THE RATE OF ACQUISITION AND EXTINCTION OF A PASSIVE AVOIDANCE RESPONSE AS A FUNCTION OF LEVEL OF TRAINING AND AGE IN RATS

By

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ABSTRACT

It has been reported that young rats are slower to acquire and faster to extinguish a simple passive avoidance response than adults. Such results have been interpreted through the assumption that young subjects have difficulty in inhibiting active responses. The extinction data are difficult to interpret since level of acquisition was not held constant across age. The present investigation explored the contributions of an inhibitory deficit and the level of acquisition to the rate of extinction in preweanling and adult rats. Latency of response was employed as the dependent measure.

The design of the experiment was a 2 x 2 x 3 factorial, including factors of age (18 days and 100 days), level of training (one acquisition trial and two acquisition trials), and treatment condition (experimental or response-contingent, Pavlovian control or placed, and stimulation control). Level of training was varied in order to examine its effects both within and between age groups on extinction rate. Since some evidence suggests that young and adult subjects may respond differently to Pavlovian and instrumental contingencies involved in passive avoidance settings, the Pavlovian control group was employed. In addition, there is also evidence which suggests that handling and shock may increase the activity level of young rats compared to that of adults. Thus, a yoked stimulation control group was used to partial out the effects of these procedures.

No age differences were found in acquisition level or extinction rate. Two training trials produced longer crossover latencies in acquisition than one training trial. In addition, subjects in the response-contingent training condition had longer crossover latencies in acquisition than subjects in the Pavlovian and stimulation control groups after two training trials. Extinction rate was independent of acquisition level. Furthermore, extinction rate was the same for both the experimental and Pavlovian groups, suggesting that Pavlovian conditioning is importantly involved in passive avoidance.

The lack of age differences as reflected in acquisition was related to the use of apparatus which was scaled to the size of the animal. In previous studies, with the use of unscaled apparatus, age differences have been reported. The use of scaled apparatus may have facilitated acquisition of the response in young subjects. The lack of an age difference in extinction rate appeared to be the result of the same type of learning (i.e., Pavlovian fear conditioning) in both age groups. A further investigation of the effects of apparatus size on the acquisition of a passive avoidance response in both young and adult rats is suggested.

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CHAPTER ONE: THE NATURE OF THE PROBLEM

The importance of early experience to an organism's subsequent development and adult behaviour has been a major concern of psychologists. Investigators have explored the effects of stimulation (Ader, 1959; Denenberg, 1964), rearing conditions (Harlow & Harlow, 1962), and deprivation conditions (Cooper & Zubek, 1958) on adult behaviour. In addition, the development of learning (Campbell, 1967) and memory processes (Campbell & Spear, 1972) have been the object of investigations.

Some evidence from experimentation concerning the ontogeny of learning in rats suggests that young organisms differ quantitatively, and perhaps qualitatively, from adult organisms (Riccio & Marrazo, 1972). It has also been suggested that age differences may be explained, at least partially, with reference to inhibitory capacities, subsequent competing responses, and activity level (Campbell, Lytle & Fibiger, 1969; Egger, Livesey & Dawson, 1973; Fibiger, Lytle & Campbell, 1970; Mabry and Campbell, 1974). A number of questions remain unanswered, however. Qualitative differences in learning behaviour have not been substantiated experimentally. The contribution of amount of training has been investigated minimally (Kirby, 1963) and requires further clarification. The effect of apparatus size has been, for the most part, ignored even though Feigley and Spear (1970) have provided evidence of its importance. Each of these (i.e., qualitative differences in learning behaviour, amount of training, and apparatus size) may affect, or be affected by, inhibitory capacities. Thus, the present investigation was designed to explore further the role of inhibitory capacities in age differences in learning.

Inhibitory Deficits in Young Rats

Inhibition Hypothesis

Carlton (1963) has suggested that some inhibitory system in the brain acts to antagonize that system in the brain which in normal situations activates behaviour. He hypothesized that the activation system controls "the tendency for all responses to occur" (p. 27) but that the inhibitory system would "antagonize this action on nonreinforced responses" (p. 27). A central cholinergic system was the inhibitory system that Carlton suggested was involved in this process.

Carlton (1963) cited neuropharmacological research with adult rats and mice which supported his hypothesis. The administration of atropine, a drug known to block cholinergic activity in the brain, resulted in the exhibition of behaviours that were rarely produced in a Sidman avoidance learning situation. Responding during extinction, and perseveration of response topography were noted after the administration of cholinergic blocking agents, suggesting a lack of inhibition. In addition, animals were unable to extinguish irrelevant and competing responses during acquisition of a complex learning behaviour after a cholinergic blocking agent had been administered to them.

If young rats have an inhibitory deficit, then, according to the system outlined by Carlton (1963), young rats would continue to respond even though such responding is no longer reinforced (i.e., during extinction). In addition, acquisition of a response by young animals would be slower compared with adults because a young animal would have relatively greater difficulty inhibiting competing responses.

Carlton (1963) demonstrated that since cholinergic inhibitory activity aids in the habituation process and leads to an inhibition of nonrewarded responses, anticholinergic drugs such as scopolamine and atropine, which can block the influence of the cholinergic inhibitory system, can lead to the disinhibition of certain responses. It follows from such a suggestion that if young rats have an inhibitory deficit, then anticholinergic drugs would produce no observable effect on their behaviour. Of course, in adults a disruption of behaviour would be produced.

Age Differences in Inhibitory Control: Neuropharmacological Evidence

A number of investigators have evaluated the hypothesis that young rats have inhibitory deficits by studying age differences in the effects of anticholinergic drugs on such unlearned behaviours as activity level and spontaneous alternation in a T-maze. Campbell et al. (1969) found that the anticholinergic drug scopolamine only increased the activity level of rats which were 20 days of age or older whereas the stimulant drug amphetamine produced a dosage-dependent increase in activity level of all ages of rats in the study (i.e., 10-, 15-, 20-, 25-, and 100-day-old rats). These results imply that activation processes are salient in rats as young as 10 days of age but that inhibition processes are not able to influence behaviour until some time between 15 and 20 days of age.

Fibiger et al. (1970) investigated the development of inhibitory processes in rats by testing the effects of pilocarpine, a cholinomimetric drug, on amphetamine-induced arousal of rats 10, 15, 20, and 25 days of age. No effect of pilocarpine could be detected in the 20-day-old group; and a marked effect could been seen in the 25-day-old-group. Fibiger et al. inferred a gradual development of cholinergically mediated inhibition between 15 and 25 days of age in rats. Egger et al. (1973) investigated the effects of scopolamine on spontaneous alternation behaviour and found that the drug increased spontaneous alternation in 50- and 100-day-old rats, but did not affect the behaviour of 16- and 24-day-old rats. Two hypotheses are supported by the results of this experiment: young rats have an inhibitory deficit in comparison with mature rats, and the lack of inhibitory control does lead to perseveration of responding.

Mabry and Campbell (1974) evaluated the development of a serotonergic inhibitory process and its effects on behavioural arousal. They obtained results which imply that a serotonergic inhibitory process is functional, and does have a certain degree of effect on behaviour by the time a rat is 15 days of age. However, the inhibitory process does not appear to be fully developed at 15 days of age, since a greater effect on behaviour was found in 20- and 25-day-old animals.

An inhibitory deficit which would result in at least some age differences in the acquisition and extinction of a response seems to be present in young rats. In all of the investigations described above it has been found that young animals had an inhibitory deficit (Campbell et al., 1969; Egger et al., 1973; Fibiger et al., 1970; Mabry & Campbell, 1974). Some inhibitory control seems to be present at about 15 days of age (Mabry & Campbell, 1974), but a deficit, as measured by activity level (Campbell et al., 1969; Fibiger et al., 1970) and perseveration of responding (Egger et al., 1973) seems to remain until at least about three weeks of age. The deficit should be reflected probably in terms of rate of acquisition and extinction of various learning tasks.

The Relationship Between Inhibitory Deficits and Learning Tasks

In all of the investigations described above, the finding of an inhibitory deficit in the unlearned behaviour of young rats (Campbell et al., 1969; Egger et al., 1973; Fibiger et al., 1970; Mabry & Campbell, 1974) implies that an inhibitory deficit could result in at least some age differences in acquisition and extinction of a learned response.

In reviewing the literature on age differences and learning, it is important to note that different learning tasks may involve different processes or combinations of processes. Since different tasks may call into play different learning processes, it should not be assumed that age differences in inhibitory control will be reflected in all learning tasks. Some tasks seem more suitable than others in the investigation of age differences in learning capacities, and the contribution of inhibitory deficits. Schulenburg, Riccio, and Stikes (1971) have commented that the passive avoidance technique is sensitive to certain developmental changes which affect learning ability, but they do not attempt to specify the processes which would be involved, such as the development of inhibitory control.

The Task of Interest

Although the components of the passive avoidance task and age differences in acquisition and extinction of a passive avoidance response will be described below, the reasons for choosing this particular learning task will be presented here.

Passive avoidance learning involves training the subject to remain stationary in order to avoid receiving an aversive stimulus such as shock. Such a task minimizes age differences in locomotor ability, since it is the lack of movement which constitutes the objective of the task. The technique has been used extensively in the literature on the ontogeny of learning.

Consideration of Variables of Interest

If inhibitory deficits in young rats are to be examined adequately be the use of a passive avoidance technique, then a number of important variables, other than inhibition, that may contribute to age differences in passive avoidance behaviour should be considered. A listing of such relevant variables would include (1) level of learning; (2) Pavlovian conditioning control; (3) stimulation control; (4) apparatus size; and (5) extinction behaviour.

Level of Learning

Carlton (1969) has suggested that inhibitory capacities may be measured by rate of extinction of a learned response, since the ability to extinguish a learned response may in part be controlled by such processes. However, in any evaluation of extinction of a learned response, the original level of acquisition must be taken into account, especially if a trials to criterion measure of extinction is employed. If the level of acquisition is not considered, then the number of trials taken by a subject to reach an extinction criterion may be erroneously interpreted. For example, an animal which has a low level of acquisition and a high or moderate level of resistance to extinction may reach the extinction criterion in fewer trials than another animal which has a higher level of acquisition and a low level of resistance to extinction. If an investigator simply measured the number of trials to an extinction criterion, he would probably draw the conclusion that the former animal was less resistant to extinction than the latter. With the exception of Kirby (1963), in the context of an active avoidance procedure, the effect of level of acquisition on extinction rate has not been investigated. Kirby found a nonsignificant trend for resistance to extinction to be greater in young rats as compared to adult rats when the groups were unmatched for level of acquisition. When the groups were matched for acquisition level, no differences among age groups were apparent. Kirby concluded that extinction of an active avoidance response was invariant across age.

There is evidence that differences in acquisition level may occur as a function of age. For example, Snedden, Spevack, and Thompson (1971), in an investigation of conditioned suppression, found that 15-day-old rats did not suppress licking any longer than 15-day-old rats which received the conditioned stimulus (CS) unpaired with the shock. Experimental animals which were 22, 35, and 70 days old suppressed licking significantly more than control animals of the same ages which received the CS unpaired with the shock. The authors concluded that young rats were not as capable of learning a contingency as adult rats, thereby resulting in age differences in acquisition levels. Thus, in any investigation of age differences in extinction rate, level of acquisition must be examined.

The use of a trials to criterion measure of rate of extinction fails to take into account differences in the level of acquisition. Most experimenters attempt to equate acquisition levels across experimental groups, either by administering an equal number of trials to each subject or by imposing an acquisition criterion, but then fail to test for equal levels of acquisition by examining first trial extinction behaviour. If the contributions of both an inhibitory deficit and the level of learning are to be evaluated, then some method of differentiating their effects must be devised.

Pavlovian Conditioning Control

The use of the passive avoidance conditioning technique requires some evaluation of the possible contribution of different types of associations to overall performance. It is not certain, without the use of proper control procedures, whether the subjects are associating the shock with the situational cues of the shock compartment or with the response of entering the shock compartment. It is possible that a subject that has associated the shock with certain cues in the environment will exhibit a conditioned emotional response (CER) or Pavlovian conditioning to the situational cues as opposed to a punishment effect (i.e., instrumental conditioning), as follows:

Blanchard and Blanchard (1968) administered passive avoidance training to adult rats and then administered the same number of shocks, at the same frequency, to subjects in a yoked control condition. A third group of subjects received treatment identical to that of the yoked control group except that no shock was administered. When the three groups of animals were tested for passive avoidance of the shock compartment, the experimental and yoked shock control groups both took a significantly longer amount of time to enter the shock chamber than the third group. The yoked control group latencies were not significantly different from those of the experimental group, suggesting that passive avoidance in this experiment was based on conditioned fear.

Randall and Riccio (1969) have presented evidence which suggests that both punishment and fear conditioning occur when rats learn a passive avoidance response. They hypothesized that a delay of punishment gradient, which is a weakening of response strength as the response-shock interval increases, would reflect a punishment effect in passive avoidance training. A delay of punishment gradient was obtained, but even with a 60 second response-shock interval, the response strength of experimental animals was greater than that of naive control animals. These results suggest that conditioned fear is also a factor in passive avoidance conditioning (Randall & Riccio, 1969).

In a second experiment, Randall and Riccio (1969) hypothesized that if conditioned fear was present, then response strength would diminish as a function of time spent in the fear chamber. The hypothesis was confirmed. Randall and Riccio concluded that both instrumental and Pavlovian conditioning components are involved in passive avoidance learning.

The results of the two studies just reported (Blanchard & Blanchard, 1968; Randall & Riccio, 1969) both imply that passive avoidance responding is probably a result of both a punishment effect and a CER. This, in itself, is not of any particular concern. However, punishment effects have been found to be less resistant to extinction (Church, 1963) and more effective for the suppression of a response than a CER (Church, Wooten & Matthews, 1970). The possibility thus arises that age differences may reflect not a difference in either inhibitory control or level of acquisition but a difference that is due to young and adult subjects attending to different experimental cues. Certainly some theoretical models of early experience effects allow the inference that young subjects would attend to the Pavlovian components and adult subjects would attend to the instrumental components of a passive avoidance learning situation (Bronson, 1965; Razran, 1961; Thompson, 1966). Furthermore, Riccio and Marrazo (1972) detected certain age trends in a delay of punishment situation which prompted them to hypothesize that the young subjects were attending to the Pavlovian aspects of the situation whereas the adult subjects were attending to the instrumental aspects. (This study is described more completely in the review of the literature of age differences in passive avoidance learning (see p. 20).)

Stimulation Control

In addition to separating the effects of Pavlovian and instrumental conditioning in the passive avoidance learning situation, it is also imperative to separate the non-associative effects of stimulation from the learned response. Handling and shocking animals may not only affect the activity level of subjects, but also affect young animals more than adult animals. Denenberg (1964) has suggested that handling increases the activity level of animals and that handling before the subject is weaned is more effective in increasing activity level than handling after weaning. As well, some evidence indicates that shock administration may differentially affect the activity level of young and adult rats (Ader, 1959; Meyers, 1965). If this is the case, then it is possible that young subjects will be less able to remain stationary than adults. Such an effect would be reflected in slower acquisition scores and faster extinction scores by young than adult subjects in a passive avoidance task.

Apparatus Size

The size of the apparatus in relation to the size of the animal may affect learning of a response, since in a larger apparatus, cues may be less prominent. That is, young rats, because they are smaller than adult rats, may not notice apparatus compartment differences. Also, movement from one compartment to another compartment may not be noticed by young animals if they are placed in an apparatus which is scaled in size and generally designed for adult rats. Furthermore, age differences in activity level may contribute to apparent age differences in learning if the size of the apparatus is not taken into account.

Feigley and Spear (1970) have presented some evidence that the size of the apparatus in relation to the size of the animal is an important variable in the evaluation of age differences in passive avoidance learning. When both young and adult animals were given passive avoidance acquisition training in the same compartment, the young animals required significantly more trials to reach the acquisition criterion than the adult animals. When young animals received passive avoidance acquisition training in an apparatus which was scaled to their size, no significant age differences were found. (This study is described more completely in the review of the literature of age differences in passive avoidance learning (see p. 17).)

Carlton (1963) has reported experimental results with adult rats which suggest that inhibitory deficits become more prominent as size of the learning chamber increases in proportion to size of the animal. As larger apparatus were employed, lower dosages of scopolamine were required in order to disrupt performance.

Extinction Behaviour

The examination of extinction behaviour of young and adult rats is necessary in order to detect age effects which may not be a result of age differences in inhibitory control. In order to determine whether the response-contingent subjects attend predominantly to the instrumental or Pavlovian cues of the learning situation, extinction rate must be examined in comparison to extinction rate of Pavlovian control animals. Such information would not be available from evaluation of acquisition behaviour. As well, acquisition behaviour may be affected by age differences in inhibitory capacity, whereas extinction behaviour may be controlled by other factors, such as type of learning or activity level. Therefore, in order to investigate the role of inhibitory capacities in age differences in learning, both acquisition and extinction behaviour must be examined.

Summary

A number of investigators have become interested in analyzing early experience effects in terms of factors governing age differences in learning. One factor which has received considerable attention is inhibitory ability, which may control a subject's behaviour in situations such as acquisition of conditioned responses, suppression of activity, and extinction of learned responses. Of interest in the present thesis is the role of inhibition in early learning, as manifested in the acquisition and extinction of a passive avoidance response. It has been observed, however, that in any adequate investigation of passive avoidance behaviour, attention should be paid to control over several extraneous variables. Otherwise, age differences in passive avoidance learning may be attributed to (1) different levels of acquisition across age groups; (2) the behaviour of some animals reflecting a punishment effect and the behaviour of others reflecting a CER; (3) handling or shocking of subjects which is involved in the experimental procedure, and which may differentially affect activity levels of animals in different age groups; and (4) the greater activity levels of the young subjects than those of adult subjects, irrespective of any stimulation effects.

CHAPTER TWO: AGE DIFFERENCES IN PASSIVE AVOIDANCE RESPONDING

The results of studies of age differences in passive avoidance responding suggest that young rats are slower to acquire the response than adults. Also, the young animals appear to be less resistant to extinction than adults. These age difference effects seem to be related to factors involving the ability to inhibit an unrewarded response. However, several difficulties arise from such an analysis, as follows: (1) the contribution of level of acquisition to rate of extinction has been ignored; (2) proper control procedures for Pavlovian conditioning, stimulation, and activity level have in general been ignored; (3) the use of apparatus which is scaled to the size of the animal has been inconsistent; and (4) a measure of rate of extinction has not been employed. These inadequacies in individual investigations will be detailed in the following literature review. The review is divided into five sections, each of which contains material relevant to age differences in passive avoidance learning. The five sections are (1) acquisition of a passive avoidance response as a function of number of acquisition trials; (2) extinction of a passive avoidance response; (3) punishment of an active avoidance response; (4) passive avoidance after active avoidance training; and (5) physiological mechanisms.

Literature Review

Acquisition as a Function of the Number of Acquisition Trials

Brunner (1969) examined age differences in one trial passive avoidance learning using rats 20, 25, 30, 35, 40, 45, 50, 55, 60, and 120 days old. A step-down task was employed. The step-down latency for each subject was measured during one training trial and two test trials, which occurred 24 and 48 hours after the training trial. No age differences in latency of stepping down were found for the training trial, indicating that age differences in activity level were not present. Comparisons of the step-down latencies between the 20 day old and every other age group revealed that the youngest group had significantly shorter latencies in both test trials than groups which were 40 days of age or older.

Because appropriate control groups were not employed in order to assess the contribution of Pavlovian conditioning, stimulation effects, level of acquisition, or possible age differences in retention, it is difficult to determine whether age differences reported by Brunner (1969) were due to age differences in inhibitory control, original level of learning, or memory.

Riccio, Rorbaugh, and Hodges (1968) studied passive avoidance using rats which were 16, 19, 25, 32, or 90 to 120 days old. In one segment of the study, one training trial was administered and then the animals were tested for passive avoidance of the shock side of the apparatus either 2 minutes or 24 hours later. In another segment of the study, half of the subjects in the three youngest age groups received acquisition trials until they failed to enter the shock compartment within 10 minutes of the beginning of the trial.

Because no age differences due to retention interval were observed, the data were pooled across this condition. The results for the acquisition procedure of administering one trial revealed that younger rats moved from the safe to the shock side of the apparatus after a shorter period of time than the older rats. Differences in latency were, in fact, significant for all adjacent and nonadjacent age groups. The trials to criterion results indicated that the three younger groups were capable of learning the passive avoidance response, but only after a greater number of shocks had been delivered. The youngest group of animals received the largest number of trials in order to achieve the acquisition criterion.

The results of a third portion of the study (Riccio et al., 1968) in which an active avoidance task was employed, suggest that 19-day-old animals are slower than adult animals to learn an association between a stimulus and a response, since young animals required significantly more trials to acquire a simple active avoidance response. Therefore, age differences found in passive avoidance responding were probably not simply the result of age differences in the capacity to inhibit active responding, but also the result of age differences in learning a contingency. In addition, no control groups for the effects of Pavlovian conditioning, stimulation, age differences in activity level, or level of acquisition were employed in this study. As well, the apparatus was not scaled to the size of the animals. The results, then, may reflect the effects of a variety of factors rather than age related inhibitory ability _per se_.

Riccio and Schulenburg (1969) attempted to sort out some of the variables contributing to age differences in passive avoidance conditioning by the use of appropriate control measures. The apparatus was scaled to the size of the animal. The first of two experiments was designed to determine age differences in rate of acquisition of passive avoidance responding. The rats were 10, 15, 20, 30, or 100 days old when training began and each response contingent subject received training until it did not step down from the safe side to the shock side of the apparatus for 180 seconds. Control animals placed in the shock side of the apparatus received the same number of shocks at the same time intervals as those of their matched response contingent animals. The test for passive avoidance acquisition was a single test trial in which the step-off latency for each subject was measured.

The increase in latency relative to the first trial and the number of trials to criterion were the acquisition measures employed. The 10 and 15 day old response contingent rats were found to be considerably slower than all the older animals in acquiring the response. In most cases, the adults acquired the response in only a single trial. Riccio and Schulenburg concluded that the results reflected a punishment contingency since the placed control animals exhibited little evidence of the passive avoidance response. The behaviour of the placed control animals is surprising since Brunner, Roth, and Rossi (1970) found conditioned suppression of licking within one trial with adult animals. Also, Blanchard and Blanchard (1968) found no differences between the passive avoidance responding of experimental and matched control groups in their study outlined previously. It is unclear why passive avoidance of the fear chamber was not found in the control group in the study by Riccio and Schulenburg (1969).

In a second experiment, Riccio and Schulenburg (1969) attempted to determine whether or not making an escape response from the shock compartment would improve passive avoidance performance. The animals were 12, 15, 18, and 21 days old. The apparatus was scaled to the size of the subject. The procedure for the inescapable group was the same as that in the first experiment for the response contingent passive avoidance condition. In the escape condition, the procedure was identical except that if the animal had not returned to the safe side of the apparatus within 14 seconds, it was pushed back.

The three younger groups required significantly more trials than the oldest group to learn the response in both the escapable and inescapable conditions. Those animals in the escape group tended to require slightly fewer trials in order to learn the response. However, control groups, whose behaviour would reflect the effects of age differences in activity on acquisition levels were not employed. Therefore, any conclusions concerning age differences in ability to inhibit responding based on these data would be premature.

Feigley and Spear (1970) investigated retention of active and passive avoidance responses in a study which involved three experiments. Only the passive avoidance experiments will be reported here. In the first experiment in which a passive avoidance task was used, the animals were 21 to 25 and 95 to 105 days old. Each of the rats received training at one of three different shock levels. The warning signal was a flashing light, followed by shock when the animal entered the passive avoidance shock chamber. Avoidance of the shock chamber for 60 seconds on two consecutive trials constituted the acquisition criterion. Retention tests occurred 1 and 28 days after training. On the retention trials the animals were retrained to the acquisition criterion, using acquisition parameters.

The crossover latencies on the first trial did not differ significantly as a function of age, indicating that activity levels for the two age groups were similar. The number of trials to reach criterion decreased as the shock intensity increased in both age groups. The young