

FAILURE TO DELAY GRATIFICATION FOLLOWING SEPTAL LESIONS IN RATS: IMPLICATIONS FOR AN ANIMAL MODEL OF DISINHIBITORY PSYCHOPATHOLOGY

JOSEPH P. NEWMAN,¹ ETHAN E. GORENSTEIN² and JOHN E. KELSEY³

¹Department of Psychology, University of Wisconsin, Madison, WI 53706;

²Columbia University, NY 10027 and

³Bates College, Lewiston, ME 04240, U.S.A.

(Received 21 April 1982; accepted in revised form 24 May 1982)

Summary—It has been proposed that dysfunction within a neural system composed of the medial septum, the posterior hippocampus and the orbito-frontal cortex (SHF system) may constitute the physiological basis of several disinhibitory syndromes in humans—psychopathy, hyperkinesis, alcoholism and extraversion. Consequently, the syndrome produced by lesions of the SHF system in animals is offered as a tentative behavioral model that may elucidate basic psychological components of human disinhibitory psychopathology. As predicted from this model, rats with septal lesions, like disinhibited humans, were less likely to delay gratification than controls when given a choice between waiting 10 sec for an assured reinforcement and an immediately available, though infrequently delivered, reinforcement. Inquiry into the nature of this deficit suggested that these rats are subject to an interference effect, such that the influence of future rewards on behavior could be disrupted or 'eclipsed' by the presence of more immediate, prominent, motivationally significant cues. The possibility that various disinhibitory syndromes in humans may also be due to a similar rigid focus of attention upon the most immediate or prominent motivationally significant event was briefly discussed.

It has been proposed that dysfunction within a neural system composed of the medial septum, the hippocampus and the prefrontal cortex (SHF system) may constitute the physiological basis of psychopathy (Hare, 1970), criminality (Trasler, 1978; Williams, 1969), hyperkinesis (Rosenthal and Allen, 1978), alcoholism (Tarter, 1976) and extraversion (Gray, 1972)—in short, syndromes that may be characterized as primarily disinhibitory in nature. This speculation is founded partly upon the observation that the behavior of animals with lesions of this system resembles behavioral aspects of each of these human syndromes. For example, Hare (1970) compared the poor passive avoidance and diminished conditioned suppression in animals having septal lesions to the poor passive avoidance and diminished autonomic anticipation of electric shock among psychopaths, suggesting that both psychopaths and animals with septal lesions are deficient in anticipatory fear conditioning (see also Gray, 1972).

In addition to behavioral characteristics reminiscent of animals with SHF dysfunction, psychophysiological anomalies observed in disinhibitory psychopathology have also been cited to support an SHF hypothesis. Specifically, abnormal patterns of EEG waves (Williams, 1969), and autonomic and cortical reactivity indicative of autonomic imbalance (Porges, 1976) have been observed in disinhibited patients and have been interpreted as implicating dysfunction within the SHF system (see Mawson and Mawson, 1977, for a review).

Unfortunately, current theorizing about the role of the SHF system in various disorders has not advanced beyond the level of tentative speculation. This is principally because confirmation of the SHF hypothesis depends upon direct physiological evidence in humans which remains unavailable. Although one can anticipate little progress in directly confirming the role of SHF dysfunction in human disinhibitory syndromes, Gorenstein and Newman (1980) suggest that the similarities between animals with SHF lesions and disinhibited humans may nevertheless have important implications for understanding disinhibited behavior in man. These authors suggest that even if we are unable to determine whether dysfunction of the SHF system is the physiological substrate of these human disinhibitory syndromes, the SHF syndrome may nevertheless offer a valid behavioral model of human disinhibition. It is proposed that the perceptual, motivational, attentional, learning and other psychological peculiar-

ities inferred from the behavior of animals with SHF dysfunction can provide clues to basic psychological components constituting the common denominator of several human disinhibitory syndromes.

The experiments that follow utilize the syndrome created by SHF dysfunction as a model for discovering basic processes in disinhibitory psychopathology. Specifically, a behavioral style regarded by many as the *sine qua non* of disinhibition, failure to delay gratification (e.g. Hare, 1970; Mischel, 1961; Unikel and Blanchard, 1973) is explored in rats with septal lesions. The hypothesis is that septal lesions will reduce the tendency of rats to defer rewards.

EXPERIMENT 1

This experiment was designed to determine if rats with septal lesions, relative to controls, prefer to enter the arm of a Y-maze in which water reinforcement is immediately available, but only on some of the trials (partial reinforcement, PRF), or prefer to wait 10 sec (i.e. delay gratification) to enter another arm in which water is available on every trial (continuous reinforcement, CRF). The prediction is that, if septal lesions produce a disinhibitory deficit similar to that occurring in disinhibited humans, rats with septal lesions will fail to delay gratification and will choose the arm providing immediate, but infrequently available reinforcement more often than the controls. To assess the effect of the density of partial reinforcement, the probability of reinforcement in the partial reinforcement arm was systematically varied.

Method

Subjects

The Ss were 11 experimentally-naive, male Sprague Dawley rats. All animals weighed 375-425 g at the outset of the experiment. Subjects were maintained in separate cages in a colony that was lighted between 7 a.m. and 7 p.m. each day. The rats were given free access to food, but were between 22- and 24-hr water-deprived at the start of each experimental session.

Surgery

The rats were injected with 2.5 cc/kg Chloropent (Fort-Dodge) anesthetic prior to surgery. Five of the 11 animals received bilateral septal lesions. These were made by passing 1.5 mA of anodal direct current for 10 sec through a stereotaxically-positioned stainless-steel No. 1 insect pin that was completely insulated except for the flattened cross section of the tip. Six animals were assigned to the operated control group. These rats underwent the same surgical procedure with the exception of electrode insertion.

Apparatus

The apparatus was a wooden Y-maze with a galvanized-steel floor. The start box was 27-cm long and 10.2-cm wide and was separated from the choice area by a black opaque guillotine door. The choice section was pentagon-shaped with 10.2-cm long sides. The two goal arms were separated by 90°, were 14.2-cm long and 10.2-cm wide, and were separated from the choice section by clear Plexiglas doors which could be pivoted upward into the goal arms. In the middle of each arm, 1.8 cm from the back wall, a 2-cm diam. brass cup was mounted on the floor to hold the water reinforcement. The walls of the apparatus were 17.5-cm high. The start box and the choice section were covered by clear Plexiglas and the goal arms were covered by white, opaque Plexiglas.

Procedure

The experiment was divided into three parts: "pretraining", to expose the rats to the maze and the contingencies; "assessment", during which the rats' knowledge of the reinforcement contingencies was evaluated and "delayed CRF vs immediate PRF", during which the rats' preference for the various delay and reinforcement contingencies was measured.

Pretraining. The 6 days of pretraining began 10 days after surgery, on the first day of water deprivation. On the first day, each rat was allowed to explore the maze for 10 min in the absence of water and was randomly assigned to subsequently receive CRF at either the right or left goal box and PRF at the opposite goal box. On each of the next 5 days, the rats were forcibly exposed to the reward contingencies existing in each arm of the maze. A block of wood was placed behind the Plexiglas door of the PRF goal, blocking the entrance to that goal box and forcing the rats to the open CRF arm where they received 1/5 cc of water in the brass cup on every trial. Following 10 consecutive such trials, the block was moved behind the closed Plexiglas door of the CRF goal box, forcing the rats for 10 consecutive trials to enter the open PRF arm in which they received 1/5 cc water on only 3 of the 10 trials (PRF = 30%). Immediately following the end of a trial, the rat was returned to the start box, and the next trial was begun approx. 4 sec later by raising the start-box door. In order to accustom rats to the delay that would precede entry into the CRF arm of the maze during delayed CRF vs immediate PRF, on days 5 and 6 of pretraining, the rats were required (by virtue of a closed door) to wait 5 and 10 sec, respectively after leaving the start box before being allowed to enter the arm associated with CRF. As before, entry into the PRF arm was not delayed. Reinforcements consisted of 1/5 cc of water during all three phases of the experiment.

Assessment. On the following day (day 7), rats were given an assessment session to determine if they had learned and remembered which arm of the maze was associated with CRF and which was associated with PRF. It was reasoned that if equal delays were imposed before the rats could enter either arm, the rats should select the arm that had been associated with CRF. To evaluate this, the rats were given 10 assessment trials in which the entrance to both arms were closed for 5 sec. Five seconds after leaving the start box, both arms were opened simultaneously. A choice of CRF on 7 of the 10 trials was taken to indicate that a rat was correctly discriminating the CRF from the PRF side. In the rare event that a rat failed to meet the 70% criterion, it received further pretraining until it did so. Furthermore a similar 10-trial assessment was repeated after each 3-session block of the experiment proper to assure that the rats maintained this discrimination throughout the experiment.

Delayed CRF vs immediate PRF. This phase was designed to determine whether rats prefer to immediately enter the arm of a Y-maze in which water reinforcement is available on only a certain percent of trials (PRF) or prefer to wait 10 sec (i.e. delay gratification) and enter an arm in which water reinforcement is available on every trial (CRF). During this phase, the rats received 20 trials per day. On each trial, a rat was released from the start box into the choice point area of the maze where it was faced with two doorways: an open one that led to a goal box that might or might not contain a water reinforcement on that trial (PRF); and another that was closed, to be opened 10 sec after the rat left the start box, and led to a goal box where water reinforcement was a certainty (CRF). The rat, therefore, could enter only the PRF arm for the first 10 sec after arrival at the choice point, and if it did so, a door closed behind it and the trial ended with the rat either receiving reward or not depending on the PRF schedule. If the rat refrained from entering the PRF arm for 10 sec, however, the door to the CRF arm would open, permitting access to that arm as well. Upon the animals' entering either alley, a door closed behind it and the trial ended. The rat was then returned to the start box and the guillotine door was opened approx. 4 sec later beginning the next trial.

After every fifth trial, rats were forced to enter the goal box opposite to the one they had just chosen. This was accomplished by placing a wooden block behind the closed, clear Plexiglas door to the most recently chosen goal box. These interspersed forced trials were in addition to the 20 daily trials of delayed CRF vs immediate PRF and were intended to ensure that all animals sampled both sides of the maze to some extent each day.

Delayed CRF vs immediate PRF was conducted in 5 blocks of 60 trials at 20 trials per day. The probability of reinforcement in the PRF arm was varied sequentially by blocks: 30% for Block 1, 15% for Block 2, 0% for Block 3, 30% for Block 4 and 15% for Block 5. Thus, throughout Block 1 for example, the rat could choose to wait 10 sec for an assured reward or, alternatively, to enter the PRF arm immediately with a 30% chance of receiving a reward. During Block 2 the PRF percentage was changed to 15%, during Block 3 to 0%, etc. and a 10-sec wait before entry into the CRF goal box was required throughout. After animals

completed Block 3 (PRF = 0%), they were given one day of 20 forced trials, 10 to delayed CRF and 10 to PRF, in which the PRF = 50%. This was designed to reinstate sampling of the PRF side after extinction in Block 3.

Reinforcement schedules for the PRF arm were prepared using a random number generator. For the 30% PRF schedule, 6 reinforcements were randomly distributed throughout a daily session of 20 trials with the restriction that 3 reinforcements were scheduled for the first 10 trials and 3 for the second 10 trials. For the 15% PRF schedule, 3 reinforcements were randomly distributed throughout a daily session of 20 trials with the restriction that at least 1 reinforcement must be scheduled for the first and at least 1 for the second trials. Reinforcements on the PRF arm were scheduled to occur at a given trial such that, if an animal chose the PRF arm on that trial, it would receive the reinforcement; if it chose to wait for CRF, that reinforcement would be lost. Under such circumstances, the percentage of reinforced entries into the PRF goal box could conceivably range from 0 to 100% for a given 20-trial session but would average 30% during 30% blocks and 15% during 15% blocks. All animals received the same PRF schedule on a given day. During the assessment trials, instituted to test knowledge of the prevailing reinforcement contingencies immediately after each of the 5 blocks, the probability of reinforcement in the PRF arm always corresponded to that in the preceding delayed CRF vs immediate PRF session.

Results

Histology

The lesions were confined to the septal area and destroyed most of the medial and lateral septal nuclei (see Fig. 1). Also extensively damaged were the medial parolfactory area, the dorsal extension of the diagonal band of Broca, the hippocampal commissure, and the fimbrial septal nucleus. The descending columns of the postcommissural fornix were usually undamaged.

Behavioral testing

Assessment. Throughout the 6 10-trial assessment sessions, in which the CRF and PRF doors were opened simultaneously after 5 sec, both septal and control rats demonstrated consistent preference for CRF. Thus, both groups exhibited the appropriate discrimination, the septals choosing CRF on 94.3% of the assessment trials and the controls on 94.4%.

Two rats from the septal group and two from the control group did not reach the 70% criterion (i.e. choosing the CRF rather than the PRF arm) on the first 10-trial assessment session. These rats received further pretraining until they did so. One rat in each group also failed to reach the 70% criterion on the second assessment session, which followed Block 1. These animals underwent further pretraining and began the experiment anew, starting with the first assessment and continuing on through Block 1 etc. At no other time in any of the experiments did any rat fail to reach the 70% criterion during assessment sessions.

Delayed CRF vs immediate PRF. The results of Blocks 1-5 support the hypothesis that rats with septal lesions are less likely than control rats to wait for an assured reward when an immediate, but variable, reward is available. As shown in Fig. 2, the septal rats overwhelmingly preferred the PRF side as opposed to waiting 10 sec for CRF. In contrast, the controls continued to demonstrate a preference for the CRF arm of the maze and consequently obtained more reinforcements than the rats with septal lesions. A two-way analysis of variance of Groups \times Blocks, with repeated measures across Blocks, confirmed that there was a significant Groups effect ($F(1,9) = 18.28, P < 0.002$). There was also a significant effect of Blocks ($F(4,36) = 26.28, P < 0.0001$) indicating that animals were sensitive to alterations in the probability of reinforcement at the PRF goal box. The Groups \times Blocks interaction was not significant. Analysis of simple main effects indicated that rats with septal lesions were less likely than controls to wait for CRF on all trial blocks (P at least < 0.01 except for PRF = 0% where $P < 0.05$).

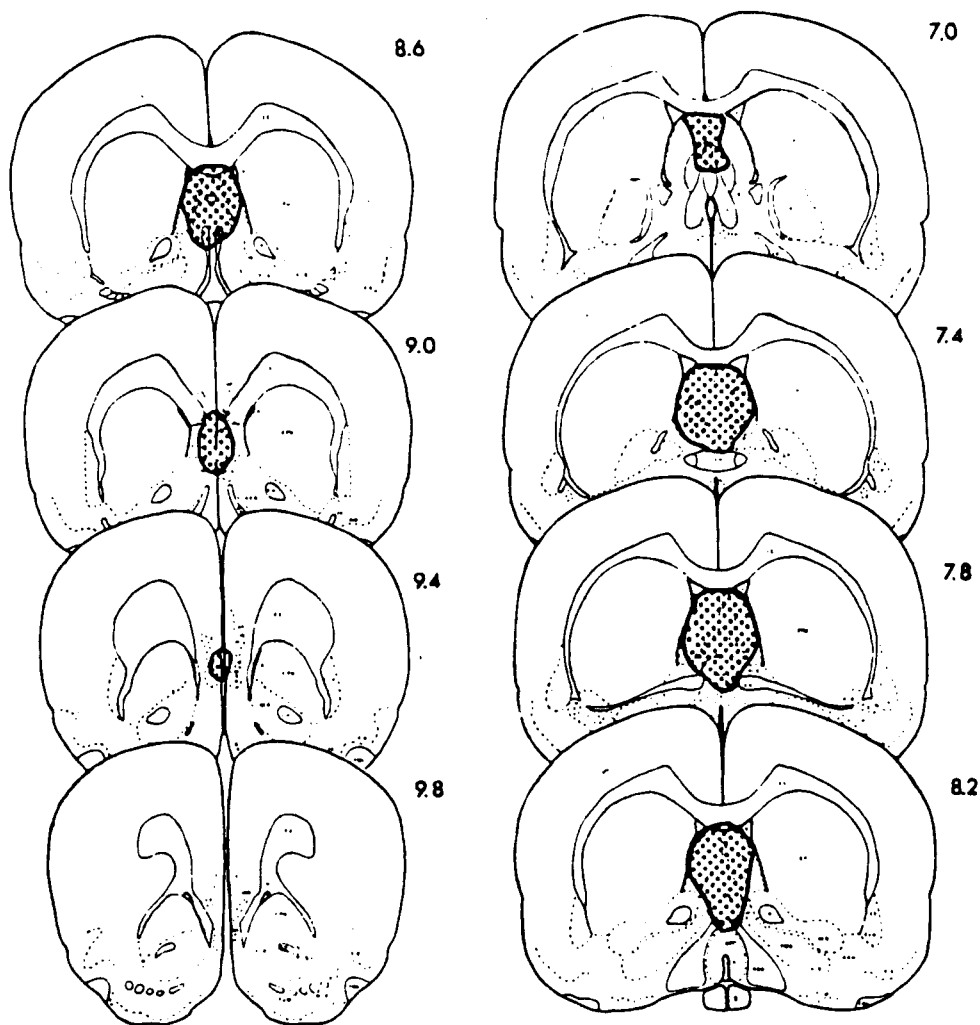


Fig. 1. Reconstruction of the typical septal lesions of Experiments 1 and 2 (the numbers refer to anterior-posterior coordinates; Pellegrino and Cushman, 1967).

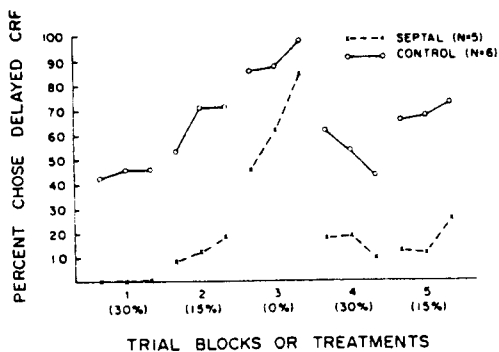


Fig. 2. The mean percentage of trials on which the controls and rats with septal lesions selected the delayed CRF arm of the maze as a function of the PRF schedule. In this experiment, the CRF arm could not be entered until 10 sec after leaving the start box.

Discussion

Analysis indicated that rats with large bilateral septal lesions were less likely than controls to wait for a more attractive alternative when a less attractive alternative was immediately available, even when such behavior resulted in an overall loss of reinforcement. Like antisocial adolescents and human psychopaths, then, rats with septal lesions are less likely to delay gratification. Such a conclusion rests, of course, on the assumption that rats with septal lesions treat the CRF arm of the maze as the more attractive arm when equal delays are imposed. This assumption was clearly supported by the results of the assessment sessions, when an equal 5-sec delay was imposed at both arms, since both the rats with septal lesions and the control rats chose the CRF side on over 94% of the trials.

What are the psychological peculiarities entailed by septal dysfunction that account for the failure to delay gratification observed in rats with septal lesions? One hypothesis has already been eliminated, namely, that rats with septal lesions fail to discriminate or are not affected by the difference in value between partial and continuous reinforcement. There are, however, two other hypotheses, derivable from previous research using rats with septal lesions, that seem to offer viable explanations for the results observed in this experiment. The first hypothesis is that rats with septal lesions suffer from a deficit in behavioral inhibition (e.g. McCleary, 1966). That is, there may be a deficit in the inhibitory processes that enable the normal animal to refrain from making an active response during the 10-sec delay. The second, that rats with lesions of the septum may fail to wait for CRF because they are deficient in anticipating rewards that are delayed by 10 sec (White, 1974). Experiment 2 addresses these two hypotheses.

EXPERIMENT 2

In order to test whether a deficit in behavioral inhibition could account for the choice behavior of rats with septal lesions in Experiment 1, the task was altered so that the required 10-sec wait for CRF was not imposed until after animals had already entered the CRF arm. Thus, upon emerging from the start box, animals were faced with two open alleys, both of which could be entered immediately. The animals, therefore, are not required to spend 10-sec waiting at the choice point in the face of temptation to proceed to PRF.

Method

Subjects

The Ss were 11 experimentally-naive male Sprague-Dawley rats weighing 375–425 g. Five rats received bilateral septal lesions and 6 were operated controls. Surgical and histological procedures were the same as in the first experiment.

Apparatus

The same Y-maze as in Experiment 1 was used. However, water reinforcement (1/5 cc) was delivered in a brass cup, attached to a piece of wood, and inserted through a door in the back of each goal box. This modification was necessary to allow for the introduction of reinforcements into the CRF goal box after the delay interval had elapsed.

Procedure

As in Experiment 1, this experiment consisted of three phases—“pretraining”, “assessment” and “delayed CRF vs immediate PRF”. The essential difference between the two experiments was the place where the 10-sec delay for the CRF arm was imposed. Whereas in Experiment 1, the delay was imposed prior to the selection of the CRF arm, in Experiment 2, it was imposed after the rat entered the CRF arm. Consequently, rats in Experiment 2 could proceed into the CRF goal box immediately, at which point the door to the goal box was closed and the 10-sec delay prior to delivery of reinforcement was begun. Thus, unlike the procedure of Experiment 1, the procedure of Experiment 2 did not require behavioral inhibition to choose CRF.

Pretraining consisted first of 10 min of free exploration in the maze for each rat. On each of the following 4 days rats were forced 10 trials to CRF (delivered immediately) and then 10 trials to PRF = 30%. On the sixth day, rats were given 20 assessment trials of free choice between immediately delivered CRF and PRF. On each of the following 2 days rats received 10 forced trials to CRF in which, after the rat entered the arm, the alley door was closed behind it and water reinforcement was placed into the goal box 10-sec later. Rats were then forced 10 trials to the PRF side.

On the following day, the rats commenced the delayed CRF vs immediate PRF phase which, similar to that of Experiment 1, was conducted in 6 blocks of 60 trials at 20 trials per day. In this phase the rats were allowed to choose either the open CRF arm, in which reinforcement was given 10 sec after the arm was entered, or the PRF arm in which reinforcement was immediately available on a certain percentage of trials. The probability of reinforcement in the PRF arm was varied sequentially for the 6 blocks as follows: Block 1A, PRF = 30%; Block 1B, PRF = 30%; Block 2, PRF = 15%; Block 3, PRF = 0%; Block 4, PRF = 30%; Block 5, PRF = 15%. In contrast to Experiment 1, an additional Block, 1B, was added at the beginning because the animal's behavior did not yet appear stable during Block 1A. Specifically, the septal group appeared to be decreasing their percentage choice of CRF and it was considered inadvisable to change the PRF schedule until they stabilized. As in the first experiment, following Block 3 (PRF = 0%), the rats were forced 10 trials to CRF and 10 trials to PRF = 50% to reinstate sampling of the PRF arm. Also, as in Experiment 1, rats were forced, after every fifth trial, to go to the opposite goal box for one trial.

Results

Histology

The septal lesions were similar to those of Experiment 1, except that the maximal extent of the lesions was about 0.3 mm more posterior (see Fig. 1).

Assessment

The results of the 20 trials assessing preference for CRF or PRF (both delivered immediately) indicated that as in Experiment 1 both the septal and control groups demonstrated overwhelming preference for CRF. The mean percentage choice of CRF was 94.0% for rats with septal lesions and 85.0% for the controls. A *t*-test indicated that these two means were, in fact, significantly different ($t(9) = 2.49, P < 0.05$). Thus, any concern that rats with septal lesions might be deficient in discriminating the greater value of CRF relative to PRF should be dispelled by these results.

Delayed CRF vs immediate PRF

Despite the septal group's greater preference for CRF when no delay was involved (assessment), the results of this experimental phase suggest that rats with septal lesions are less likely than controls to wait for a more attractive alternative even when behavioral inhibition is not required to do so. As shown in Fig. 3, the septal group was much less likely than controls to select the CRF arm in which delivery of reinforcement was delayed by 10 sec than to select the PRF arm in which reinforcements were immediately available but only on some of the trials. Consequently, as in Experiment 1, the rats with septal lesions received fewer reinforcements than the controls.

An analysis of variance of Groups \times Blocks, with repeated measures across Blocks, confirmed that there was a significant Groups effect ($F(1,9) = 7.17, P < 0.03$). There was also a significant effect of blocks ($F(5,45) = 8.46, P < 0.001$), indicating that rats were sensitive to alterations in the probability of reinforcement at the PRF goal box. The Groups \times Blocks interaction was also significant ($F(5,45) = 2.64, P < 0.04$).

Simple main effects tests indicated that the rats with septal lesions were less likely than controls to select the CRF arm when PRF = 30% (Block 1B, $P < 0.05$) and when PRF = 15% (Blocks 2 and 5, $P < 0.01$), but not when PRF = 0% (Block 3).

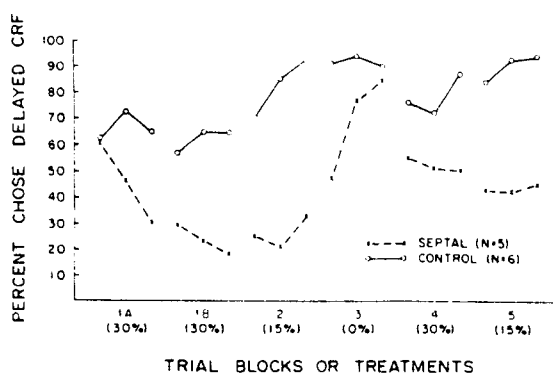


Fig. 3. The mean percentage of trials on which the controls and rats with septal lesions selected the delayed CRF arm of the maze as a function of the PRF schedule. In this experiment, both the CRF and PRF arms could be entered immediately. However, reinforcement was not given in the CRF arm until 10 sec after that arm had been entered.

Discussion

The results of this experiment suggest that the inability to delay gratification exhibited by rats with septal lesions is not due to a deficit in behavioral inhibition. Rats with septal lesions continued to choose the immediately available, but less attractive, alternative even when a capacity for behavioral inhibition was not required to select the more attractive but delayed alternative.

In addition, these results are not consistent with an hypothesis that rats with septal lesions are unable to perceive the connection between a response and reinforcement delayed by 10 sec. The septal group selected the delayed CRF arm approximately as often as controls when $PRF = 0\%$. This finding indicates that the septals are capable of anticipating delayed reinforcement; they made the appropriate response even though reinforcement did not occur until 10-sec afterward.

GENERAL DISCUSSION

In view of compelling evidence that the syndrome produced by lesions of the septum in animals bears a fundamental relationship to human disinhibitory syndromes, it was hypothesized that rats with septal lesions, like human psychopaths and antisocial adolescents, would be less inclined than controls to delay gratification. The results of Experiments 1 and 2 provide striking confirmation of this prediction. Given a choice, rats with septal lesions were far more likely than controls to select the less attractive, but immediately available, alternative than to wait 10 sec for the more attractive one.

Several plausible explanations suggested by the literature on septal lesions and by the paradigm itself were investigated. First, the results of the assessment sessions in both experiments demonstrated that rats with septal lesions were as good or better than control rats in discriminating the differences in reward value between continuous (CRF) and partial (PRF) reinforcement. When the delivery of both CRF and PRF were delayed by an equal amount, the rats with septal lesions selected the CRF arm on more than 94% of the trials—at least as often as the controls. Although it has been suggested that rats with septal lesions are less affected by aversive events (e.g. the nonreward during partial reinforcement, Gray, 1979; Lubar and Numan, 1973), such a deficit does not appear to be present here and, therefore, cannot account for the delay of gratification deficit. Second, the results of Experiment 2 demonstrated that the failure to delay gratification exhibited by these rats was not due to a deficit in behavioral inhibition, a deficit frequently proposed to account for other effects of septal lesions (e.g. Caplan, 1970; McCleary, 1961). Even when a rat could immediately enter

the CRF, as well as the PRF arm, thereby obviating the need for behavioral restraint in making the choice, rats with septal lesions were still more likely to choose the immediate, but partial reinforcement arm when the administration of reinforcement in the CRF arm was delayed by 10 sec. Finally, the finding that rats with septal lesions selected the delayed CRF arm as frequently as controls when PRF = 0%, in Experiment 2 indicates that their preference for immediate reward, when it is available, is not due to an inability to learn under conditions of delayed reinforcement *per se* (e.g. White, 1974).

While no conclusive explanation has emerged for the delay of gratification deficit demonstrated by rats with septal lesion, these results present a clearer picture of this behavioral style and indicate conditions under which it will and will not occur. It is behavioral style characterized by relative disregard for the prospect of future rewards. The behavior of rats with septal lesion is not geared to the procurement of reinforcement that is remote in time. The present results suggest, however, that the animals' relative unresponsiveness to temporally remote reinforcement occurs only under circumstances in which other rewards are immediately available. As we have seen, the experimental rats are undifferentiated from controls in ability to procure delayed reinforcement *per se*; yet an immediately available alternative, rewarded only 1/6 as often as an alternative delayed by 10 sec, is enough to cause rats with septal lesions to abandon the delayed alternative more than twice as often as controls.

Let us consider some broader implications of this interpretation. Is it perhaps generally the case that the performance of rats with septal lesions would suffer only when a task requires that the rats shift their attention away from the more immediate, dominant cues or responses to focus on more remote, added or changed events or contingencies? These are precisely the requirements of tasks involving DRL schedules, two-bar counting, delay of gratification, contingency reversals, conditioned suppression, passive avoidance and extinction--the tasks that reveal the most well-documented septal deficits. Whereas both septal and control rats can easily learn a response that leads to immediate reinforcement, the control rats are more likely to be influenced by more remote, added, or changed contingencies that require them to wait before making a response, to inhibit a response that will lead to punishment in addition to reward, and to notice an alternative contingency when the current, dominant one is no longer appropriate. Although we recognize that such an account is more descriptive than theoretical and that it does not consider all the complexities such as changes in incentive motivation, genotype and task specificity that are required to account for all the effects of septal lesions (e.g. Donovan *et al.*, 1979), it may be a useful way to conceptualize a large number of the effects of septal lesions.

The purpose of this research and the foregoing speculation concerning the nature of the septal deficit is to utilize the septal syndrome as a model of human disinhibition to elucidate basic processes in disinhibitory psychopathology (Gorenstein and Newman, 1980). If the syndrome produced by lesion of the septum is functionally analogous to syndromes of human disinhibition, then the goal-oriented behavior of disinhibited humans may also be subject to interference by conspicuous motivationally-significant stimulus cues. Thus, it is suggested that psychopaths may not be insensitive to punishment *per se*, but rather may be less sensitive to more remote, added or changed contingencies whatever their motivational sign or significance.

That rats with septal lesions, like psychopaths and antisocial adolescents, demonstrate a delay of gratification deficit in addition to the frequently cited avoidance deficits not only extends the functional analogy between the animal syndrome and human disinhibition, but also suggests a broader interpretation of the psychological consequences of these lesions and their implications for human disinhibitory psychopathology.

REFERENCES

- CAPLAN M. (1970) Effects of withheld reinforcement on timing behavior of rats with limbic lesions. *J. comp. physiol. Psychol.* **71**, 119-135.
- DONOVAN P. J., BURRIGHT R. G. and BENGELLOUS W. A. (1979) The septal region and behavior: an example of the importance of genetic and experimental factors in determining effects of brain damage. *Neurosci. Bio. Behav. Rev.* **3**, 83-98.
- FOWLIS D. C. (1980) The three arousal model: implications of Gray's two-factor learning theory for heart rate, electrodermal activity, and psychopathy. *Psychophysiology* **17**, 87-104.

- GORENSTEIN E. E. and NEWMAN J. P. (1980) Disinhibitory psychopathology: a new perspective and a model for research. *Psychol. Rev.* **87**, 301-315.
- GRAY J. A. (1972) The psychophysiological nature of introversion-extraversion: a modification of Eysenck's theory. In *Biological Bases of Individual Behavior* (Edited by GRAY J. A. and NIBYLLISYS V. D.). Academic Press, New York.
- GRAY J. A. (1979) A neuropsychological theory of anxiety. In *Emotions in Personality and Psychopathology* (Edited by IZARD C. E.). Plenum, New York.
- HARI R. D. (1970) *Psychopathy: Theory and research*. Wiley, New York.
- LUBAR J. F. and NUMAN R. (1973) Behavioral and physiological studies of septal function and related medial cortical structures. *Behav. Biol.* **8**, 1-25.
- MAWSON A. R. and MAWSON C. D. (1977) Psychopathy and arousal: a new interpretation of the psychophysiological literature. *Biol. Psychiat.* **12**, 49-73.
- MCCLEARY R. A. (1961) Response specificity in the behavioral effect of limbic system lesions in the cat. *J. comp. physiol. Psychol.* **54**, 605-613.
- MCCLEARY R. A. (1966) Response-modulating function of the limbic system: initiation and suppression. In *Progress in Physiological Psychology*, Vol. 1 (Edited by STELLAR E. and SPRAGUE J. M.). New York.
- MISCHEL W. (1961) Preference for delayed reinforcement and social responsibility. *J. abnorm. soc. Psychol.* **62**, 1-7.
- PELLEGRINO L. J. and CUSHMAN A. J. (1967) *A Stereotaxic Atlas of the Rat Brain*. Appleton-Century-Crofts, New York.
- PORGES S. W. (1976) Peripheral and neurochemical parallels of psychopathology: a psychophysiological model relating autonomic imbalance to hyperactivity, psychopathy, and autism. *Adv. Child Dev. Behav.* **11**, 35-65.
- ROSENTHAL R. H. and ALLEN T. W. (1978) An examination of attention, arousal, and learning dysfunctions of hyperkinetic children. *Psychol. Bull.* **85**, 689-715.
- TARTER R. E. (1976) Empirical investigation in psychological deficit. In *Alcoholism: Interdisciplinary Approaches to an Enduring Problem* (Edited by TARTER R. E. and SUGARMAN A. A.). Addison-Wesley, Reading, Massachusetts.
- TRASLER G. (1978) Relations between psychopathy and persistent criminality: methodological and theoretical issues. In *Psychopathic Behavior: Approaches to Research* (Edited by HARI R. D. and SCHALLING D.). Wiley, New York.
- UNIKH I. P. and BLANCHARD E. B. (1973) Psychopathy, race, and delay of gratification by adolescent delinquents. *J. nerv. ment. Dis.* **156**, 57-60.
- WHITE N. M. (1974) Effects of septal lesions on responding for delayed brain stimulation reinforcement. *Brain Res.* **65**, 185-193.
- WILLIAMS D. (1969) Neural factors related to habitual aggression: consideration of differences between those habitual aggressives and others who have committed crimes of violence. *Brain* **92**, 503-520.