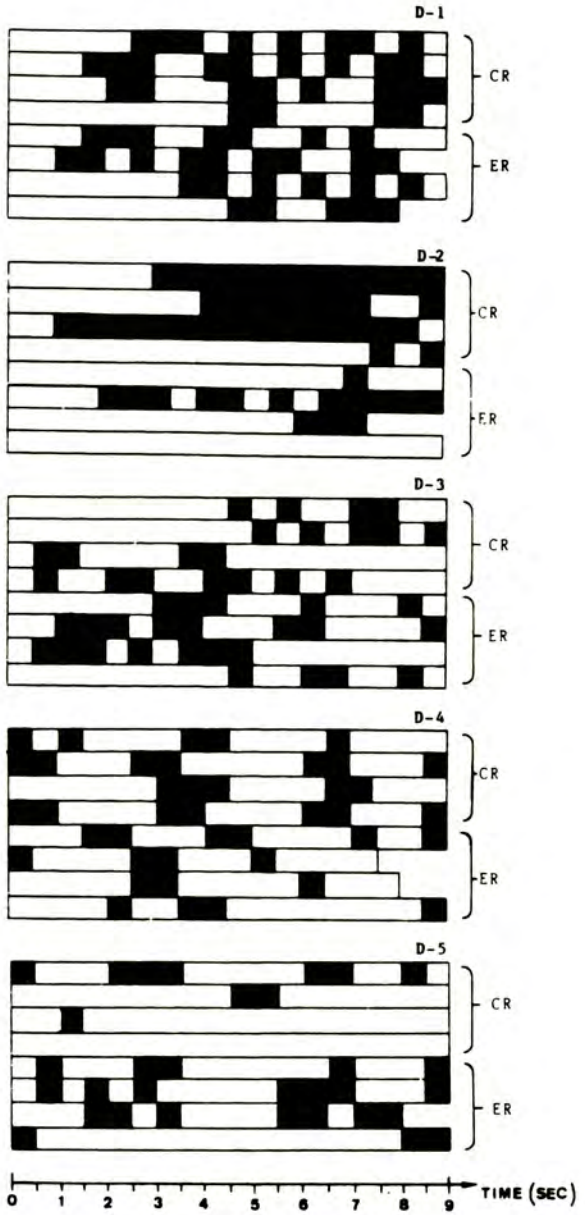

Figure 7. Sequences of collateral activities of the different subjects for several successful or unsuccessful trials without S^- between 3 and 6 seconds. (■ = presence of collateral behaviour; □ = absence of collateral behaviour).

of the frequency of collateral behaviour throughout the delay. This variability also occurs intra-individually in the diversity of the sequences of collateral behaviour. Thus Wilson and Keller (1953) 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".

In a 21 sec DRL, Hodos et al. (1962) had noted that one of their Rhesus subjects displayed characteristic head movements which decreased during the time delay. These movements could inform the individual about the state of muscular tension correlative to the temporal experience or, if one prefers, to the waiting situations that this experience stems from.

The hypothesis of the behavioural chain, invalidated by Dews (1965) in FI, has been questioned by Herrnstein (1970), Pouthas (1979), Richelle and Lejeune (1980), Staddon (1977) in other procedures like DRL. Our findings also help to undermine this hypothesis. The sequential analysis reveals considerable intra-individual variability even for successful trials without a negative stimulus, successively during a single session. Therefore, it was not useful to measure this variability for the successful trials using the negative stimulus, as an additional variable was introduced as a result of the movements produced in reaction to this stimulus. According to Staddon (1977), it is difficult to attribute to collateral activities the role of mediatory behaviour if one takes into account their variability both in sequential terms and in terms of duration. And he concludes: "How can an animal estimate time with the help of so unreliable a clock?"

By means of the "disinhibition" theory, Mc Farland (1966) and Van Iersel and Bol (1958) explain how a balance between two conflicting activities reduces the ability to inhibit a third activity and leads to displacement activity. It emerges from our findings that collateral behaviour would be better interpreted in terms of displacement activities. The evolution of the frequency of collateral activity for the group reveals a significant difference at the precise moment when the negative stimulus is applied. This difference is largely due to subjects D1, D2 and D5. The evolution of D3 and D4 is uneasily interpretable. The fact of remaining on the board at this moment constitutes a response in itself which can lead to increased activity at the behavioural level. In fact, the behavioural conflict between the motivation to hold the inhibition or to release it is maximal; the individual might then find in the increased intensity of its collateral behaviour an outlet, a way of channelling its

excitation. We can thus corroborate the main conclusions of Richelle and Lejeune (1980) for whom collateral behaviour is motor discharge activity coming to compensate the inhibitory mechanisms at work in the temporal spacing of operant responses. "It is not correct to say that collateral behaviour inhibits operant responding. The terms must be inverted: operant responding is inhibited by the periodic structure of the temporal requirements of the situation and collateral behaviour develop as by-products of this inhibitory state" (Richelle & Lejeune, 1980).

The appearance of intense activity in the animal during the execution of the procedures with temporal cues, the marked increase of this behaviour at the time of stimulation requiring inhibition are two arguments which underline the active character of the inhibitory processes involved to differing degrees in all temporal regulation schedules.

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