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JUVENILE RETENTION DEFICITS FOR A CONDITIONED EMOTIONAL RESPONSE IN RATS: IMPLICATIONS FOR INFANTILE AMNESIA

by

ALVIN M. BERK

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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date

Herbert D. Saltzstein
Executive Officer

Anthony Sclafani Anthony Sclafani
Eric Heinemann Eric Heinemann
Arthur Reber
Supervisory Committee

The City University of New York

Abstract

JUVENILE RETENTION DEFICITS FOR A CONDITIONED EMOTIONAL RESPONSE IN RATS: IMPLICATIONS FOR INFANTILE AMNESIA

by

Alvin M. Berk

Adviser: Professor Arthur Reber

Nineteen-day-old and adult rats were given off-baseline tone-footshock pairings so that tone presentation during licking 48 hr later produced equal suppression in both ages. Controls showed the suppression to be due to associative factors. Despite suppression equal to adults' at 48-hr testing, pups displayed significantly poorer retention (infantile amnesia) when compared with adults 8, 16, 32, or 64 days after conditioning. Suppression on 48-hr tests could be reduced in pups but not adults if nonreinforced off-baseline presentations of the tone were interposed in the retention interval. This off-baseline extinction procedure also reduced suppression by pups when the nonreinforced tone presentations differed in acoustic frequency from the conditional stimulus. With the same frequencies, excitatory generalization tests disclosed significant and similar generalization gradients for both ages, suggesting that the greater memorial interference observed in pups stemmed more from their heightened susceptibility to off-baseline extinction than from differences between ages in generalization. Collectively, these studies suggest that extinctionlike processes could contribute to ontogenetic retention deficits usually classified as "infantile amnesia."

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Although psychologists have grown increasingly wary of theories of learning or memory that purport to apply to both humans and infrahumans, at least one such effort has met with limited acceptance in the last decade. The phenomenon in question is infantile amnesia, which has been commonly accepted since being described by Freud (e.g., Freud, 1938) and has been broadly defined as the rapid forgetting of acquired information by immature organisms, human and nonhuman (Campbell & Spear, 1972). Despite its name, infantile amnesia is not pathological; memory retention deficits for specific information in the very young commonly are seen as an inherent and possibly beneficial attribute of development. So while the origins of infantile amnesia continue to be explored by researchers (see Campbell & Coulter, 1976, for a comprehensive discussion), there is an implicit recognition that this exploration will lead not to remediation of human infantile memory deficits, but to a better understanding of the normal development of memory.

Infantile Amnesia in Humans

Little, if any, of the published evidence for infantile amnesia in humans is experimental. Nevertheless, the anecdotal literature is extensive and compelling (e.g., Dudycha & Dudycha, 1941; Salaman, 1970; Schachtel, 1947; Waldfogel, 1948). Earliest memories of most adults date from the third year of life onward (Dudycha & Dudycha, 1941), and reports from the first year are rare enough to be remarkable (Crovitz & Quina-Holland, 1976). But despite the alleged universality of human infantile amnesia, the absence of controlled experiments makes it impossible to directly determine the extent or sources of this developmental memory deficit without relying on animal models. To understand why there are no human experimental data, one need only examine the accepted experimental definition of infantile amnesia: retention deficits by infants relative to adults given equal initial acquisition of the _same_ _to-be-remembered_ material. Campbell and Spear (1972) have discussed the problems inherent in this approach, notably, the difficulty of locating a task easy enough to be mastered by the young but capable of precluding rapid overlearning by adults.

Outside the experimental paradigm, memory comparison across ages in humans becomes feasible, but the data yielded are suggestive at best. Levy (1960), in an attempt to discover the ages and intervals at which medical innoculation would be most readily accepted by infants, traced the development of memory of prior innoculation by examining about 2000 treatment records for reports of crying and other fear signs. Excluding all incidents except those in which a child began crying upon the first innoculation and again commenced crying upon _sight_ of the needle at the second innoculation session, Levy concluded that memory for injections begins at 6 months of age and increases until age 3 years, after which time fear of innoculation apparently disappears, or, as Levy notes, is manifested differently.

More commonly, infantile memory deficits are inferred from the inability of adults to remember their childhoods. In a recent survey, Crovitz and Quina-Holland (1976) asked 199 college students to recall specific memories from their youth cued by association with selected English nouns. The results failed to reveal a single memory ascribed to the first year of life; moreover, the proportion of memories reported from each age increased steadily, thereby confirming the data gathered by Waldfogel (1948) using an exhaustive free recall method. Crovitz and Quina-Holland acknowledge the deficiencies of both methods, semantic cuing and exhaustive free recall: specifically, the impossibility of verifying the accuracy of recollections. Unfortunately, the only clearly reliable survey methods available for assessing very long-term memories, the event questionnaires of Warrington and Silberstein (1970), and Squire and Slater (1975), cannot tap memories from earliest childhood; as infants could not be expected to be cognizant of the dated events probed by these techniques (among them, short-run television shows). If Sesame Street were not the perennial success it is, Squire's subjects in the 1990s could be expected to provide new insight into infantile memories for 7-foot birds and bright blue cookie monsters.

Just as it is almost impossible to verify the events in personal memories, it is difficult to accurately date them. The events in a memory may have been personally experienced, or may have been confabulated or constructed from the accounts of others; and even if genuine, a memory may have been rehearsed many times prior to present recall. Indeed, the salience of some childhood memories provokes their frequent recall; each recounting is itself a rehearsal that strengthens the memory and obscures what would otherwise be the "natural" destiny of the recollection. Given these verification problems, it is not surprising that retrospective studies have become less common in recent years. And because controlled experiments are beset with great methodological and ethical difficulties, relevant experimental data from humans are rare.

Infantile Amnesia in Infrahumans

In contrast to the paucity of experimental data from human beings, a wealth of evidence for infantile amnesia has emerged from animal studies. As Campbell and Spear (1972) and Campbell and Coulter (1976) have already furnished comprehensive reviews of this literature, the present paper will not attempt to repeat their work. It will instead focus on a few representative studies that illustrate the interpretational problems facing researchers, most of which stem from difficulty in assuring that original learning of a to-be-remembered task is equated across age groups. In the course of this selective review, a possible role for retroactive interference in understanding infantile amnesia will be examined, and an experimental approach to discerning among several explanatory hypotheses will be described.

Underlying Assumptions

The basis for all traditional studies of learning and memory, developmental or not, is the belief that a quantitative measure of what has been learned or remembered can be inferred from a quantitative measure of observed performance. Since Hull (1943), molar attempts to formally relate learning and performance have been increasingly viewed with skepticism, although most researchers continue to assume that whatever the learning-performance transform is in a particular study, it will remain constant within the limits of that study. To this end, "performance" variables such as motivational level and reinforcement magnitude are strictly controlled, and experimenters carefully qualify their conclusions to the particular species, strain, sex, age, and prior history of their experimental subjects. It is when the subject pool ceases to be homogeneous, as in the case of interspecies or interage comparisons, that difficulties arise.

To understand the magnitude of the difficulties involved in ontogenetic (age) comparisons, it might be useful to first examine problems that have emerged in phylogenetic comparisons. The simplest approach to such comparisons is to experimentally induce changes in behavior relative to a "baseline" level at which the two or more species to be compared have been "equated," while taking care to equate the experience of the subject species in all possible respects. Attempts to do this, or "control by equation" (Bitterman, 1960), are rife with difficulty because any pair of species differ in a multitude of ways beyond the knowledge or control of the experimenter. Any of these differences may affect the outcome of a particular comparison while going unnoticed. To cite a trivial but useful example, even two genera as closely related as _Rattus_ and the gerbil _Meriones_ differ completely in their tolerance to water deprivation; equation of thirst for these beasts is therefore at best difficult, and at worst a meaningless concept.

If phylogenetic comparisons of learning are difficult, so are ontogenetic comparisons, involving subtle but significant differences between age groups. Unfortunately, the difficulties, while acknowledged in the developmental literature, are rarely dealt with satisfactorily. The most obvious problems have been extensively discussed elsewhere, such as the equating of motivation across ages (Campbell, 1967). But a great many less evident issues have been ignored or minimized. [Note, however, such exceptions as Etienne's (1973) discussion of the development of object permanence in animals.] Thus, while age differences in gross sensorimotor abilities are almost always considered in the design of experiments, possible developmental changes in selective attention or associative potential of stimuli frequently are not. Despite a growing appreciation that many stimulus aspects of a situation contribute to the effective stimulus complex (e.g., Wagner, 1968), only a few studies (e.g., Brennan & Barone, 1976; Egger & Livesy, 1972; Frieman, Rohrbaugh & Riccio, 1969; Klein & Spear, 1969; Porter & Thompson, 1967; Riccio & Marrazo, 1972) have paid attention to the way in which age-related changes in stimulus selection affect acquisition. And while developmental changes in "unlearned" response hierarchies have been carefully detailed in other contexts, few authors (e.g., Bolles, 1970; Bronstein & Hirsch, 1976) have successfully attempted to integrate these findings into studies of learned behaviors in the laboratory.

Ontogenetic memory research introduces additional assumptions, each with its own problems. For example, long-term retention losses are measured relative to some arbitrarily chosen time at which initial acquisition is assessed. The choice of *when* to measure initial acquisition is not trivial; yet few experimenters bother justifying their choice, relying instead on the comforting knowledge that they have provided an operational definition sufficient to allow attempts at replication. What is the ideal time for the determination of initial acquisition? At first glance, it seems that tests during or immediately following acquisition (e.g. Campbell & Campbell, 1962; Riccio, Rohrbaugh, & Hodges, 1968) are the obvious choice, but consideration of short-lived systemic sequelae of training (particularly, of the ubiquitous motivator electric shock) suggests that "immediate" tests will be contaminated by generalized neurohormonal responses that may differ across ages. Thus, initial acquisition is best equated at some "later" time, but because of cyclical changes such as the Kamin (1957) effect, this later time should probably be some multiple of 24 hrs. Unfortunately, the processes that underlay changes in retention undoubtedly have begun long before 24 hours have elapsed, so that any progressive monotonic age differences in memory detected on some later retention test will appear less profound relative to a 24-hour posttraining assessment of acquisition than they would relative to an earlier standard. About undocumented nonmonotonic differences, no assumptions are supportable.

Although hypothesized ontogenetic changes in stimulus selection already have been mentioned in a developmental context, they must again be discussed here because of their possible intrusion whenever retention is measured over long intervals. In their simplest form, such changes could mimic growth-induced generalization decrements (see p.17). Ontogenetic changes in selective attention or association could result in different cues controlling behavior during initial acquisition and subsequent retention tests. Put in human cognitive terms, these changes correspond to changes in "coding," the occurrence of which is an accepted phenomenon in human development. Remarkably, infrahuman animals are rarely credited with a comparable process, although experimental confirmation of such changes, should they exist, is within our capability. Conditioning in long-term retention studies could be done to explicitly-determined multimodal stimulus complexes, each element of which could be independently presented on testing; similarly, this approach could be incorporated into simple cross-sectional developmental comparisons of original learning to assess the impact on acquisition of age-related coding changes. In fact, Spear (1979) reports a study by his student James Wolz that addresses this question, with results suggesting that infant and adult rats differ in their tendency to form associations to olfactory and visual cues when both are made available in the same experimental context.

One should note one final assumption made by ontogenetic memory researchers: that biological time and physical (i.e., atomic or celestial) time retain the same relationship in animals of different ages. To the extent that the salient "time-givers" for experimental animals are internal, depending on metabolic rate and/or rate of neurological change, psychological time may be different for adults and infants. Indeed, the common observation among humans that the "same" elapsed time seems shorter as we grow older (e.g., James, 1890) suggests that from a phenomenological point of view, infantile memories may persist just as long as adult memories do. Nevertheless, we too shall conform to the convention of measuring retention against physical, as opposed to psychological, time, so as not to deny the existence of the phenomenon we wish to investigate.

Infantile Amnesia for Appetitively-Motivated Tasks

The literature in this area is sparse because of its many procedural problems. Major barriers to appetitively-motivated ontogenetic comparisons of learning or memory include the identification of tasks physically appropriate to both infants and adults, and the equation of motivation across age groups. Where aversive motivators such as electric shock are used, physical parameters can be easily varied, and titration to achieve at least equivalent behavioral effects can be rationally attempted (e.g., Campbell, 1967). Where appetitive motivation is concerned, however, manipulation of drive or incentive variables is severely constrained by the qualitative differences in diet and vastly disparate metabolic rates of infant and adult animals. Nevertheless, several strategies for equation of motivation have been attempted. The simplest method, equalization of the duration of deprivation (e.g., D'Amato & Jagoda, 1960) is usually inappropriate in ontogenetic comparisons because it produces faster percentage weight loss, and possible debilitation, in young animals than in adults (Bolles & Treichler, 1977). In view of this, an equal-percentage-weight-loss strategy has also been considered, implemented through deprivation schedules tailored to the individual age groups concerned. In the case of rapidly-growing younger animals, weight loss must be measured relative to nondeprived age-mate controls. And, even with such efforts, rat pups and adults may change their activity differentially when equivalent weight is lost (Campbell & Cicala, 1962; Campbell, Teghtsoonian, & Williams, 1961; c.f. Bolles, 1975; Bronstein, 1972).

Despite these problems, several attempts have been made to compare infant and adult animals on learning the same task. D'Amato and Jagoda (1960) trained thirsty rats on a brightness discrimination task in a Y-maze. All animals, whether 30, 60, or 90 days old, were deprived of water for 22 hours before running each day; all age groups were allowed 1.5 sec to drink. Speed of acquisition, as measured by running speed in the maze, was inversely related to age. The experimenters noted the possibility that motivation was unequal for the different age groups and qualified their conclusions heavily.

More recently, Amsel and Chen (1976), and Burdette, Brake, Chen, & Amsel (1976) have approached the motivational problem by giving proportionately more food to older (and therefore larger) subjects than to younger ones. They generally have observed that younger rat pups learn a straight-alley run faster than older animals do, when learning is measured by how soon near-asymptotic terminal speeds are achieved. Of course, as Amsel and his colleagues admit, possible motivational inequities confound the results.

Bronstein and Spear (1972) taught a spatial discrimination to juvenile (33 day-old) and adult (100-120 day-old) rats, varying the amount of food reward orthogonally with age. Adults learned uniformly better than youngsters, and proved marginally less susceptible to changes in deprivation. Within the range explored, greater deprivation produced faster learning. It is not clear why this study yielded results so different from those by D'Amato and Jagoda (1960), Amsel and Chen (1976), and Burdette et al. (1976), but is is by no means alone in demonstrating juvenile acquisition deficits using appetitive motivation. Campbell, Jaynes, and Misanin (1968) found that 23-26 day-old rats learned a light-dark lever-press discrimination more slowly than adult animals did when confined continuously to operant chambers for a 5-day acquisition period; all food depended on the success of their responding. In this case, however, the experiments suggest that the difficulty of the lever-press itself may have contributed to slower pup learning.

Ernst (1972) used a different, admittedly arbitrary, approach to attempt to equate motivation. Ernst trained rat pups and adults on a Y-maze alternation task prior to investigating the suppressive effects of shock. Here too pups showed acquisition deficits relative to adults, making significantly more repetitive responses. Ernst's method of equating motivation was to maintain adult animals at 90-95% of their ad lib weight and feed pups enough to allow them to grow 3-4 grams per day. It is problematic whether these tactics produced equivalent motivation in the two age groups.

And in a notable gesture to extend ontogenetic studies of learning beyond humans and rodents, Cogan, Inmam, and Gambrel (1971) trained parakeets from 1 to 12 months old on a visual discrimination in a Y-maze. All birds were deprived for 23 hours before each daily session; no significant age differences in acquisition were found.

Because it is difficult to meaningfully equate appetitive motivation across ages, comparisons of memory for tasks demonstrably equally-learned by infants and adults are very hard to accomplish, and even harder to interpret. This review has discovered only one attempt, that by Campbell et al. (1968). After training rat pups and adults to a criterion of 80% correct discrimination responses, Campbell et al. examined responding in extinction either 0, 1, 38, 75, or 150 days later. As mentioned earlier, animals were confined during acquisition to operant chambers where they had to earn all food. Although pups performed just as well as adults after 0 days delay, their performance fell off dramatically over longer retention intervals. Nevertheless, the youngsters did not completely forget the discrimination, even after 150 days.

The difficulty in interpreting these data, as Campbell et al. point out, lays in the fact that pups emitted fewer correct responses over the 5 days of acquisition than did adults, despite their eventual attainment of the 80% criterion by the final day. Thus it is problematic whether the pups actually learned as well as the adults did; their poorer retention could be attributed to possible acquisition deficits (e.g., less "overlearning"). The infantile amnesia that may have been demonstrated in this study would have been more impressive, but still not conclusive, had the pup retention deficits come after acquisition performance superior to that of the adult animals.

In sum, there seem to be no unambiguous data supporting infantile amnesia for an appetitively-motivated task. This lack places a heavy burden on aversively-motivated paradigms, and suggests limits to the generality of the infantile amnesia syndrome in rodents.

Spatial Avoidance Tasks Requiring an Active Response

One of the earliest demonstrations of infantile amnesia in animals was by Campbell and Campbell (1962), who trained rat pups and adults on a shock-motivated spatial avoidance task requiring an active shuttling response in testing (Experiments 1 and 3), or on a CER (Exp. 2). Although infants forgot both tasks more rapidly than adults, the authors' age comparisons must be qualified because ceiling effects may have hidden differences in initial acquisition. Notably, Campbell and Campbell failed to find differences between the age groups for extinction of the spatial avoidance task, a point we will return to later.

Ceiling effects were avoided by Kirby (1963) in training 25-, 50-, and 100-day old rats on active avoidance in a straight alley. Immediately following acquisition, in which pups showed no significant deficits compared to adults, Kirby tested some animals in extinction and found no differences between age groups. Other animals given retention tests 25 or 50 days after acquisition, however, showed significant test deficits if trained as pups, but not as adults. But these may not have represented truly memorial effects. The majority of rats trained at 50 or 100 days of age failed to make a single avoidance response in 30 trials when tested in extinction one day later, even though median avoidances on the 60 acquisition trials one day earlier had exceeded 40. This result is not easily interpreted as a memorial failure, and raises the possibility that the poor avoidance performance at 50 days of age by animals trained 25 days earlier may also have resulted from whatever factors hurt 1-day test performance by their older counterparts. Very possibly, the adult 1-day test results reflect "freezing" induced by a high level of fear; this, in turn, may depend on the age of the animal at testing. (Kirby reported that a majority of animals failed to leave the start compartment on testing.) Comparable immobility by the 25-day-olds given 1-day tests seems to have been less common, judging by Kirby's data (1963, Figure 5), which may represent incomplete maturation of generalized fear (Candland & Campbell, 1962). However, by the time these pups received their 25-day retention tests, and were 50 days old, not a single animal left the start box within Kirby's 15-second criterion, suggesting that considerable generalized fear was present. It should be noted that to avoid handling subjects after each trial, Kirby took the goal box containing the animal and interchanged it with the start box. This compartment shift avoidance procedure (McCleary, 1966) has been shown to resemble 1-way avoidance for adult rats, but seems to yield data more like those of 2-way avoidance when cats are the subjects (Olton, 1973). Just possibly, ontogenetic differences may parallel the species differences just noted. A test of this comparison across rats of different ages would be a useful adjunct to understanding Kirby's results.

The Kirby (1963) study and the earlier one by Campbell and Campbell (1962) share another problem. As suggested by Perkins (1965) and by Thompson, Koenigsberg, and Tennison (1965), the great physical growth of young animals over long retention intervals may cause their perception of an apparatus to change between training and testing, thereby introducing an additional source of forgetting not experienced by slower-growing adults. Thompson, et al. (1965) found that when apparatus sizes were graded to remove the major source of this generalization decrement, age differences in retention disappeared. But so did retention in all age groups. Thus we cannot know whether the apparatus size adjustment actually reduced infantile forgetting. It is possible that the absence of age differences in the Thompson, et al. rats resulted from the additional training required by pups to reach adult acquisition criteria. A subsequent study by Feigley and Spear (1970, Exp. 3) failed to attenuate pup forgetting of passive avoidance through the use of apparatuses graded to size, but possibly the task was less dependent on the specific spatial cues that generalization decrement is likely to affect than was the active avoidance required in the earlier-cited work.

Feigley and Spear (1970, Exp. 1) did observe infantile amnesia for active avoidance. However, their acquisition data are difficult to interpret. After training rats to a criterion of five successive avoidances, which weanlings and adults reached at the same rate, Feigley and Spear examined relearning either 1 or 28 days later. First-trial latencies 1 day after training appear to show the pups at a disadvantage at two of the three shock intensities used (data were presented graphically only). We cite these data because Feigley and Spear draw their infantile amnesia inferences from a comparison of 1- and 28-day scores; i.e., they not unreasonably treat the 1-day scores as if these, and not training day scores, are the standard against which to evaluate long-term forgetting. In terms of trials to criterion after 1 day, both pups and adults relearned so well (one to three trials) that comparisons with the 28-day scores are compromised by what is essentially a ceiling effect. Ideally, parameters could be chosen that would increase the difficulty of the relearning task, so that equal initial acquisition across ages could be verified.

In contrast with the Feigley and Spear (1970, Exp. 1) report of infantile amnesia, a subsequent study from Spear's laboratory (Parsons & Spear, 1972) failed to show infantile retention deficits in a similar active avoidance paradigm. A procedural difference between the two studies may explain the apparent discrepancy. Parsons and Spear started both active avoidance training, and testing-by-retraining, with a single escape trial for each animal. This may have facilitated relearning for pups sufficiently to reduce age differences that would otherwise have proven significant.

Retention of active avoidance must be evaluated in light of what we understand about acquisition and its measurement. Most commonly, this is done by a trials-to-criterion method. In a recent examination of the effect of criterion level on acquisition and retention of active avoidance in young (23-25 days old) and adult rats, Potash and Ferguson (1977) observed infantile amnesia in animals trained to a 5/5 criterion, but failed to disclose age differences in retention in rats trained to 15 consecutive avoidances. This result could just as easily suggest that pups and adults trained to an equal, low number of consecutive avoidances may not, in fact, have achieved equal learning. If we assume, as Potash and Ferguson did, that each successful avoidance amounts to an extinction trial, and that pups extinguish faster than adults, then the observed difficulty in bringing pups to a 15/15 avoidance criterion is explained. Moreover, if one accepts these assumptions, one can account for infantile amnesia in terms of deficits in effective learning by the time the final criterial trial has been reached; presumably pups have already extinguished part of their acquired fear while adults have not. The difficulty of extinguishing active avoidance in adult rats (e.g., Clark, 1966; Theios, 1963) seems consistent with this argument, but it may alternatively indicate that successful avoidance trials do not actually constitute extinction treatment, as the reinforcing contingency of escape from an aversive situation remains in effect. Perhaps 2-factor theory applies to adults, but not to pups: Potash and Ferguson suggest that infantile retention deficits disappear when a 15/15 criterion is used because, to reach that standard, pups have had to experience many more shock trials than adults. In essence, they are taking note of a possible ceiling effect. A similar argument can be made for the failure to observe infantile retention deficits for active avoidance in Egger and Livesey (1972), where a moderately stiff criterion of

10/10 avoidances resulted in significantly more shocks for pups than for adults in acquisition. Unfortunately, neither study allowed for the exact assessment of these effects, as short-term (e.g., 24 hr) active avoidance retention tests were not administered.

An acquisition criterion of five consecutive avoidances was used by Wilson, Phinney, and Brennan (1974). The authors report having found no age-related differences in acquisition of active avoidance, but evidently reached this conclusion by lumping together data from animals that received CS preexposures and those trained conventionally. Considered separately, it appears that 21-23-day-old pups without preexposure took significantly longer than adults to reach the 5/5 avoidance criterion (27.1 trials, vs. 18.0 for the adults). Unfortunately, no statistical test of the relevant data was presented.

In a recent assessment of active avoidance learning and memory in developing rats, Myslivecek and Hassmanova (1979) noted an improvement in acquisition between 14 and 28 days of age, as measured by trials to reach a 9/10 criterion. Although one-month retention was measured only after retraining, extinction, and more training sessions, making data interpretation difficult, an inverted U-shaped pattern could be discerned, with memory improving as age at conditioning increased from 2 to 8 weeks, only to fall significantly in rats conditioned at 3 months of age. Short-term (24-hour) retention, however, peaked at 4 weeks of age; performance by older animals was not different from that of 2- and 3-week-olds.

The complexity of active avoidance as a task is reflected by some apparently anomalous data reported in the studies just reviewed. For example, Feigley and Spear (1970) found that, although adult rats relearned after 28 days about as fast as they had after only 1 day, their latency to first crossover on nonshock test trials increased significantly over the longer retention interval. Moreover, while pups showed significant decrements in relearning at 28 days compared to 1 day, their 28-day first-trial crossover latencies showed no significant increase, possibly because forgetting was balanced by motor maturation. [Contrast this with Kirby's (1963) results mentioned earlier.] Thus, although relearning scores implied infantile amnesia, crossover latencies suggested adult memory deficits. Feigley and Spear suggest that the surprisingly high 28-day crossover latencies shown by adults may have resulted from situationally-aroused fear that immobilized the animals at a time when specific response contingencies had been forgotten. Implicit in this explanation, as in that offered for the Kirby (1963) 1-day data, is the recognition that the adult rat will frequently "freeze" in a fear-inducing situation (Bolles, 1970). Freezing was also suggested by Feigley and Spear to explain why their adult animals receiving 2.5 mA footshocks in training did not cross over faster 1 day after training than they had as naive animals.

It is clear that freezing plays a role in active avoidance by rats, so that this task, as well as passive avoidance and the CER, must be considered in the light of possible juvenile response-inhibition deficits and the development of species-specific defense reactions (SSDRs; Bolles, 1970) when age comparisons are being made. Conceivably, an ontogenetic change in priority of the SSDRs emitted in a given situation (i.e., a transition from fleeing to freezing) could produce comparable active avoidance performance in animals differing in amount learned about direct response contingencies. As the available data (e.g., Feigley & Spear, 1970; Myer, 1971) suggest that high fear levels cause an increased incidence of freezing in adult animals, it is reasonable to expect that adults, more than pups, will have to overcome a tendency to freeze in order to actively avoid. The associative learning required to do this would necessarily be greater than that needed by pups for comparable performance. The fact that freezing does seem to increase with age (Bronstein & Hirsch, 1976) implies that adults do have to learn active avoidance better than pups do to reach a given performance criterion. Similarly they might also be expected to extinguish more slowly.

As evidence for infantile amnesia, each of the active avoidance studies available using rodent subjects must be qualified. Unfortunately, none showing infantile retention deficits has unequivocally demonstrated that age differences <u>in original learning</u> were not also present. It is not even clear that this goal is in principle obtainable. Probably the work that has come closest to successfully dealing with this problem is the study by Feigley and Spear (1970), but even there, floor effects may have obscured acquisition differences across ages. At this time, while the weight of the data suggests that infantile memory deficits for active avoidance do exist, the possibility of confounding age differences in original learning has not been resolved.

Age Effects in Learning and Remembering Passive Avoidance

If, as suggested, infant rats "freeze" less than adults do in a fearful situation, the young animals should show greater difficulty in performing passive avoidance (PA), where movement must be withheld to prevent shock or other noxious treatment. Pups in fact do display this deficit (e.g., Brunner, 1969; Campbell, Misanin, White, & Lytle, 1974; Feigley & Spear, 1970; Riccio, Rohrbaugh, & Hodges, 1968; Riccio & Schulenburg, 1969; Schulenburg, Riccio, & Stikes, 1971). The typical pattern seen in ontogenetic studies of passive avoidance acquisition by rats shows juvenile deficits up to about 25 days of age (Feigley & Spear, 1970). In most direct comparisons between pups and adults, pups acquire less well, although Feigley and Spear (1970) were able to alleviate juvenile acquisition deficits by training weanlings in a smaller apparatus. In trying to account for this effect, Feigley and Spear hypothesize that pups receiving footshock in an apparatus compartment much larger than themselves might not associate the shock with the compartment itself, but just with the part of the compartment where the shock was taken. In rodent species other than rats, juvenile acquisition deficits have not been noted. Nagy, Thaller, and Mazzaferri (1977) report that 16-, 19-, and 25-day-old mice show no PA acquisition deficits relative to adults using a single test trial either 1 minute or 1 or 24 hours after one-trial training, despite the use of an adult-scaled apparatus. When animals were given repeated training trials until a 5-minute PA criterion was met, adult mice took *more* trials to learn than did pups. Although acquisition rates were not measured by Campbell, et al. (1974) in their study of passive avoidance in the guinea pig, a nonreinforced test 2 days after training showed no age-related deficits. In sum, then, although general conclusions cannot be reached, passive avoidance acquisition *in rats* seems to improve with age.

Among the hypotheses traditionally advanced to explain apparent juvenile passive avoidance acquisition deficits in rats, several have stressed age differences in nonassociative factors such as spontaneous locomotion. Moorcroft, Lytle, and Campbell (1971) found that activity levels, as measured by stabilimeter cages scaled to animals' sizes, were 10-20 times higher for 15-20 -day-old pups than they were for adults. Higher activity presumably makes it difficult for pups to achieve the immobility that successful passive avoidance demands. Despite this, comparisons of pups and adults on their tendency to step off or cross over in actual PA apparatuses have disclosed no age-related differences (e.g., Riccio, Rohrbaugh, & Hodges, 1968; Riccio & Schulenburg, 1969; Schulenburg, Riccio, & Stikes, 1971). Moreover, when approach tendencies have been explicitly equated across ages (e.g., Riccio & Marrazo, 1972), rat pups still show strong passive avoidance acquisition deficits relative to adults. In sum, it does not seem as if age-related baseline activity differences alone can account for infantile PA acquisition deficits.

An alternative, non-exclusive, explanation for infantile passive avoidance acquisition deficits is that young animals cannot effectively inhibit ongoing behavior in general. Underlying the behavioral explanations have been a number of physiological hypotheses. One influential account was based on a suggestion by Carlton (1963, 1968) that much of behavior is activated by an adrenergic system and selectively inhibited by an antagonistic cholinergic system. Within that framework, Campbell and his colleagues (e.g., Campbell, Lytle, & Fibiger, 1969; Fibiger, Lytle, & Campbell, 1970; Moorcroft, 1971; Moorcroft et al., 1971) have demonstrated that cholinergic forebrain inhibitory centers do not fully develop until 15-25 days of age in the rat: the same time that infantile passive avoidance deficits vanish. Further implicating a cholinergic inhibitory system in the development of passive avoidance, Feigley (1974) found that scopalamine disrupts PA in animals over 20 days of age, but not in 16-day-olds. The hippocampus has been discussed as the site of adult inhibition by a number of writers (e.g., Altman, Brunner, & Bayer, 1973; Douglas, 1967; Kimble, 1968; cf. Nadel, O'Keefe, & Black, 1975), and has been frequently suggested as the late-developing mediator of passive-avoidance behavior in general (e.g., Brunner, 1969; Douglas, Peterson, & Douglas, 1973; Schulenburg, Riccio, & Stikes, 1971). However, in a more recent evaluation of the response inhibition hypothesis, Campbell and Coulter (1976) have noted that at least one task requiring response suppression, the conditioned emotional response (CER), presents no problems for pups; neither does passive avoidance in a conditioned taste aversion (CTA) context (Grote & Brown, 1971). Campbell and Coulter attribute this to the stimulus-stimulus (S-S) contingency represented in CTA learning, as contrasted with the stimulus-response (S-R) contingency present in the majority of passive avoidance paradigms that use footshock as reinforcer. To examine the proffered distinction between S-S and S-R is beyond the scope of this paper; we wish to note, however, that classification of CTA learning as either S-S or S-R is problematic at least. In any event, CTA learning differs from conventional PA in so many respects that to focus on their formal distinction alone is arbitrarily to ignore other, possibly more important, differences. The ease with which the CER is acquired by young animals will be examined in a later section; it does, however, cast doubt on the adequacy of the response-inhibition hypothesis.

A further difficulty with the response-inhibition hypothesis was pointed out by Riccio and Marrazo (1972), who first trained pups and adults on active avoidance and then assessed response suppression by either punishing the active avoidance behavior or by extinguishing it through nonreinforcement. Although pups showed suppression deficits when punished (they continued to avoid), they ceased responding earlier than adults when simply extinguished; this last result would not have been predicted by a juvenile inhibition-deficit hypothesis.

Perhaps the simplest and most satisfying "explanation" of juvenile passive avoidance deficits lies in the observation that successful passive avoidance is indistinguishable from "freezing," and that age-related changes in freezing are known to occur in response to fearful situations (Bronstein & Hirsch, 1976). This view is compatible with Bolles' (1970) more general hypothesis that shock-elicited responses are frequently manifestations of innate defense reactions, and not necessarily newly-learned behaviors.

Bronstein and Hirsch (1976) conjecture that passive avoidance behavior occurs initially through the association of shock-elicited freezing with contextual or kinesthetic stimuli. Presumably the absence of movement would come to predict the nonoccurrence of shock after an initial successful avoidance trial. Pup passive avoidance deficits could come either because of inadequate shock-elicited freezing or because of a difficulty in associating a freezing response with the available cues. Bronstein and Hirsch seem to think that the former explanation is the more probable, and suggest that the hippocampus, rather than subserving inhibitory functions as such, may be responsible for exteroceptive responsivity, and hence freezing, when fearful stimuli are presented.

Although age-related changes in defense reactions can neatly account for juvenile PA acquisition deficits, they are harder-pressed to explain infantile amnesia for an already-acquired passive avoidance response. The experimental evidence for such forgetting is not extensive. Nagy, et al. (1977) observed accelerated infantile forgetting by mice over retention intervals of 8 and 16 days; this was in a situation where the pups, 16 or 25 days old at training, reached an acquisition criterion *faster* than adults did. Although the authors suggest that neurological maturation at the time of training can account for the age-related memory differences, such an explanation apparently is inconsistent with the acquisition data, which show the pups superior to the adults. The demonstration of infantile amnesia is not entirely unambiguous, though, because of the possibility of generalization decrement and the absence of animals given noncontingent shock to control for generalized fear. But it does represent the attainment of infantile retention deficits in a situation where incomplete acquisition cannot account for the results.

Incomplete acquisition does not seem likely to account for the infantile amnesia seen by Feigley and Spear (1970, Exp. 2) in pups trained on passive avoidance and tested by relearning 28 days later. Feigley and Spear brought all animals to the same criterion of two consecutive 60-second avoidances. Pups tested 1 day later showed *higher* first-trial latencies than adults, while those tested after 28 days showed performance deficits compared with older animals. The forgetting observed in this study, then, cannot be attributed to quantitative acquisition deficits by pups, although the possibility of qualitative differences in original learning remains.

In contrast with the Feigley and Spear (1970) demonstration of equated acquisition, Egger and Livesy (1972) never showed pups and adults to perform comparably on passive avoidance. Egger and Livesy first trained their adults and pups on *active* avoidance in a shuttlebox; then they tested some animals at each age on passive avoidance of the shock compartment, immediately or 25 days later. Although weanlings acquired active avoidance as well as adults, their passive avoidance performance was poor when tested immediately *or* after 25 days. As evidence of infantile amnesia, therefore, this study is faulted by a failure to equate across ages on initial acquisition of the passive avoidance behavior, the best available approximation to equation of original learning. Egger and Livesy noted that retention of active avoidance, however, as measured by retraining 25 days later, was as good for pups as for adults. They suggested that the active avoidance test procedure allowed for reinstatement of memory, which could alleviate any infantile amnesia that would otherwise have been apparent. Invocation of reinstatement to explain differences between active and passive avoidance retention, in a situation where <u>acquisition</u> of PA was never equated across ages, seems unnecessary.

Initial acquisition of passive avoidance was equated for 15-, 21-, and 90-120-day-old rats by Schulenberg, Riccio, and Stikes (1971), who trained all animals until they reached a 300-second PA criterion. Acquisition improved with age, consistent with other reports. Retention testing disclosed deficits only by the youngest group, and only after 12 days. In another experiment (Exp. 3), the retention interval was stretched to 24 days, with animals either 19-20 or 90-120 days old at training. With the PA criterion extended to 600 seconds, pups 19-20 days of age displayed significant PA deficits over the long retention interval. No acquisition data were presented.

The Schulenberg, et al. (1971) study leaves open the question of comparing retention across ages when (1) ceiling effects have been eliminated (they may be present whenever animals are trained to a PA criterion), (2) possible growth-induced generalization decrement is ruled out, and (3) rate of learning is roughly comparable (it was not). An attempt to avoid the second of these problems was that by Campbell, et al. (1974, Exp. 3), who scaled apparatus size to subjects during training. Then, after a 21-day retention interval, rats that had been trained as pups in a small apparatus were tested in a larger apparatus scaled to their now-adultlike dimensions. Although the apparatus switch itself may have contributed to performance decrement over longer retention intervals, tests after only 1 day, in the small apparatus, showed pup deficits before any appreciable physical growth had occured. Campbell and his colleagues infer from this that true memorial deficits were being displayed by the pups. However, this conclusion rests on the assumption that original learning had been equal across age groups. It may not have been, due to weaknesses in the spatial PA paradigm itself.

Passive avoidance behavior in a shuttlebox may comprise several different components. Animals given shock upon entry into an apparatus compartment from another, safe, location, may hesitate to enter the shock compartment on a subsequent trial because (1) they remember that the shock compartment was an unsafe place, (2) they remember that their past locomotion in this context had been punished, or (3) they remember that this situation was a dangerous one in general, and they now "freeze" in a species-specific way, as they would in any dangerous situation. Note that this last mechanism does not assume any specific memory relating to the shock compartment, only to the "safe" compartment and to the experimental situation in general.

Age-related differences in the learning of passive avoidance may reflect developmental differences in any or all of these components. Pups that acquire slowly (as was the case in the Campbell, et al., 1974 study) may do so because they are deficient in place association, locomotion association, or in generalized fear-induced immobility linked to the overall experimental context. The relative performance deficit shown by pups tested 1 day after training in the Campbell, et al. (1974) experiment may not reflect loss of memory specific to the shock compartment or to punished locomotion in the experimental situation. Compared to adults, the pups may have remembered the contingencies just as well after 1 day, but may have been "deficient" in their expression of generalized fear. Unfortunately, the noncontingently-shocked animals that could have controlled for this effect were never run, so the implications of the Campbell, et al. study for infantile amnesia are clouded.

In sum, the existing data from passive avoidance studies seem inadequate to independently and fully support assertions of infantile amnesia in rodents. Clearly, the demonstration of such amnesia must be done under circumstances where growth-induced generalization decrement is unlikely, where ceiling effects are eliminated, and where proper controls are run to rule out generalized fear effects.

The Conditioned Emotional Response

Probably the most attractive aversively-motivated task used for ontogenetic comparisons of learning and memory in nonhumans is the conditioned emotional response (CER) paradigm. It generally requires that an animal perform some repetitive behavior, e.g., pecking, licking, or bar-pressing, which is then interrupted by the presentation of a stimulus that previously had been linked with electric shock. Assessment of conditioning is by the amount of suppression produced; nonassociative effects are inferred from suppression in animals for which conditional stimulus (CS) and shock (US) presentations never had been paired. The advantages of this paradigm for ontogenetic comparisons are its minimal physical requirements (even very young rat pups can interrupt their licking), and the latitude it affords the experimenter in choosing a CS. If an auditory CS is used, problems of growth-induced generalization decrement are less than if the CS is visual or tactual.

The CER paradigm can be implemented so that conditioning of the CS-US occurs during performance of the baseline repetitive behavior (on-baseline), or while baseline behavior is prevented, either by removal of reinforcer, manipulandum, or the subject itself to another apparatus (off-baseline). Moreover, it is feasible to condition an animal long before establishing the baseline behavior against which such conditioning will be measured. Thus, the CER procedure affords the experimenter an unusually flexible tool for the discovery of ontogenetic patterns of learning or memory. Casual inspection of such patterns first seems to suggest infantile acquisition deficits.

Frieman, Warner, and Riccio (1970) used an off-baseline CER procedure to compare 17-and 90-120-day-old rats on acquisition, retention, and generalization of a tone-footshock association. Conditioned animals received 15 shocks embedded within 12 1-minute long tone presentations. Immediate lever-press tests disclosed better acquistion by adults than by pups.

A similar result was achieved by Snedden, Spevack, and Thompson (1971) using 10 CS-US pairings per day for 3 days. Here, the youngest animals, 15 days old at start of conditioning, showed less lick suppression than their older counterparts upon presentations of the tone-light CS. Notably, though, 22-day old weanlings showed no deficits relative to 70-day-old adults.

Using only a single tone-footshock pairing, Brunner, Roth, and Rossi (1970), achieved reliable lick suppression in 50-and 120-day-old rats, but failed to observe any CER in 25-day-old weanlings. In another study, using three CS-US pairings, Wilson and Riccio (1973) found a similar acquisition deficit in 23-day-old pups relative to 30- or 90-day-old animals.

At first glance, therefore, it seems as if young rat pups acquire a CER less readily than adults whether few or many CS-US pairings are used. The only available data showing an opposite effect, adult deficits, are from McGaughey and Thompson (1975), who presented evidence for greater heart-rate changes in weanlings than in adults in response to tones that previously had been paired with footshock. It democracy rules, then, the preponderance of the data for fixed numbers of CS-US pairings indicate infantile acquisition deficits for the CER.

Studies parametrically varying the number of CS-US pairings needed to produce reliable conditioned suppression do not consistently disclose infantile deficits, however. Frieman, Frieman, Wright, and Hegberg (1971) delivered on-baseline tone-footshock pairings until animals met a criterion of 90% lick suppression for three consecutive trials. Frieman, et al. found no significant differences between adult and 18-20-day-old rats in their speed to reach this criterion; in fact, pups did marginally better then adults. In the single available primate study, Green (1962) noticed no differences in the degree to which neonate, 30-, and 300-day old monkeys altered their activity in response to a conditioning tone. As an ontogenetic memory probe, the CER paradigm promises to provide data somewhat easier to interpret than those from spatial avoidance tasks. The primary reason for this is the CER's common use of auditory CSs, which are presumably less likely than visual cues to appear different to animals of differing ages. With a visual (or tactual) CS, what was learned by a young, physically small, animal may not be recognized by that same animal when it is returned to the experimental context full-grown after an extended retention interval. This growth-induced generalization decrement (Perkins, 1965) is considered less likely to occur if purely auditory cues are used, as they can be in a CER. Off-baseline conditioning in an apparatus different from the test location further minimizes the possible role of generalization decrement of generalized fear associated with the conditioning context.

Campbell and Campbell (1962, Exp. 2) used a white-noise CS to condition their 25-day-old rat pups and adults off-baseline; retention testing 0, 21, or 42 days later was by drink-contingent punishment by the CS over an 80-minute trial in the same apparatus used for conditioning. This technique is not typical of most CER work; usually CS presentation in testing is not dependent on momentary performance of the baseline task. The difference is of theoretical interest because the Campbell and Campbell technique constitutes a clear operant punishment (and extinction of punishment) situation, whereas customary CER studies, particularly those using only a single short test trial, minimize (but do not wipe out) the effects of age-related differences in learning occurring on the test trial.

The results of the Campbell and Campbell (1962) experiment were clear weanling retention deficits after 21- and 42-day test intervals, while adult retention was perfect throughout. However, the value of these findings as evidence for infantile amnesia is mitigated somewhat by the possibility of contextual generalization decrement and by the results of the immediate tests: here both weanlings and adults showed near-100% cessation of drinking, obscuring any possible age-related inequities in learning that may have contributed later to long-term retention differences.

Avoidance of generalization decrement was a major consideration in the design of experiments by Coulter, Collier, and Campbell (1976), in which pre- and post-weanling rats were given off-baseline tone-footshock pairings in one chamber and were tested for bar-press suppression in a dissimilar apparatus. Using a total of 12 CS-US pairings spread over 3 days, Coulter and her colleagues observed substantial 42-day memory in pups conditioned when 17-19 or 20-22 days old, suggesting that earlier demonstrations of infantile amnesia, such as that by Campbell and Campbell (1962), may have been contaminated by generalization decrement for apparatus stimuli. Pups conditioned when 11-13 or 14-16 days of age, however, showed no evidence of memory after 42 days, even though, in a later experiment, 14-16-day olds showed strong suppression after a 5-day interval.

Although no adult rats were included in the Coulter, et al. (1976) studies, the experiments nevertheless make a strong case for the existence of infantile amnesia for the CER in 14-16-day-old rats. The authors' assertion that retention deficits in rats 17-19 days of age and older will vanish when sources of generalization decrement are removed, however, is more difficult to accept in view of the extensive conditioning given (12 trials over 3 days), and the absence of any direct comparison with adult animals.

Extinction and Retroactive Interference

There is a compelling formal similarity between the memory-impairing technique known as retroactive interference and the conditioning manipulation called extinction. Nevertheless, for reasons that are more historical than substantive, extinction is not usually interpreted as a memorial phenomenon. Experimental extinction, which involves the re-presentation of stimuli or conditioning in the absence of the "reinforcer" or unconditional stimulus (US), can be procedurally indistinguishable from the interpolation of stimuli between training and testing known as retroactive interference. To the extent that retroactive interference plays a role in infantile amnesia, an examination of age differences in extinction might offer clues to the origins of juvenile memory deficits.

Unfortunately, despite the well-documented existence of memory retention deficits in infants relative to adults (Campbell & Coulter, 1976; Campbell & Spear, 1972), developmental comparisons of susceptibility to extinction have yielded no consistent pattern. Brennan and Barone (1976), Ernst (1972), Riccio and Marrazo (1972), Schulenberg, Riccio, and Stikes (1971), and Wilson, Phinney, and Brennan (1974) presented evidence showing that rat pups extinguish faster than adults in a variety of aversively motivated tasks. On the other hand, Egger (1974), Frieman, Frieman, Wright, and Hegberg (1971), and Snedden, Spevack, and Thompson (1971) found adult rats to extinguish faster in aversive situations, and Amsel and Chen (1976) showed this relation to extend to an appetitively motivated task as well. Moreover, Campbell and Campbell (1962), Frieman, Rohrbaugh, and Riccio (1969), Kirby (1963), and Thompson, Koenigsberg, and Tennison (1965) found no differences between pups and adults in rate of extinction. To better understand the implications of these varied results, a close examination of several key studies is appropriate.

Appetitive Tasks

The bulk of the information available about age differences in extinction for appetitively-motivated tasks comes out of Amsel's laboratory at the University of Texas (e.g., Amsel & Chen, 1976; Burdette, Brake, Chen, & Amsel, 1976). Using a food-motivated straight runway task, Amsel and his colleagues tracked acquisition and extinction in rats ranging from 17 to 65 days of age at the onset of training. The measure of extinction used by Amsel and Chen (1976) was a proportion derived by dividing runway speed for each animal by its terminal speed on the last eight trials of acquisition; analyses of variance were done on these proportions. By this measure, Amsel and Chen (1976, Exp. 1) found that 18-22-day-old rats acquired the runway response faster than the oldest group, and then lost it more slowly in extinction.

Burdette, et al. (1976), looked at rats aged 18 to 36 days at training, using speed measures that had not been transformed, and observed similar patterns. Relative to near-asymptotic terminal acquisition speeds, the youngest animals learned fastest and extinguished least. Seen from another point of view, however, the extinction data from Burdette, et al. (1976) yield a different conclusion. If terminal near-asymptotic extinction speeds, instead of acquisition speeds, are used for within-subject comparison purposes, the youngest animals appear to extinguish just as fast as their older counterparts (1976, Fig. 2). Moreover, comparison of the slopes of the speed measures across ages is biased by the physically-imposed limit on the maximum speed attainable by the youngest animals. And, inasmuch as the proportion scores used by Amsel and Chen also depend on absolute speeds which differed across ages (1976, p. 811), slope comparisons in that study too are inherently biased. Finally in neither study is there any independent demonstration of the equivalence of motivation across age groups, a point which Amsel and Chen themselves acknowledge.

Active Avoidance

Campbell and Campbell (1962) and Kirby (1963) observed no age differences in extinction of active avoidance. Campbell and Campbell (1962, Exp. 3) obtained this result after fear conditioning rats to one side of a two-compartment shuttle box. After two sessions of 15 inescapable shocks on one side of the apparatus, alternated with two safe intervals spent on the other side, 25-, 50-, or 100-day-old rats were given five daily 30-minute free choice position preference tests, with the first one occurring immediately after conclusion of the fear conditioning. Extinction of fear was evident by the second session in all age groups, and proceeded apace thereafter.

Two features of the Campbell and Campbell (1962) study are worthy of note. First, the experimenters took pains to heighten the distinctiveness of the fear and safe compartments by covering the grid floor of the safe side with a sheet of aluminum, thus presumably minimizing chances of age-related discrimination deficits. Second, training was sufficient to produce "ceiling"-level avoidance of the fear compartment by all age groups on the first 30-minute test. Thus, it is unclear whether age differences in subsequent extinction would not have been disclosed had a more sensitive means of equating initial acquisition been used.

In one respect, however, the results of Campbell and Campbell (1962) are easier to interpret than those of Kirby (1963), who used a conventional active avoidance task in a straight runway. Kirby gave 25-, 50-, and 100-day-old rats 25 training sessions, then matched groups according to acquisition performance, and tested all animals immediately to a criterion of four out of five trials in which reaching the goal box took longer than 15 seconds. Extinction was slow and variable, taking about 50 trials to complete for all age groups; no developmental differences were found. These results raise questions about the utility of active avoidance as a task for the investigation of developmental (or any other) differences in extinction. The Kirby training procedure, in which successful avoidances were interspersed with escapes and punished nonavoidance trials, actually constitutes a partial reinforcement (PRF) schedule for the classical CS-US component of conditioning, which might be expected to introduce variability to the course of extinction of CS-linked fear. Possibly, age differences in extinction were not visible because of this variability. In view of this, investigators of extinction of fear might be better advised to eschew active avoidance, and use tasks such as Campbell and Campbell's that insure a continuous reinforcement (CRF) schedule in acquisition.

Despite the use of a CRF schedule, Frieman, Rohrbaugh, and Riccio (1969) failed to find age-related extinction differences in rats given 10 inescapable shocks in the presence of a 450-Hz tone in one compartment of a shuttle-box. Over the course of 20 4-minute test sessions during which entry into the fear compartment was punished by the sounding of the training tone or a frequency variant, a progressive extinction effect was observed, equal in animals trained at age 19-23 days or as adults.

Several other ontogenetic comparisons of extinction of active avoidance have yielded more consistent evidence for faster extinction by younger animals. Riccio and Marrazo (1972), after bringing 20-22-day-old and adult rats to a criterion of 5/5 active avoidances in a straight runway, ran the animals in extinction until they failed to enter the goal box on five consecutive trials. Although pups and adults reached the acquisition criterion equally rapidly, the younger animals extinguished faster. Paradoxically, other equally-trained animals who were punished for making the active avoidance response showed the opposite age relationship: Pups continued running longer than adults. It is this result that Riccio and Marrazo interpret as evidence for infantile deficits in passive avoidance learning following experimental equation of approach tendencies.

After training their rats to a 5/5 active avoidance criterion, Wilson, et al. (1974) instituted extinction until animals met a new criterion of five consecutive 12-second trials without responding. Weanling rats extinguished significantly faster than adults, whether or not they had received CS exposures prior to training. Wilson, et al. suggest that age differences in original learning may have existed despite attainment of a uniform performance criterion, and may have produced the observed inequities in resistance to extinction.

Brennan and Barone (1976) report results that closely parallel those of Wilson, et al. (1974). Weanling and adult rats were trained in a shuttlebox to a criterion of eight consecutive active avoidances and were then immediately extinguished until five consecutive trials passed without a response within 12 seconds of CS onset. Acquisition data from this study suggest that adults learned marginally faster than pups, although statistical analysis shows no differences. In extinction, however, huge age differences emerged, pups extinguishing much faster than their older counterparts.

Half the animals at each age in the Brennan and Barone (1976) study had been trained using a compound CS consisting of the door opening and the onset of a loud pure tone, which terminated upon successful avoidance or escape. For the other half of the animals at each age, the door opening alone, 5 seconds before shock onset, served as the CS. Presumably this arrangement was continued into extinction (it is not specified). Of particular interest is the finding that the interaction between age and type of CS closely approached significance ($\underline{p} < .10$). Adults trained on the compound CS extinguished faster than those for whom the door opening had served as the sole cue. Pups, on the other hand, were unaffected by the type of CS employed. Cumulatively, these results suggest that learning or extinction differed qualitatively across age groups in terms of the stimuli effectively controlling behavior.

A clue to the nature of possible age differences in stimulus control was offered by Brennan (1979, Exp. 2). Brennan trained weanlings and adults on a 2-way avoidance task in which *place* was irrelevant as a cue, using as a CS a compound of tone and light. During acquisition a successful avoidance resulted in termination of the compound CS. In extinction, however, a "correct" response failed to terminate one or the other of the CS elements. Presumably this change in procedure aided animals in discriminating the onset of extinction. Brennan discovered that CS element continuation accelerated extinction in both age groups, although more so in weanlings. In its absence, however, pups and adults took equally long to extinguish. Most importantly, Brennan noted that adult extinction was accelerated more by tone continuation than by light continuation, while pups responded equally to both manipulations. This implies that the stimulus elements were differentially salient for older animals but not for weanlings. The broader meaning of this result is also clear: Age differences in stimulus salience (or associability) may account for many of the ontogenetic inequities in the learning literature. Such age differences will produce differential extinction when the effective stimulus complex in extinction is different from its composition in acquisition. Inasmuch as the effective stimulus complex undoubtedly includes apparatus and handling cues to varying degrees in different studies, such manipulations as whether extinction is carried out on- or off-baseline, or in or out of the training apparatus, will produce differential rates of extinction in pups and adults.

In sum, the weight of the evidence from active avoidance studies suggests weakly that young rat pups extinguish faster than adults. Although this age difference seems primarily associative in origin, it could also be related to "nonassociative" factors such as tendency to "freeze" in a fearful situation, or to trivial effects such as pup susceptibility to fatigue during multiple extinction trials. To assess these possibilities, age relationships in extinction must be examined using other tasks, preferably those yielding predictions opposite to active avoidance. Two such tasks are passive avoidance and the CER.

Passive Avoidance

Schulenburg, et al. (1971) extinguished passive avoidance (PA) in rats by confining them to the shuttlebox compartment where they had experienced shock in the course of PA training. All animals had been conditioned to a 300-second PA criterion; extinction exposures were 0 (handling only), 30, 60, or 300 seconds. Immediately after extinction exposure, each animal was tested for passive avoidance, and if the acquisition criterion was still met, it was given another extinction exposure. This extinction-test cycle was repeated until a rat crossed within 300 seconds.

The effectiveness of the extinction exposure was roughly inversely related to age. Animals 15, 21, or 27 days old at conditioning extinguished fastest, while adults took considerably longer. Oddly enough, though, the biggest age differences in extinction came from the 0-second condition, where only 2-3 seconds of handling constituted each extinction treatment. Adults responded very slowly to this; young animals considerably faster. For the youngest pups, handling proved as effective as any of the actual apparatus exposure conditions in extinguishing PA behavior.

The Schulenburg, et al. extinction procedure, in which animals were <u>placed</u> into the shock compartment, could reasonably affect fear associated with place, but not with response. And what was extinguished in the 0-second exposure condition could only have been generalized fear associated with handling and/or the experimental context. The age differences observed in susceptibility to this treatment are strongly suggestive. Either pups and adults differ in the speed with which they <u>lose</u> generalized fear, or they differ in the degree to which generalized fear (as opposed to fear of place and fear of response contingencies) contributed to passive avoidance performance in the first place. Unfortunately, the non-contingently shocked control animals that could have shed light on this question were not run in this study.

The Conditioned Emotional Response

The CER paradigm excels among aversively-motivated tasks as a tool for ontogenetic comparisons. Its most attractive features are the ease with which stimulus modality and salience can be manipulated, and its unique facility for having contextual cues rendered irrelevant through the use of dissimilar apparatuses for conditioning and testing. If on-baseline conditioning is used, however, the CER may be subject to the same possible context-dependent problems as are active and passive avoidance: uncontrolled conditioning to apparatus cues as elements of a stimulus complex, and, in long-term retention studies, growth-induced generalization decrement (due to perceptual changes) of that contextual conditioning.

Snedden, Spevack, and Thompson (1971) conditioned rats off-baseline, but did so in the same apparatus later used for testing. Animals aged 15, 22, 35, or 70 days were given 30 pairings of a tone-light complex and shock; 5 days later they received their first lick suppression test trial. The same animals were tested atgain a week later, and then at age 70 days for the three youngest groups, and age 105 days for the oldest animals. Thus, the Snedden, et al. paradigm confounded extinction with loosely-defined retention tests. The results were an absence of acquisition for the youngest animals, equal acquisition by all others, and extinction/ forgetting proportional to age. Notably, however, animals given unpaired CS-US presentations and other controls given no training showed the same age relationship in suppression as the conditioned rats, albeit uniformly less so. This strongly suggests that a significant part of the extinction pattern was attributable to age-related changes in habituation.

Using an on-baseline procedure, Frieman, et al. (1971) gave 18- and 100-day old rats CS-US pairings until a criterion of 90% lick suppression was reached, and immediately subjected each animal to 12 30-second CS presentations in extinction. For one-third of the subjects at each age, the CS in acquisition and extinction was a tone; for one-third, a light. The remaining animals were trained to the tone and extinguished to the light. A suppression ratio was calculated comparing licking during CS presentation with pre-CS lick rates; presumably this was expected to take account of any conditioning to the apparatus that had developed. Although this procedure clearly does factor out any conditioning of fear to the apparatus alone, it does, not, in and of itself, eliminate any contribution by the apparatus to the stimulus complex formed with the nominal CS (tone or light). And, to the extent that age differences exist in stimulus salience, the effective stimulus complex for adults may not be the same as it is for pups.

Frieman, et al. (1971) found no difference between the effects of tone and light: with either cue, adults extinguished faster than pups. To what extent this was caused by true extinction and to what extent by progressive reduction in pup baseline lick rates over the course of the single prolonged test session cannot be told; no baseline lick data are presented.

In summary, it appears that age relationships in extinction are inconsistent. Where appetitive tasks are used, adult animals tend to extinguish faster than pups (Amsel & Chen, 1976; Burdette, et al., 1976). Where aversive motivation is employed, however, pups either seem to cease responding earlier than adults (Brennan, 1979; Brennan & Barone, 1976; Riccio & Marrazo, 1972; Schulenburg, et al., 1971; Wilson, et al., 1974) or later than adults (Egger, 1974; Frieman, et al., 1971; Snedden, et al., 1971), or show no differences (Campbell & Campbell, 1962; Frieman, et al., 1969; Kirby, 1963; Thompson, et al., 1965), depending on the specific situation.

The apparent lack of reliability of the extinction paradigm probably stems from the absence of any consistent methodology and may also be indicative of a weak phenomenon: Adults and infants may simply not differ much in their overall susceptibility to nonreinforced stimulus exposures. This last possibility, however, is at odds with at least one hypothesis advanced to account for infantile memory deficits, which asserts that young animals are more susceptible than adults to retroactive stimulus interference (Campbell & Spear, 1972). Attempts to evaluate this hypothesis have yielded equivocal results, consistent with the extinction literature. Parsons and Spear (1972) trained adult and weanling rats on an active avoidance task and then subjected animals from both age groups to an enriched retention environment. Although exposure to this environment exacerbated forgetting over a 60-day retention interval, it appeared to do so equally for animals trained as pups or adults. Unfortunately, there were no untrained control animals included in this study. In an earlier experiment with rats, Smith (1968) used relearning to test retention of a discriminated escape task 75 days after training and found inferior savings in those animals initially trained as pups. To evaluate the role of retroactive interference in this forgetting, he trained pups and adults and then forced some of each to learn a competing response on the following day.

Tested 1 day later, pups given the interpolated training made more errors on the original task than did equivalently treated adults. Smith's interpretation of these data was that pups were more susceptible to the retroactively interfering effects of the interpolated learning than were older animals, but an alternative explanation is possible. Because adults and pups differed in performance and hence experience on the interpolated task, Smith's data could have been a consequence of differential proactive interference with reacquisition rather than differential retroactive interference with retention.

Developmental Differences in Generalization

The prevailing explanation for the presumed juvenile susceptibility to retroactive interference (Campbell & Spear, 1972) is that relative to adults, young animals find greater novelty in the retention environment and therefore do more information processing that is potentially detrimental to retention of a target association. Another potential source of differential retroactive interference could arise from ontogenetic differences in perceived similarity. As the degree of interference between two memory traces is a function of their similarity (E. Gibson, 1941), it could be expected that young organisms would be particularly susceptible to retroactive interference, relative to adults, if they are specially prone to confuse the stimuli in a learning event with other nonreinforced stimuli experienced subsequently.

The general developmental trends reported in children toward increasing perceived stimulus specificity (E. Gibson, 1969; Werner, 1961) and narrowing generalization gradients with increasing age (J. Gibson & E. Gibson, 1955; Mednick & Lehtinen, 1957; Riess, 1946) are consistent with this hypothesis. Even the phyletically distant domestic chicken also shows a pattern of perceptual sharpening over the first 9 days after hatching (Rubel & Rosenthal, 1975). The albino rat, however, seems to show an opposite trend, a broadening of generalization gradients in older animals. This tendency has appeared whether the task has been spatial avoidance without auditory cues (Rohrbaugh & Riccio, 1968), spatial avoidance with auditory cues (Frieman, Warner, & Riccio, 1969), or tone-induced conditioned suppression (Frieman, Warner, & Riccio, 1970). Common to all three studies was the experimenters' conclusion that adult rats retained high fear levels even when cues were altered, while younger animals lost some of their fear as stimuli were changed. It is not clear, however, whether developmental differences in stimulus generalization actually accounted for the observed behaviors.

Rohrbaugh and Riccio (1968), for example, inferred generalization differences across ages when 18- and 23-day-old rats, trained on a shuttlebox spatial avoidance task, showed greater losses in performance than adults did as testing was switched from the training apparatus to a second, similar, apparatus. The nominal cue in this situation was compartment color (black or white) although odor cues were undoubtedly available as well. What makes interpretation of this study difficult is a failure by the youngest animals to learn the task completely, coupled with control group performance in the other two age groups that closely paralleled the behavior of trained animals. Thus, it is not certain that what was being shown was the presence of age differences in generalization of learned information. Nor is it clear that animals of different ages had used the same cues to learn the avoidance; the "generalization" difference across ages may actually have reflected qualitative differences in original learning made possible by the redundancy of cues.

Frieman, et al. (1969) added a tonal cue to the spatial avoidance task used by Rohrbaugh and Riccio (1968), and complicated the situation further by testing half the animals at each age (weanling and adult) in a gray-walled apparatus. The reported result, sharper frequency generalization in pups than in adults, is difficult to accept at face value. Equation of acquisition across ages was achieved by discarding animals that "froze" (5 subjects, all adults) or those that displayed the opposite response, inadequate fear (5 subjects, all pups). Moreover, the tones used (230, 450, and 1000 Hz.) are at the limit of audibility for the adult rat (Kelly & Masterton, 1977). Finally, the absence of any differences between animals tested in the grey apparatus and those tested in the black-white shuttlebox raises questions about the salience of those color cues in a situation frankly patterned after Rohrbaugh and Riccio (1968), where they were reported to have had effect.

The third study in this series from Riccio's laboratory, Frieman, et al. (1970), controlled stimulus saliency by using a conditioned suppression design with off-baseline conditioning. Adult rats showed broader generalization around the 1000 Hz CS than did pups, as well as higher suppression overall. It is unfortunate that this acquisition difference appeared in what otherwise could have been a convincing demonstration of age differences in tone generalization.

Brennan and Riccio (1972) compared rat pups and adults on frequency generalization by using a two-way active avoidance task with 300 training trials cued by a 3000 Hz CS. No age differences in generalization were found, although overall performance by adults exceeded that of pups. Brennan (1975), using the same basic task, replicated these results with animals given intensity discrimination training interpolated between avoidance training and testing.

Using heart-rate changes as the dependent variable in a CER paradigm, McGaughey and Thompson (1975) trained rats of 20-22 and 78-80 days of age to a 1200 Hz tone paired with shock. Pups showed a sharp frequency gradient around the CS, while adults did not. Unfortunately, neither did the adults show heart-rate changes to the CS itself, mitigating the value of this study as a developmental comparison of generalization.

The apparent contradiction between results of the rat studies and the evidence from other species may be due to procedural differences, as only the rat data have been based on the use of aversive stimulation. Moreover, the rodent studies are difficult to interpret because of inadequate evidence of equivalent learning across age levels. Despite these reservations, however, the data from Riccio and his colleagues collectively suggest that infants may <u>not</u> have broader generalization gradients for excitation than do adults.

Experimental Plan

Carried to its logical extreme, the relation between stimulus similarity and retroactive interference asserts that as an interfering stimulus approaches identity with a to-be-remembered stimulus, interference will increase as it approaches the conditions necessary for experimental extinction (Osgood, 1949). Extinction and forgetting, usually conceived of as distinct phenomena, may have certain bases in common. To test the contribution of this mechanism to infantile amnesia, it would be useful to evaluate the effects of nonreinforced presentations of the conditioned stimulus "off-baseline," that is, prior to, rather than merely during, testing. Then, with the same preparation, nonreinforced stimuli *different* from the CS could be introduced to determine whether they exacerbate performance decrements in juvenile anijmals relative to adults. If such infantile susceptibility to generalized extinction were found, it could be argued, by extension and analogy, that infant organisms will probably also be more susceptible than adults to the interfering effects of stimuli encountered casually in a retention-interval environment. This last assertion is clearly a step beyond the previous one, but its distance is in degree only.

The first experiment in the present series attempts to equate acquisition of a task by rats across age levels. The next study determines that the observed bahavioral changes are associative. Experiment 3 ascertains whether the preparation does, in fact, yield infantile amnesia without explicit stimulus exposure during the retention interval. Experiments 4 and 5 examine the susceptibility of adults and pups to off-baseline extinction. Experiment 6 concerns the generalization of this extinction and, by extension, retroactive interference to infantile amnesia. Experiment 7 examines excitatory generalization gradients of pups and adults in the same preparation in order to distinguish differences in susceptibility to off-baseline extinction from differences in stimulus generalization.

Experiment 1

Method

Subjects. The subjects were 96 naive male CD albino rats (Charles River Breeding Laboratories, Wilmington, Massachusetts) from two age ranges. At the time of conditioning, adults were 75-130 days old and pups were 19 days old. The older animals were housed in 24-hr light in individual wire mesh cages. Pups were cross-fostered into all-male litters of 10 within 4 days of birth and remained with their foster mothers until weaned at 17 days of age. They were housed thereafter in individual wire mesh cages similar to those occupied by the adults except for a smaller mesh size and the presence of glass bowls for nesting; room temperature was maintained at 29°C to compensate for their inadequate thermoregulatory abilities. Both age-groups were provided with ad lib Purina pellets and water except while in the experimental apparatus, and the animals were handled during daily weighing. Adults received additional gentling for 1 min twice a week for 2 wk prior to the start of each study.

Apparatus. Three distinct types of apparatus were used: one for conditioning, another for lick testing, and a third to deliver shocks to control animals. The conditioning apparatus was a rectangular clear Plexiglas box, 8.4 X 23 X 12.5 cm, with a hinged ceiling and a grid floor formed by 4.6-mm-diam. bars 1.3 cm apart.

Each side wall was perforated by seven 1.19-cm-diam. holes to allow sound penetration and ventilation. The test apparatus was each animal's stainless steel home cage, 18 X 24 X 18 cm, with a glass lick tube mounted in place of the usual water bottle. All animals were offered sweetened condensed milk (Magnolia or Eagle brands) diluted with two parts tap water. A lick-counting circuit (LVE 221-05) monitored each animal's lick rate. Data loss through uninterrupted lick tube contact was avoided by supplying the circuit with a 6.5 count/sec electronically generated pulse as long as each animal's mouth remained in contact with the lick tube orifice. This rate represented a close approximation to the average momentary rate of adults and pups as measured in our own laboratory and verified by Wells and Cone (1975). During conditioning and testing, the appropriate apparatus was inserted into a BRS/LVE sound-attenuating chamber fitted with additional sound-absorbent paneling and door gaskets. The conditioning apparatus was centrally placed on the floor of the chamber, whereas the test cage was suspended 5 cm above the floor. Fresh bedding was placed beneath each animal. Acoustic stimuli were supplied by a 4-in. (10.2-cm), 45-ohm loudspeaker at the right rear corner of the floor aimed slightly upward toward the acoustically reflective front door of the chamber. The speaker was driven by a Heath Model IG-21 audio generator and a power amplifier. Six identical chambers and apparatuses of each type were constructed.

In addition to the conditioning and testing apparatuses, the present study and Experiment 2 used a rectangular black Plexiglas box, 8.4 X 30.2 X 12.5 cm, with a grid floor for the delivery of footshock to control group animals. This control shock box was housed in a room different from that containing the sound-attenuating chamber used for training and testing, and it had no chamber of its own.

Procedure. Experiment 1 had a 2 X 3 factorial design in two equal replications. At each of two ages, adult and weanling, independent groups (n=12) received either 1, 2, or 3 Pavlovian tone-footshock pairings and were tested for lick suppression 48 hours later. Two additional groups (n=12) were run as explicitly unpaired controls. The actual procedure comprised three stages: adaptation, conditioning, and testing.

Adaptation consisted of exposing each animal to the conditioning apparatus and the test situation prior to conditioning, On Day 1, when pups were 15 days of age, all animals were inserted into the test situation for 10 min with milk-filled lick tube present. On Day 2, each animal was placed into the conditioning apparatus for 6 min and 2-4 hr later, was placed into the test situation for 15 min with the lick tube present. On

Day 3, each animal was again exposed to the conditioning apparatus for 6 min and 2-4 hr later, was inserted into the test situation and allowed 15 min to locate the lick tube and an additional 10 min to drink. Day 4 procedures were identical to those on Day 3. Amount drunk and latency to emit Licks 7-57 were recorded to furnish information for group assignment.

In each age level, group assignments were made by counterbalancing Day 4 adaptation lick rate, amount drunk and body weight. Pup groups, however, were first counterbalanced for litter of origin and for any temporary weight loss occurring after weaning. (All pups recovered from any such weight losses relative to unweaned pups prior to testing.) Only animals emitting Licks 7-57 on Adaptation Day 4 in less than 15 sec were included in the conditioning phase of the experiment. Over all studies, 24.6% of the pups and 18.2% of the adults failed to meet this criterion and required replacement.

Conditioning on Day 5 consisted of inserting each animal into the conditioning apparatus for 1, 2, or 3 pairings of a 15-sec, 2400-Hz pure tone, 18-20 dB above ambient levels of 58-63 dB produced by ventilating fans (re 20 $\mu N/m^2$) and a 2.0-sec, 1.5-mA constant-current footshock. The shocks were delivered through grid bars linked in series by NE2 neons. Tone and footshock were coterminous. Animals remained in the apparatus 5 min for each tone-footshock pairing, which was initiated between 90 and 180 sec after the start of the 5-min period. Animals receiving multiple tone-footshock pairings remained in the apparatus until the completion of the designated number of conditioning periods.

The control animals were treated just as were the conditioned animals except that they received only the CS during "conditioning," three times for adults and twice for pups. Approximately 90 min later, each animal was inserted into the control shock apparatus and was given as many footshocks of 1.5 mA for 2.0 sec as it had received CSs. Shocks were 30 sec apart.

Testing occurred 48 hr after conditioning. Each animal was carried in its home cage, without water bottle, to a sound-attenuating chamber and was inserted, still in its cage, into the chamber. A lick tube filled with sweetened condensed milk was then introduced, and the chamber door was closed. Upon Lick 7, a tone identical to that heard during conditioning, but with intensity adjusted to 18-20 dB above background as measured in the current test situation, was sounded. The tone remained on until the animal emitted 50 more licks or until 1 hr of tone presentation had passed. Each animal was tested only once. To normalize the data, we converted raw latencies to emit Licks 7-57 to natural logs. Extending the tone duration during testing beyond the 15 sec used in training permitted the possible interaction of generalization decrement along the CS duration dimension with learning and retention, but it avoided the larger problem of a ceiling effect obscuring real differences between groups.

Results and Discussion

Latencies from Lick 7 to Lick 57 on the last day of adaptation were 7.37 sec and 7.83 sec for adults and pups, respectively, corresponding to natural log (Ln) values of 2.00 and 2.06. This high similarity $t(94) = .62$, $p > .50$, speaks for the equality of the behavioral baseline across age levels. The Day 4 scores in all the remaining studies were so similar to these that they are not repeatedly stated.

After conditioning, lick latencies increased drastically for all conditioned animals. As shown in Figure 1, adults suppressed more readily than weanlings, although by three conditioning trials, the difference due to age was minimal. Analysis of variance on log latencies of the six experimental groups revealed significant effects of age $F(1, 60) = 13.00$, $p < .001$, and trials, $F(2, 60) = 12.37$, $p <.001$, but no replication effects or interactions (all ps $> .25$). The similar test performances of adults and pups given three conditioning trials were not due to a ceiling effect: only one animal (an adult) suppressed for the entire 60-min test.

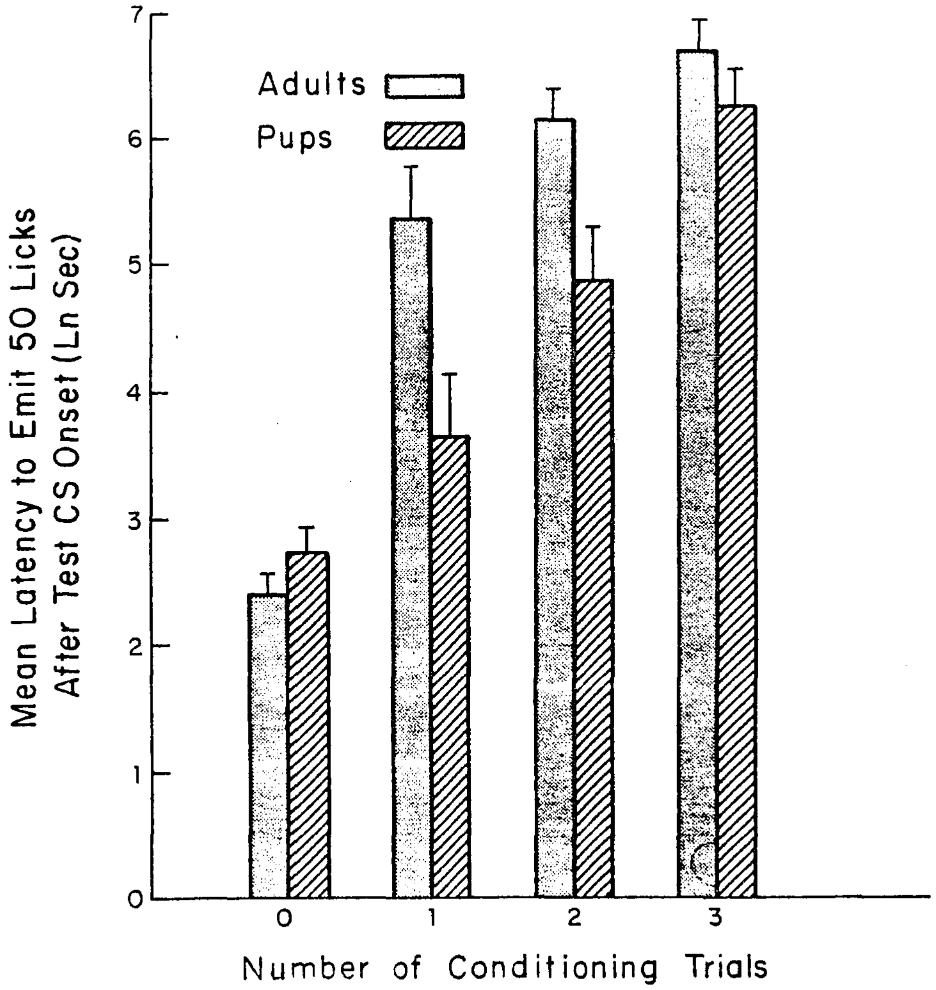

Figure 1. Experiment 1: Lick suppression by pups and adults as a function of number of Pavlovian tone-shock pairings received 48 hr earlier. (T-bars show standard errors of the mean. Animals receiving 0 trials were given two [adults] or three [pups] unpaired presentations of the tone and shock. CS = conditioned stimulus.)

Given the small (nonsignificant) trend toward greater suppression by adults than by pups after three pairings, it appeared that any subsequent demonstrations of extinction and infantile amnesia would be more impressive if measured from a baseline of initial acquisition where this trend was eliminated. Accordingly, for all subsequent studies, adult rats received only two conditioning trial and pups received three. Moreover, except when noted, the subject, apparatus and procedural specifications of Experiment 1 obtained in all subsequent experiments.

The data shown in Figure 1 include the scores of the explicitly unpaired control animals. Although these groups were omitted from the analysis of variance because their treatment was not a parametric variation of number of pairings, individual *t* tests found all six of the factorial groups to differ from these two groups, all *t*s(22) $\geq$ 2.13, *p*s < .05, which suggests that the observed suppression was due to an acquired association between the tone and footshock rather than to nonassociative factors such as sensitization to the tone or pseudoconditioning.

Experiment 2: Evidence for Associative Effects

Experiment 2 was designed to confirm the equivalent acquisition obtained by giving two conditioning trials to adults and three to pups in Experiment 1 and to introduce additional control groups for nonassociative effects.

Method

Thirty-six adults and 36 pups served as subjects. Following adaptation, groups of 12 animals at each age were given paired CS-US presentations three times for pups and twice for adults (Paired), explicitly unpaired tone-footshock exposures in the conditioning apparatus (US-In), or tone-only exposures in the conditioning apparatus and shock exposures in the shock box (US-Out). Procedures for conditioned animals were the same as in Experiment 1. The US-In and US-Out animals received no shocks during their tone exposures, which were otherwise to those received by Paired animals. About 90-100 min after their tone trials, the US-In subjects were returned to the conditioning apparatus for as many shocks as they had had tones, and the US-Out animals received the appropriate number of shocks in the supplementary shock box. Intershock interval for the US-In and US-Out animals was 30 sec; the shocks were identical to those received by Paired subjects: 2.0 sec of 1.5 mA. Testing occurred 48 hr after conditioning.

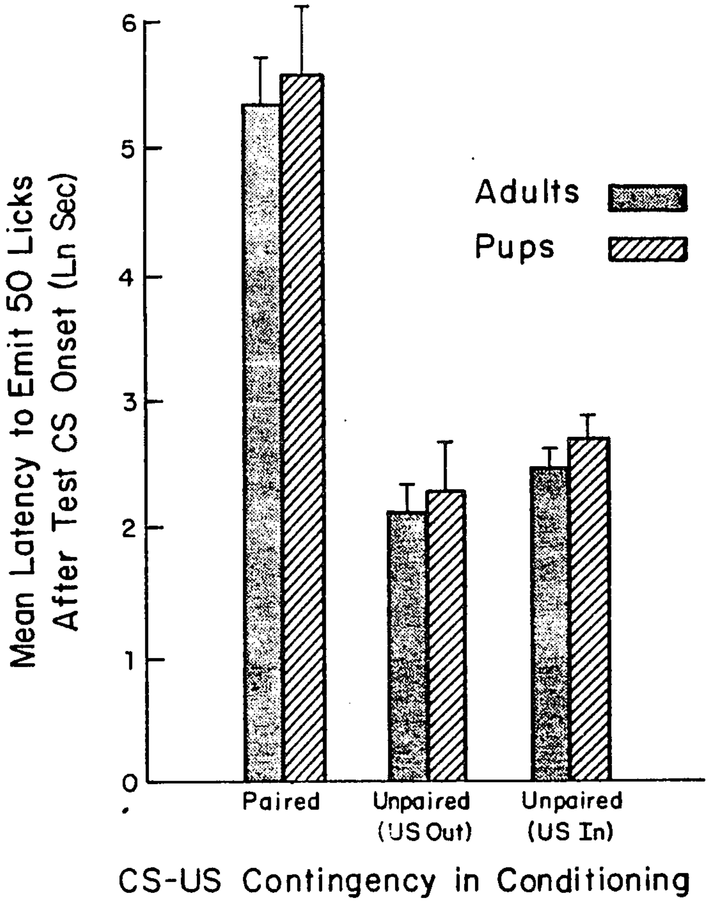

Figure 2. Experiment 2: Effect of conditioned stimulus-unconditioned stimulus (CS-US) contingency on lick suppression 48 hr after conditioning. (Pups received three CS-US pairings; adults received two. Shocks for control animals receiving unpaired presentations were given either inside [US-In] or outside [US-Out] the conditioning apparatus. CS presentations occurred within the conditioning apparatus for all subjects. T-bars show standard errors.)

Results and Discussion

Postconditioning mean Ln latencies to emit Licks 7-57 in the presence of the CS were 5.41 and 5.56 for Paired adults and weanlings, respectively, $t(22) = .49$, $\underline{p} > .50$, corroborating the equivalent acquisition performance across ages seen in Experiment 1. As illustrated in Figure 2, pups in US-In and US-Out groups showed mean values of 2.68 and 2.27, and adults in these conditions yielded suppression scores of 2.43 and 2.09. Each of these scores differed from its same-age Paired groups, $\underline{t}s(22) = 4.18, 5.44, 6.88$, and 8.40, respectively, all $ps < .001$, but did not differ among themselves, all $ts(22) \leq 1.02$, $\underline{p}s > .20$, or from preconditioning scores for the same animals, all $\underline{t}s(11) < 1.56$, $\underline{p}s > .10$.

The essentially equal lick suppression obtained in weanlings given three and adults given two conditioning trials provides a baseline measure of acquisition from which extinction and long-term retention losses will be assessed in future studies. The significantly lower suppression in US-In and US-Out groups at both age levels suggests that the effects observed in Paired animals were truly associative and not the result of shock-induced sensitization to the tone. However, the short intershock interval used for control animals could have obscured sensitization effects that might otherwise have been visible had different time parameters been used.

Experiment 3

Age-Dependent Long-Term Retention

Our ability to generate hypotheses about the ontogeny of forgetting depends on the demonstration that the task employed in one that produces infantile memory deficits under ordinary circumstances. Experiment 3 utilized the conditioning parameters identified in Experiments 1 and 2, three conditioning trials for pups and two for adults, to examine long-term retention and possible infantile amnesia in the absence of explicit stimulus exposure during the retention interval.

Method

Forty animals at each age were adapted, conditioned, and assigned to be tested 2, 8, 16, 32, or 64 days later. Thus, the design was a 2 (Ages) X 5 (Retention Intervals) factorial with eight animals per cell. To minimize differences in long-term retention-interval environmental stimulation, we transferred the cage racks housing the pups from the heated (29°C) pup colony to the cooler (21°C) adult colony 1 day after conditioning. On that same day, the adults were moved a comparable distance, although entirely within the adult colony. All animals except those in the 2-day groups received an additional lick adaptation session 1 day prior to testing. This was to ensure that baseline lick latencies remained constant across ages and retention intervals.

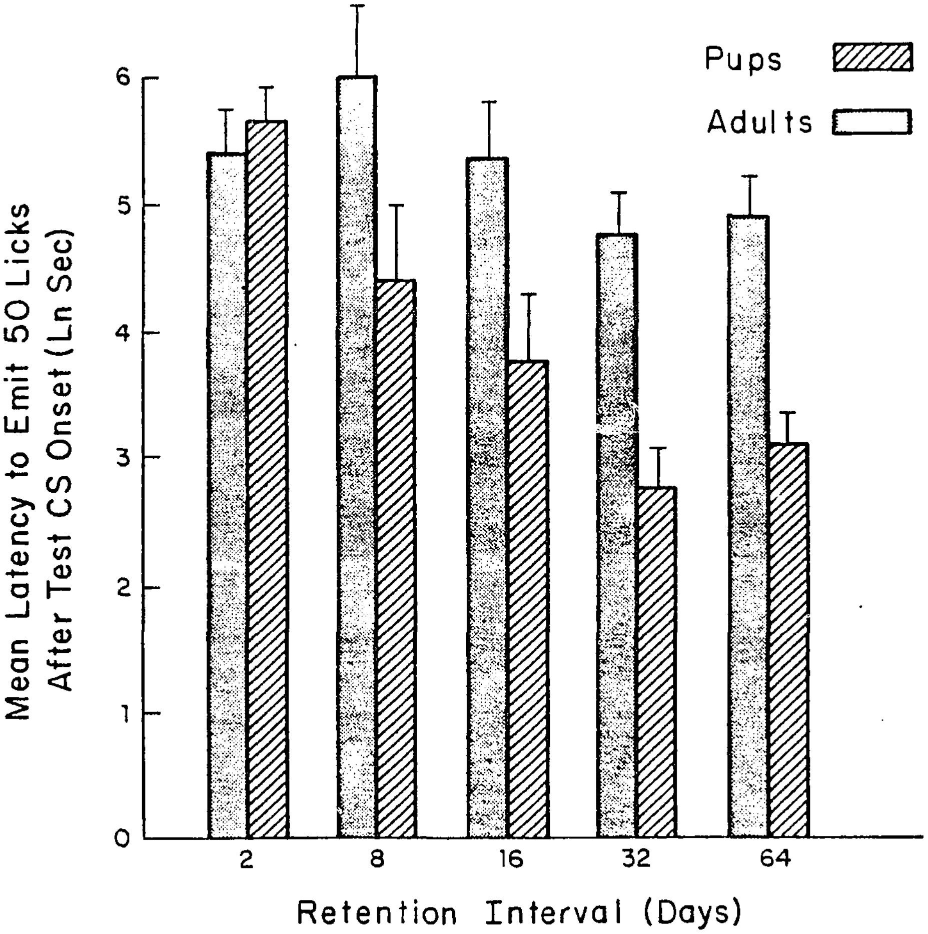

Figure 3. Experiment 3: Infantile amnesia for the conditioned emotional response. (All pups received three conditioning trials; all adults received two. Each animal was tested only once. T-bars show standard errors. CS = conditioned stimulus.)

Results and Discussion

Pretesting adaptation latencies from Lick 7 to Lick 57 did not differ across ages or retention intervals (all *ps* $> .25$). Figure 3 shows the development of long-term retention deficits in pups but not adults. Analysis of variance on transformed test latencies revealed reliable effects of age, $F(1, 70) = 26.72$, $p < .001$, retention interval, $F(4, 70) = 7.01$, $p < .001$, and their interaction, $F(4, 70) = 2.79$, $p < .05$. Individual comparisons using the mean square error from the analysis of variance as an estimate of variance showed pups and adults to differ at 8, 16, 32, and 64 days, $ts(70) = 2.65$, 2.79, 3.49, and 3.24, respectively, all $ps < .02$, but not at 2 days, $t(70) = 1.18$, $p > .20$. Moreover, relative to pups tested at 2 days, pups examined at all longer retention intervals suppressed significantly less, $ts(70) = 2.08$, 3.33, 5.09, and 4.56 for 8, 16, 32, and 64 days, respectively, all $ps < .05$, while no adult group differed from any other, all $ts(70) \leq 1.51$, $ps > .10$.

As suggested in Figure 3 and confirmed by statistical test, infantile amnesia for the CER developed rapidly, but adult memory remained robust over 64 days. This finding in a situation in which spatial stimulus generalization decrement is unimportant is inconsistent with the failure of Coulter, Collier and Campbell (1976) to obtain amnesia in rats 17-22 days of age. Those animals received 12 tone-footshock pairings, which may account for the disparity. In other contexts, for example, spatial and active avoidance, it has been suggested that infantile retention deficits are most likely to appear when training is brief and will vanish when stiff acquisition criteria are employed (Bronstein & Spear, 1972; Potash & Ferguson, 1977). A similar consideration may apply in the present situation, which used relatively few conditioning trials. In summary, the present preparation appears to be subject to infantile amnesia and thereby lends credence to the possibility that the previously observed differences in extinction between adults and pups may contribute to age-dependent differences in retention.

Experiment 4: Off-Baseline Extinction in the Conditioning Apparatus

The inconsistent pattern of results from ontogenetic comparisons of extinction has been observed almost entirely in studies using conventional, on-baseline techniques. In contrast, Smith's (1968) study used an off-baseline method in which an interfering task was interpolated between training and testing of a target task. However, Smith's design was not amenable to unidimensional variation of similarity between target task and interpolated learning. The present preparation was designed to allow systematic variation of stimulus similarity. Experiment 4 established the sensitivity of this manipulation by making an ontogenetic comparison of off-baseline extinction, using nonreinforced presentations of the original CS presented within the conditioning context during the retention interval.

Method

Forty-five pups and 45 adults were adapted, conditioned, and assigned to one of five extinction treatments: 0, 2, 4, 8, or 12 exposures to the nonreinforced CS during the day intervening between conditioning and a test 48 hr later, with conditioning for each rat occurring at the time of day corresponding to the midpoint of its extinction treatment 1 day later. On the extinction day, animals were inserted into the conditioning apparatus for each CS exposure, which consisted of a 15-sec tone identical to that presented during conditioning, but unaccompanied by footshock. Each extinction tone was initiated between 90 and 180 sec after the beginning of a 300-sec extinction trial. Fifty-five minutes intervened between extinction trials so that the longest extinction treatment took 12 hr (for the 12-exposure animals). Rats receiving no exposures were not placed in the apparatus on extinction day, which made them equivalent to the acquisition controls of preceding studies. The testing procedure was unchanged from previous studies.

Results and Discussion

Equipment failure forced five animals to be removed from the study; one additional animal (a pup) died for unknown reasons. Inasmuch as no more than one animal was lost from any group, the missing data were replaced by group means in the analysis of variance; degrees of freedom were reduced appropriately.

As can be seen in Figure 4, lick suppression by pups was markedly attenuated by nonreinforced CS exposure, whereas adult suppression was not. This impression was corroborated by analysis of variance, which disclosed significant main effects of age, $\underline{F}(1, 74) = 14.69$), $p < .001$, and number of extinction trials, $\underline{F}(4, 74) = 5.93$, $\underline{p} < .001$, and their interaction, $\underline{F}(4, 74) = 2.97$, $p < .025$.

Individual $\underline{t}$ tests based on the mean square error term of the analysis of variance revealed that pups given 2, 4, 8, or 12 extinction exposures differed from those given none, ts(74) = 3.89, 3.48, 3.99, and 4.59, respectively, all $\underline{p}$s < .001, whereas no adult group differed from any other (all ps > .10). Pups and adults differed from one another if given 2 or 4 extinction exposures, ts(74) = 2.66 and 3.43, respectively, both ps < .02, although not if they received 0, 8, or 12, $\underline{t}$s (74) = 1.12, 1.83, and 1.79, respectively, all $\underline{p}$s > .05. The absence of any age differences at 8 and 12 CS exposures

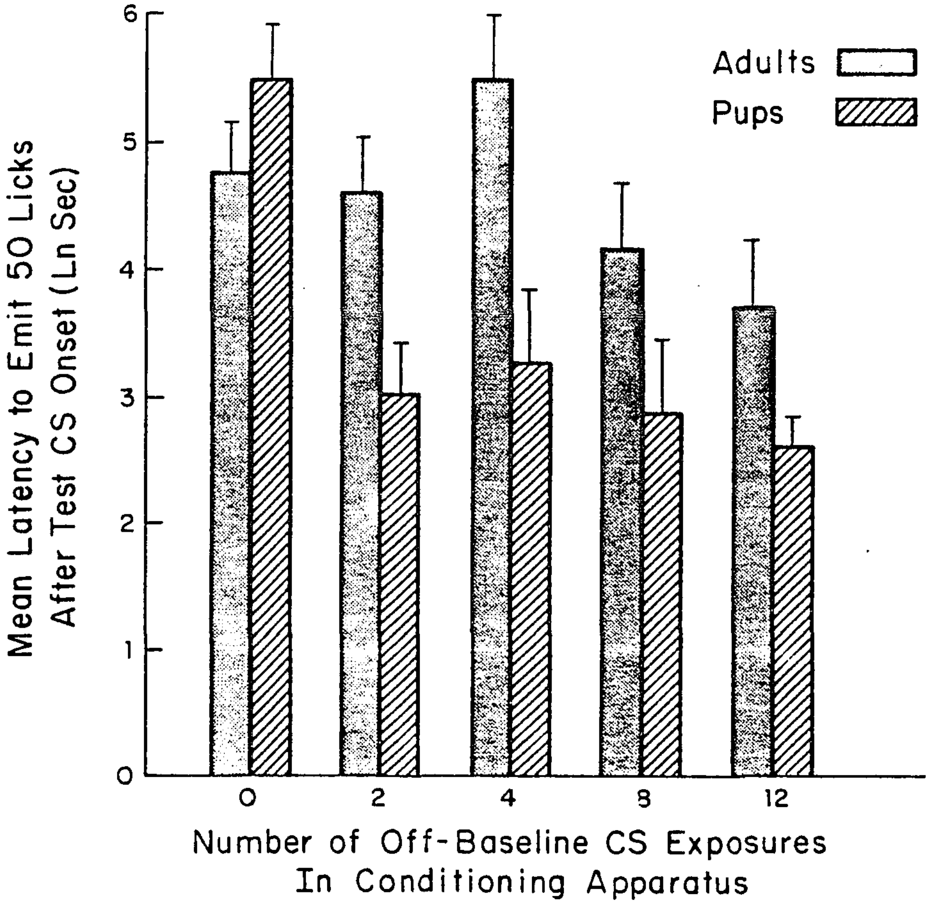

Figure 4. Experiment 4: Attenuation of lick suppression on a 48-hr test as a function of number of nonreinforced conditioned stimulus (CS) exposures given in the conditioning apparatus. (All pups received three conditioned stimulus-unconditioned stimulus pairs; all adults received two. T-bars show standard errors.)

was probably due to the onset of extinction effects in adult animals. That even more than 12 exposures would have been needed to achieve significant extinction suggests that this process is not an important component of any forgetting of aversive conditioning that does occur in mature rats.

One possibility not tested by this study is that extinction in pups was the result of differential handling. This question is directly addressed in Experiment 6. A less likely possibility is that an interaction between age, motivational level, and extinction produced the present results. In view of the extremely high motivational levels of both pups and adults, implied by their emission of several hundred licks of Magnolia milk in the absence of the CS, we prefer to interpret the present data as evidence for differential susceptibility to associative extinction across ages.

The extinction procedures used in this study, particularly those with small numbers of unpaired CS exposures, are operationally identical to the procedures sometimes employed for reinstatement (Campbell & Jaynes, 1966), in which memory losses are alleviated by retention-interval exposures to unpaired CSs or USs from conditioning. No reinstatement effects appeared in the present experiment, however, probably because our retention interval was too short for significant forgetting to occur.

Experiment 5: Off-Baseline Extinction in the Test Apparatus

The results of Experiment 4 do not address questions of CS specificity. No animals received apparatus exposure alone on the extinction day; nor were any animals exposed to nonreinforced tones different from the CS. Thus it is impossible to know the extent to which pup extinction was due to the nominal CS or to other elements of the stimulus complex present during conditioning. In Experiments 5 and 6, we examined this question in different ways: In Experiment 5 by administering extinction treatments in the test situation, in which neither tone nor shock had previously been encountered, and in Experiment 6 by systematically varying the similarity of the extinction stimuli to the CS.

Method

The design of this study was similar to that of Experiment 4 except that extinction exposures to the 2400-Hz tone were given in the test apparatus. The lick tube, however, was not present. Each exposure involved inserting an animal, in its home cage, into a sound-attenuating chamber and, between 125 and 215 sec later, sounding the CS for 30 sec. This interval was chosen on the basis of pilot work in an effort to obtain significant extinction in adult rats. Removal was 25-115 sec after CS offset; total time spent in the apparatus was uniformly 270 sec. Multiple exposures were separated by 38.5 min spent in the home cage, which was returned to the animal colony during this interval.

Forty-two animals of each age were adapted, conditioned, and assigned (n=6) to one of seven extinction conditions: 0, 1, 2, 4, 8, 12, or 16 nonreinforced exposures. Conditioning and testing were programmed to fall at the same time of day as the middle of each animal's extinction schedule, which spanned up to 11.6 hr for those subjects receiving 16 exposures.

Results and Discussion

The results, shown in Figure 5, confirm the findings of Experiment 4. Analysis of variance revealed significant main effects of age, $F(1, 70) = 10.79$, $p < .001$, number of extinction exposures, $F(6, 70) = 6.00$, $p < .001$, and their interaction, $F(6, 70) = 2.68$, $p < .025$). Individual *t* tests using the mean square error of the analysis of variance as an estimate of variance showed pups receiving 2, 4, 8, 12, and 16 extinction exposures to differ from the pup acquisition control group, *t*s (70) = 2.03, 3.30, 2.87, 4.45, and 4.52, respectively, all *p*s < .05, which in turn did not differ from adult acquisition control animals ($p > .25$). No adult group differed from any other, all $ts(70) \leq 1.36$, $ps > .10$. Pups and adults differed from one another at 4, 12, and 16 trials, *t*s(70) = 2.59, 2.77, and 2.77, respectively, all $\underline{p}$s $< .02$, but not at 1, 2, or 8, all $\underline{t}$s(70) ≤ 1.27, $\underline{p}$s $> .20$.

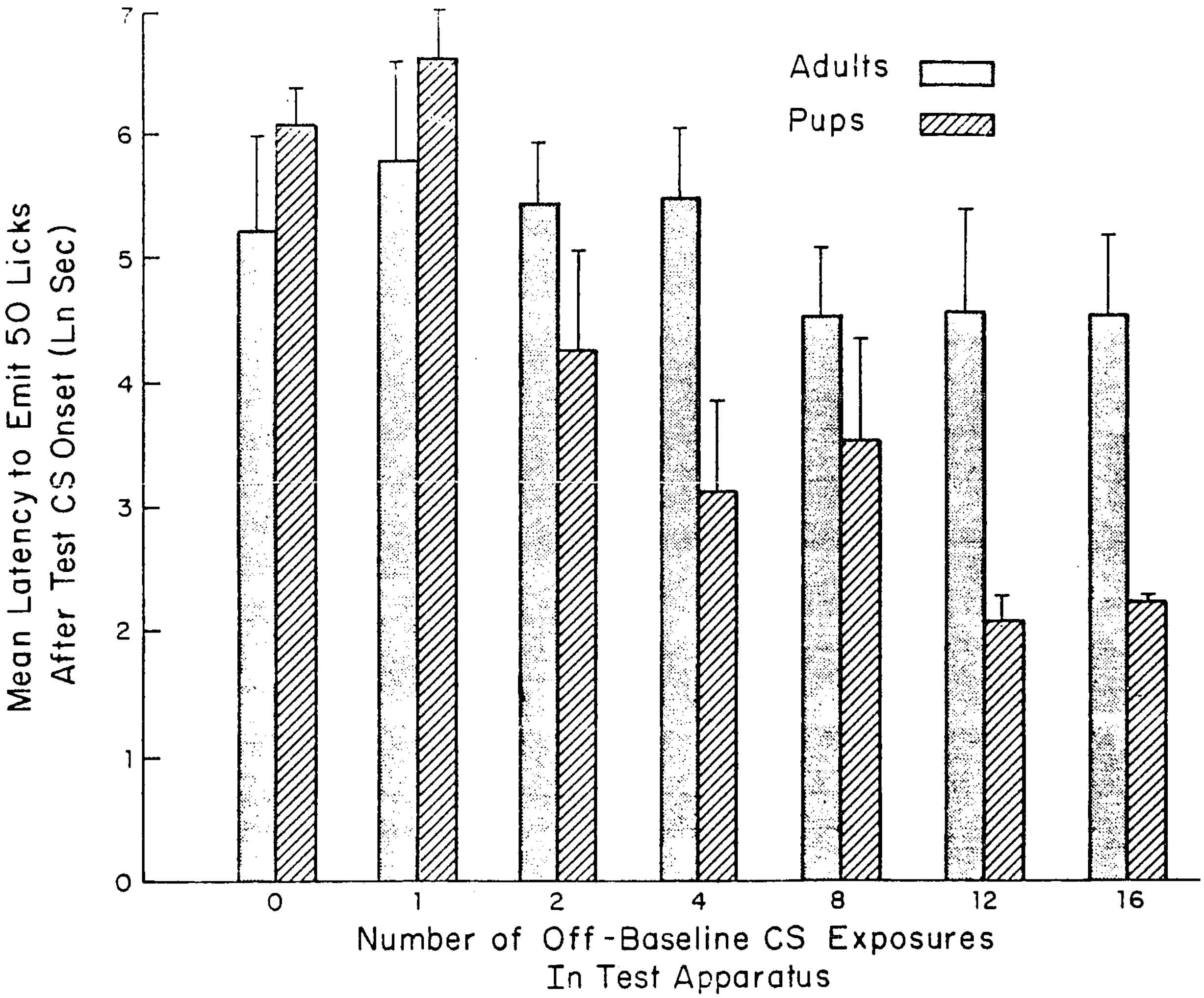

Figure 5. Experiment 5: Attenuation of 48-hr lick suppression as a function of number of non-reinforced conditioned stimulus (CS) exposures given in the test situation without the lick tube present. (All pups received three conditioning trials; all adults received two. T-bars show standard errors.)

The rapid extinction undergone by pups but not adults when presented with tones outside the conditioning context increases the generality of the findings of Experiment 4 and suggests that the age differences in extinction seen in that study are reliable. The apparent contradiction between the present work and earlier reports by Snedden et al. (1971) and Frieman et al. (1971), which noted more rapid extinction of a CER in adults than pups, is possibly due to the different types of extinction procedure employed. The Snedden et al. (1971) and Frieman et al. (1971) studies presented extinction stimuli on baseline, that is, while animals were licking, whereas the present studies (Experiments 4 and 5) used an off-baseline procedure. The principal difference between the two procedures seems to be a greater opportunity for instrumental conditioning in the on-baseline situation, in which animals can learn that licking in the presence of the CS will not produce punishment and in fact will be rewarded.

Experiment 6

Generalization of Off-Baseline Extinction

Although Experiment 5 corroborated the earlier finding that pups are more susceptible to off-baseline extinction than are adults, it does not indicate whether this infantile susceptibility could be a significant source of forgetting over long retention intervals containing sporadic and casual stimulus presentations. Such stimuli would not be likely to closely resemble a specific CS as was used in conditioning, and generalization would have to take place for extinction to play a significant role in natural forgetting. Experiment 6 examined this hypothesized process by exposing animals to one CS in conditioning and testing and to other stimuli during the off-baseline extinction procedure. Because adult rats had not shown any significant extinction when the conditioning tone itself had been used for extinction, Experiment 6 used only pups as its subjects.

Method

Fifty-four pups were adapted, conditioned and tested 48 hr later with the standard 2400-Hz tone. On the day between conditioning and testing, four groups of animals (n = 9) were returned to the test situation for two off-baseline extinction trials with the lick tube absent and were exposed to the CS or to tones differing from the CS by equal fractional log steps: 2400 Hz (CS), 4058, 6861, or 11600 Hz. The intensities of these tones were 18-20, 17-19, 18-20, and 16-18 dB above background, respectively, the variation being a result of slight apparatus differences and the limitations of the equipment. Each tone presentation lasted 15 sec and was initiated 125-230 sec after an animal in its home cage, without water or condensed milk, was inserted into its sound-attenuating chamber, where it remained for 5 min. The two extinction trials were separated by 38 min spent in the home cage in the animal colony. On the same day that the four groups received tone exposure, Group AO ($\underline{n}$ = 9) was placed in the apparatus but received no tone, and Group NT ($\underline{n}$ = 9) received no treatment. The inclusion of Group AO in the present study was intended for assessment of any extinction that accrued from being carried into the experimental room and being inserted into the sound-attenuating chamber. Group NT was equivalent to the acquisition controls of earlier studies in this series.

Results and Discussion

Figure 6 shows the generalization gradient for off-baseline extinction, which was most effective at 2400 Hz and least effective at 11600 Hz. Analysis of variance on the transformed lick latencies revealed a significant effect of the extinction treatment, $\underline{F}(5, 48) = 5.59$, $\underline{p} < .001$. Independent t tests using the variance estimate

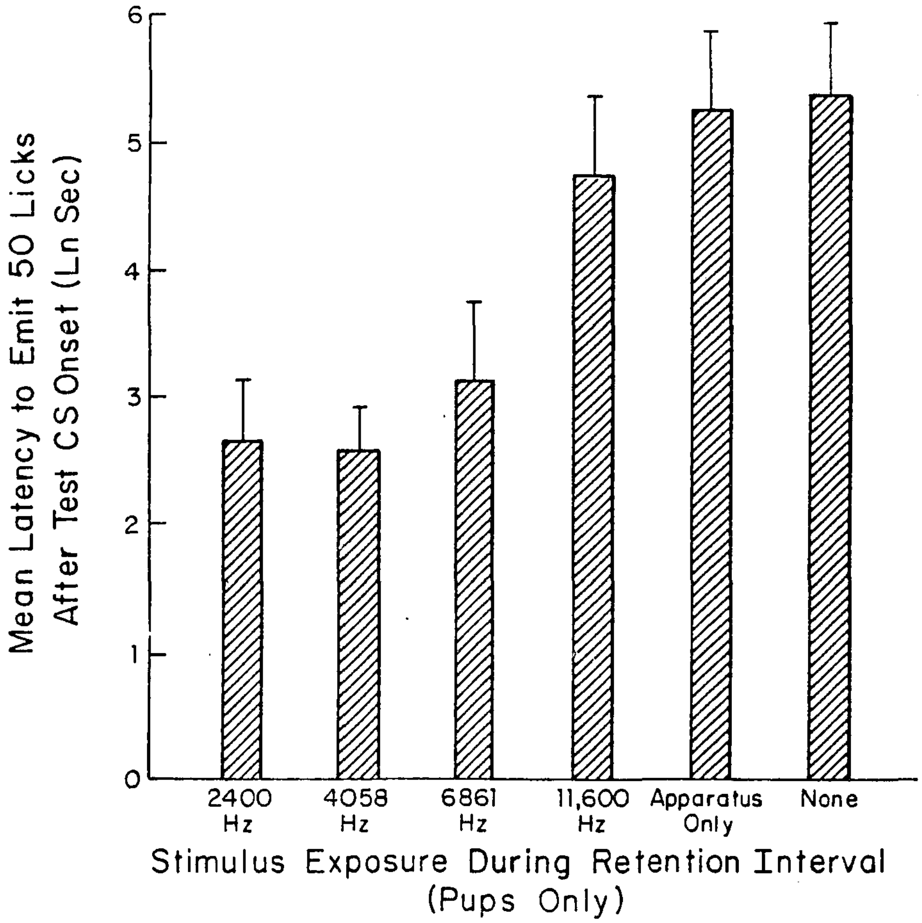

Figure 6. Experiment 6: Generalization of latent extinction in pups given three conditioning trials 48 hr prior to testing. (All animals received two non-reinforced tone exposures in the test situation with the lick tube removed. T-bars show standard errors. CS = conditioned stimulus.)

from the mean square error term showed Groups 11600, AO, and NT not to differ from each other, all ts(48) $\leq .83$, ps $> .20$, but all to differ from Groups 2400, 4058, and 6861, all ts(48) ≥ 2.04, ps $< .05$, none of which in turn differed from one another, all ts(48) $\leq .62$, ps $< .50$.

The generalization of off-baseline extinction observed in pups admits the possibility that adventitious stimulus exposure, to the extent that it is generalized to the CS, may contribute to infantile performance losses over long retention intervals spent in a stimulating environment. The potential strength of this effect is indicated by the significant attenuation of suppression produced even when the tone presented in extinction differed by almost a factor of three from the 2400-Hz tone used in conditioning and testing. The inability of two presentations of the 11600-Hz tone to effect extinction is probably a result of the great frequency difference between it and the 2400-Hz tone. It is not likely the result of the 11600-Hz tone's being less loud, despite the intensity differences between the tones. Rat hearing is considerably *more* sensitive at 11600 Hz than at 2400 Hz (Kelly & Masterton, 1977) and would more than compensate for the intensity deficit at the higher frequency.

The failure of handling and apparatus exposure (Group AO) to attenuate fear is not surprising, inasmuch as that part of the test procedure prior to tone presentation itself constitutes a treatment similar to the one received by the AO animals albeit a day later. No delay of onset of test-trial licking in conditioned acquisition control animals was noticed in any of the experiments, indicating that the absence of fear is associated with the test apparatus. Group AO, however, represents a direct control for effects of handling during the retention interval and puts to rest questions about the nature of the effective extinction stimulus raised in Experiments 4 and 5.

The absence of adults from the present study prevents us from learning whether pups differ from adults in their generalization of off-baseline extinction. Such differences, if substantial and if coupled with the assumption that retention-interval stimuli do cause extinction, could possibly contribute to age-dependent differences in memory. However, the present data do not compel this conclusion. The strongest statement that can be made at this point is that weanling rats are generally more susceptible to off-baseline extinction of a CER than are adult animals and that their greater susceptibility may extend to stimuli different from the CS itself.

Experiment 7:

Generalization of Excitatory Conditioning

A central assumption underlying Experiment 6 was that CS frequency is a salient stimulus dimension for weanling rats. The generalization decrement observed at 11600 Hz supports this assumption, as do the excitatory generalization data furnished by Riccio and his colleagues (e.g., Brennan & Riccio, 1972; Frieman et al., 1969, 1970; Rohrbaugh & Riccio, 1968). Experiment 7 examines the assumption of frequency salience in the present experimental context by the use of conventional excitatory generalization testing. Both weanling and adult rats were included to permit comparison of generalization gradients across age levels, which was not deemed possible in Experiment 6 owing to the failure of adult rats to show substantial extinction to the CS in Experiments 4 and 5.

Method

Forty-four adults and 44 pups were adapted and conditioned with the 2400-Hz CS. Forty-eight hours later, each animal was tested for lick suppression to one of four tones: 2400, 4058, 6861, or 11600 Hz. Intensities were the same as in Experiment 6; relative to background, 2400 Hz = 18-20 dB, 4058 Hz = 17-19 dB, 6861 Hz = 18-20 dB, and 11600 Hz = 16-18 dB.

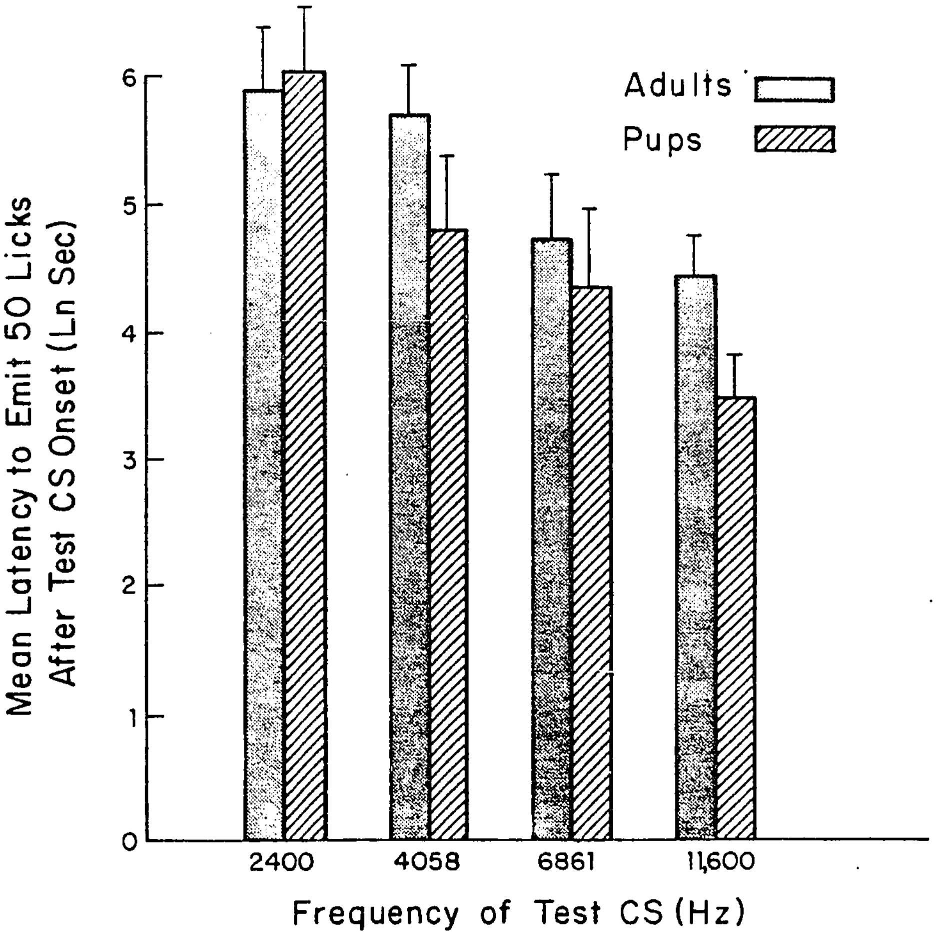

Figure 7. Experiment 7: Excitatory generalization gradients for the conditioned emotional response in adults given two conditioned stimulus-unconditioned stimulus (CS-US) pairings and pups given three. (Lick suppression testing was 48 hr after Pavlovian conditioning. T-bars show standard errors.)

Results and Discussion

The results are presented in Figure 7. The generalization gradient was confirmed by an analysis of variance, which yielded a reliable main effect of frequency, $F(1, 80) = 7.43$, $p < .001$. However, neither age, $F(1, 80) = 2.61$, $p > .10$, nor the interaction term, $F(1, 80) = 1.00$, $p > .25$, proved significant. Individual tests using the mean square error term from the analysis of variance as the variance estimate showed pup generalization decrement, relative to that at 2400 Hz, to be significant at 6861 Hz, $t(80) = 2.70$, $p < .01$, and 11600 Hz, $t(80) = 4.00$, $p < .001$, and nearly reliable at 4058 Hz, $t(80) = 1.98$, $.05 < p < .10$. Adult generalization decrements were nearly reliable at 6861 Hz, $t(80) = 1.83$, $.05 < p < .10$, and were statistically confirmed at 11600 Hz, $t(80) = 2.29$, $p < .05$. Adults and pups did not differ at any frequency, all $ts(80) < 1.47$, $ps > .10$.

The generalization gradients observed in both age groups suggest substantial stimulus control by the frequency dimension of the CS. Given the significant decrement at 6861 Hz seen in the pups, it now seems quite unlikely that the generalization decrement for off-baseline extinction observed in Experiment 6 was due to reduced sound-source intensity at 11600 Hz. No difference in generalization of frequency was observed between pups and adults, which appears to contradict the majority of the evidence from

Riccio's laboratory (Frieman et al., 1969, 1970). However, two observations may mitigate this discrepancy. First, both earlier studies used many more shock trials than the present experiment (10 and 15 pairings rather than the 2 and 3 used here). But more important, both earlier studies employed frequencies at which there is serious doubt that weanling rats can hear well, such as 230 and 450 Hz. Kelly and Masterton (1977) indicated that auditory thresholds in adult rats are at least 40 dB higher at 500 Hz than they are at 8000 Hz. Pups, with their physically smaller middle and inner ears, might be expected to show even greater sensitivity losses at low frequencies. Thus, the low-end components of the Frieman et al. (1969, 1970) generalization gradients may represent loudness differences, rather than generalization of frequency differences, that vary with age.

General Discussion

The principal outcome of the present series of studies is to confirm in a CER preparation the infantile amnesia syndrome in rats and to suggest, however tentatively, a possible mechanism contributing to that memory deficit, specifically the generalization of extinction from stimuli present in the retention environment. At least with the parameters employed in the present experimental series, this source of forgetting appears inconsequential in adult rats. Adult animals similar to those that showed no memory decrement over a 64-day retention interval (Experiment 3) showed no performance decrement at 48 hr despite up to 12 (Experiment 4) and 16 (Experiment 5) off-baseline extinction trials. Pups, in contrast, forgot the CER within 8 days spent in a conventional laboratory environment (Experiment 3) and were effectively extinguished by as few as two nonreinforced CS exposures between conditioning and a 48-hr test. Moreover, pup susceptibility to off-baseline extinction was generalizable to stimuli differing sufficiently from the CS on the frequency dimension to evoke different behavioral responses when presented during baseline licking (Experiment 6, 6861 Hz). Inasmuch as adults failed to display extinction to the CS itself within the parametric range employed, they were not tested on their propensity to generalize extinction on an auditory frequency dimension.

The central question arising from these experiments is why weanling rats should be so prone to off-baseline extinction of the CER in the first place or, alternatively, why adult rats are not so susceptible to extinction. One possible explanation is a variant of the generalization of extinction argument advanced earlier. It assumes that adult animals, with their greater experience, discriminate effectively between the extinction context and the conditioning and test situations. Pups, on the other hand, are presumed to confuse these contexts so that extinction in one generalizes to the others. This argument would be particularly convincing if conditioning and testing were carried out in one context and extinction in another, but it is hard-pressed to deal with the present situation in which conditioning and testing took place in different apparatuses, minimizing contextual control of the CER. In any case, the failure to obtain extinction in adults during Experiment 4 in which the conditioning and extinction environments were identical argues against an explanation that age-dependent differences in extinguishability are due solely to better discrimination of stimulus context by adults than pups.

Another possible explanation for the observed differences in susceptibility to off-baseline extinction assumes an interaction between age, motivational level, and extinction exposure. However, given the equal suppression, measured by conventional on-baseline extinction, that was observed across age levels in the absence of any off-baseline extinction treatment, that is, 48-hr testing of acquisition control groups in Experiments 1-5 and 7, it is hard to imagine a mechanism whereby the introduction of nonreinforced CS exposures on the day intervening between conditioning and testing could have exacerbated any motivational inequities existing between pups and adults. In any event, the approach that was used here to minimize motivational differences across ages probably comes closer than most other techniques to removing this as a source of nonassociative performance differences.

Another way to view the present data is that they may simply reflect a rapid juvenile development of disinhibition of a previously learned suppression of an ongoing behavior, an interpretation consistent with the enormous amount of literature reporting general infantile response-inhibition deficits (see Campbell, Riccio, & Rohrbaugh, 1971, for an introduction to this problem). This hypothesis, however, is not likely to explain infantile amnesia over long retention intervals, when the age of animals at testing is well beyond that at which juvenile response-suppression deficits cease to occur.

A further hypothesis attempting to explain rapid juvenile extinction simply assumes that pups learn certain things, including extinction, faster than adults do.

At first glance, the CER acquisition data presented in Experiment 1 seem to speak against this, as do the vast majority of experimental reports from the animal literature. Of 26 reports examined in conjunction with the present work, only 3 (McGaughey & Thompson, 1975; Nagy, Thaller, & Mazzaferri, 1977, Experiment 2; Paré, 1969) reported faster acquisition by younger animals in an aversive situation, and 1 of these (Paré, 1969) defined 40-day-old animals as "young." Fully 12 reports unequivocally concluded that young animals learn more slowly than adults. But despite the weight of evidence from aversively-motivated tasks arguing that young rodents do not learn faster than adults, and hence are not likely to specifically learn extinction faster either, the question is far from resolved. Of the dozen studies examined that show clear learning deficits in younger rodents, only 1 (Thompson, Koenigsberg & Tennison, 1965) used a task that did not depend on response inhibition or "freezing." As young rodents are widely acknowledged to have difficulty in inhibiting their behavior (Campbell, Riccio, & Rohrbaugh, 1971) or freezing (Bronstein & Hirsch, 1976), the apparent juvenile acquisition deficits appear to be task-specific and may not be indicative of a general juvenile learning deficiency at all. Thus it is difficult to use aversive-task juvenile acquisition deficits to support a conclusion that rat pups do not specifically learn extinction faster than adults.

Pup learning deficiencies also are not strongly supported by reports of appetitively motivated tasks, where there is only a mild suggestion of adult superiority. Bronstein and Spear (1972), Campbell, Jaynes, and Misanin (1968), D'Amato and Jagoda (1960), and Ernst (1972) reported faster learning by adults, and Amsel and Chen (1976) and Burdette, Brake, Chen, and Amsel (1976) described faster acquisition by pups. The absence of clear age effects here suggests further that the juvenile acquisition deficits seen with aversively-motivated tasks are situation-specific. And in view of the response inhibition and freezing deficits known to exist in young rodents, it would be premature to conclude that juvenile organisms generally learn more slowly than adults. A more probable conclusion would be that Age X Learning Rate interactions are task dependent and that most experimenters have tended to structure tasks and stimulus situations so that adults have an advantage over infants. in this sense, the question of acquisition rates will never be resolved, because it will always be possible to set up a learning situation to the advantage of whichever age-group one wishes.

Yet another explanation of age-dependent differences in off-baseline extinction of the CER is that younger animals specifically learn <u>safety</u> faster than adults do. This implies that on a task that is appetitively, as opposed to aversively, motivated, the faster extinction by pups shown in the present series of studies would not be visible. Although no off-baseline data presently available speak to this issue, some work by Amsel and Chen (1976) does indicate that pups extinguish more slowly than adults in an appetitively motivated standard extinction situation. A similar result was observed by Ernst, Dericco, Dempster, and Neimann (1975), whereas reports of faster extinction by pups in an appetitive situation apparently do not exist. The major limit to this learned-safety hypothesis is that it fails to predict infantile amnesia for appetitive tasks. As such amnesia was reported by Campbell et al. (1968) and supported by human anecdotal evidence (e.g., Waldfogel, 1948), acceptance of the learned-safely hypothesis would necessitate a separate explanation of amnesia for appetitive events.

Closely related to the previously described learned-safety explanation is the hypothesis that seems consistent with the broadest range of available data. Perhaps pups learn irrelevance faster than adults do. Thus, during off-baseline extinction exposures, pups would learn to ignore the previously conditioned CS. This hypothesis is clearly testable in that it predicts that pups would respond more than adults to "latent inhibition" treatments (Lubow, 1965) given prior to original conditioning, whether appetitively or aversively motivated. The only study attempting to explore this problem (Wilson & Riccio, 1973) yielded equivocal results, in that true associative conditioning was never demonstrated. But the problem seems fairly straightforward and could be examined within the present experimental paradigm.

All of the hypotheses examined here have assumed that infantile amnesia is a unitary phenomenon and has been demonstrated from a base of equivalent learning in infants and adults. It must be reemphasized that these are only assumptions. Infantile amnesia in animals may have multiple origins in different situations and at different ages, and may differ entirely in its bases from infantile amnesia in humans. Neurological maturation, in one or several of the forms reviewed by Campbell and Coulter (1976), undoubtedly plays a major role in forgetting by human infants and pre-weanling rodents. However, as maturation proceeds, and change is less easily characterized in neuroanatomical terms than it is in terms of "schemas," "concepts" or "coding" (which may be nothing but finer-grained versions of the more-visible earlier neuroanatomical changes), our hypothesized explanations for infantile amnesia also move toward the experiential. Thus, environmental factors such as the extinction-like processes described in the present experimental series probably contribute to forgetting in weanling animals more than they do in pre-weanlings.

Beyond this, a likely source of exacerbated long-term retention deficits in juvenile animals may be undisclosed age differences in the quality of original learning. Throughout all of the present experimental series, and throughout the vast majority of the examined experimental studies of the ontogeny of memory, an unstated assumption has been that original learning by adult and infant subjects has been equivalent. But infant and adult rodents, like infant and adult humans, may differ in several aspects of learning, despite equivalent performance of the task being used to demonstrate that learning. As long as experimental designs depend heavily on the use of complex situations and/or aversive stimuli, it is likely that age-related qualitative differences in learning will escape detection and will contribute an indeterminate amount to behaviors interpreted as demonstrating age differences in memory.

In sum, using a task that yielded infantile amnesia in rats, we successfully accelerated the performance decrement in weanlings by exposing them to nonreinforced presentations of the CS or similar stimuli in either the conditioning or testing context. It would be premature at this time to fully endorse any one of the hypotheses discussed; further research is needed. However, despite the lack of a clear explanation and despite some reservations about equivalence of learning across ages and about the conceptual leap between generalization of extinction and retroactive stimulus interference in the retention environment, the present data suggest that generalization of extinction may account for part of the normal long-term retention losses observed in infant rats. If this is true, the present studies would serve as another example of how experiential factors can contribute to the production of infantile amnesia, a conclusion consistent with a previous study of infantile amnesia in frogs (Miller & Berk, 1977) and with Smith and Spear's (Note 1) finding of greater susceptibility in rat pups than adults to proactive stimulus interference. Presumably, such factors supplement and interact with the maturational factors implicated by such studies as Campbell, Misanin, White, and Lytle (1974).

Reference Note

1. Smith, G.J., & Spear, N.E *Role of proactive interference in infantile forgetting*. Unpublished manuscript, 1979.

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