only if introduced within a comparatively short (100 sec) ITI. (2) UR amplitude was smaller on unpaired trials than on paired trials.

One possible explanation for the occurrence of a conditioning decrement with a short but not a long ITI is the greater massing of US presentations, paired or unpaired, that results from either shortening the ITI or increasing the number of unpaired US presentations within a fixed ITI. Hupka et al (1970) compared conditioning of an experimental group (paired and unpaired US presentations) with a control group that had the same number and pattern of US occurrences as the experimental group but that always received the US paired with the CS. The latter group conditioned more rapidly than the experimental group, suggesting that it is the occurrence of the USa independent of any simple massed trials effect that interferes with conditioning. Putting it another way, it appears as if an unpaired US operates more as an "external inhibitor" than as a source of "reactive inhibition." Yet the timing of the USa in relation to a paired trial is a critical factor, and it is this observation that points to a consolidation hypothesis.

Consolidation theory assumes that the disrupting event acts retroactively by preventing "hardening" of the CS-CR connection. Yet it is also possible that the USa acts proactively by preventing the formation of the CS-CR connection. Although the proactive and retroactive influences of the USa cannot be separated in the present experiment, it seems clear that USa trials interfere basically with "associative" rather than "performance" processes. This conclusion is based on the fact that USa disruption does not persist beyond the labile stage of conditioning. Once "consolidation" occurs, the USa loses its effect, with the result that experimental and control groups both achieve high asymptotic levels of responding.

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Differences in reversal learning between two inbred mouse strains*

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DBA/2J and C56BL/6J mice were given original learning and 11 reversals of a spatial discrimination habit. The former strain required fewer trials to shift from incorrect to correct responding after a reversal and made fewer errors on reversals. These data suggest that (1) genetic characteristics contribute to differences in reversal learning, and (2) generalizations concerning phyletic differences in reversal learning may be premature prior to testing of diverse strains within species.

Spatial reversal learning has been investigated for a wide range of species (Bitterman, 1965), but the house mouse has received relatively minor attention. This is unfortunate since strain comparisons within species have provided a useful paradigm for separating environmental and hereditary influences on learning capacity (Bovet, Bovet-Nitti, & Oliverio, 1969). Elias (1969, 1970) and Meier & Foshee (1963) have reported differences in reversal learning between mouse stocks and strains, but too few reversals were given to permit comparisons of reversal learning curves. The purpose of the present experiment was to give a sufficient number of reversals to two inbred mouse strains to allow for comparisons of learning curves. Inbred Strains DBA/2J (DBA) and C57BL/6J (C57) were of particular interest since Bovet et al (1969) have cited superior maze learning for the former as opposed to the latter strain as evidence for genetic influence on learning capacity.

METHOD

There were 12 8-week-old male Ss of

each strain. A T-maze described by Waller, Waller, & Brewster (1960) was used. It had rounded arms and no top or bottom, and was half immersed in a tank of water ($25 \pm 2^\circ\text{C}$). The front-back and top-bottom orientation of the maze in the water tank was reversed randomly between trials to control visual and olfactory cues. Ss swam from the start point at the stem end to a wire escape ladder at the end of the correct arm. The arms were curved so that the ladder could not be seen until a correct turn was made, and correction was permitted. For original learning (OL), the correct arm of the maze was defined for each S as that chosen on less than half of the 20 habituation trials that preceded testing. For Reversal 1 (R-1), the direction of the correct response was opposite to OL. For Reversal 2 (R-2), the correct response was opposite to R-1, and so on until 11 reversals were completed. Ss were given two blocks of seven immediately successive trials each day, with 15 min between blocks. As soon as a criterion of 13 out of 14 consecutive correct responses was met on a single day, S was advanced to the next stage of learning, e.g., OL to R-1, or R-1 to R-2. Performance measures were: (1) mean errors prior to reaching criterion (errors to criterion), (2) number of trials required before S shifted from incorrect to correct responding after a reversal (trials to

Fig. 1. Mean errors to criterion for the DBA/2J (DBA) and C57BL/6J (C57) strains for each stage of learning.

shift), (3) percent response shift, and (4) median swimming time from start to choice point. Analyses of variance and trend were performed for the first three measures, but nonparametric analyses were necessary for the highly skewed time scores.

RESULTS

Error scores are shown in Fig. 1. Both strains improved significantly over the 12 stages of learning ($F = 15.22$, $df = 11/242$, $p < .01$), but Strain DBA made significantly fewer errors ($F = 8.43$, $df = 1/22$, $p < .01$). Linear and quadratic trends were significant ($F_s > 25.38$, $p < .01$) for all Ss combined ($df = 1/242$) and for each strain analyzed separately ($df = 1/121$). It may be noted, however, that learning curves differed for the first three reversals. The C57 strain showed a decrement on R-1 and R-2, with marked improvement on R-3. In contrast, Strain DBA showed no decrement from OL to R-1, and marked improvement on R-2. The observed superiority of Strain DBA to Strain C57 was significant ($F = 8.43$, $df = 1/22$, $p < .01$) at R-2, but no significant differences between strains were observed at any other stage of learning.

Percent shift scores showed a gradual decrease from OL to R-11, with no differences between strains at any learning stage. For trials-to-shift scores, however, the two strains revealed notably different curves. As may be seen in Fig. 2, the DBA mice showed less decrement on R-1 and more rapid improvement from R-1 to R-5 than the C57 mice. Significant differences between strains were not observed at any learning stage, but there were significant differences ($F = 15.22$, $df = 11/242$, $p < .01$) in trials to shift over the 12 learning stages. Further, there were significant linear and quadratic trends

($F_s > 7.89$, $p < .01$) for both strains combined ($df = 1/242$) and for each strain analyzed separately ($df = 1/121$). The correlation between errors-to-criterion and trials-to-shift scores was low (Pearson $r = .32$), but significant ($p < .005$). Analyses of covariance revealed that F values for differences in errors between strains were deflated (8.42 to 4.62) and F values for differences among learning stages were reduced (15.22 to 10.57), but both remained in the significant range ($df = 1/21$, $p < .05$; $df = 11/241$, $p < .01$) when they were adjusted for the influence of trials-to-shift scores.

No decrease in median swimming time for the 12 learning stages was observed for the DBA strain. Strain C57 swam significantly slower than Strain DBA on OL (8 vs 4 sec) and R-1 (8 vs 4 sec). Mann-Whitney Us were 14.5 ($df = 12/12$, $p < .01$) and 23.5 ($df = 12/12$, $p < .02$), respectively. Swimming times did not differ for the two strains at any other stage of learning.

DISCUSSION

It appears that mice form spatial reversal learning sets with relatively few reversals, but at least two strains do not do so with equal facility. Consistent with Bovet et al's (1969) findings, the DBA mice were better maze learners than the C57 mice. However, Bovet et al gave only one trial per day and no reversals. Under the present 14-trial-per-day schedule there were no differences in errors on OL, but clear differences were observed for R-2. This suggests that the two strains do not differ with regard to habit formation under relatively massed practice conditions, but the C57 strain may be less adaptable to changing environmental demands imposed by habit reversal. The fact that the DBA strain shifted from incorrect to correct responding more quickly than the C57 strain after early reversals suggests that the former strain may be more flexible, i.e., have a greater tendency to test new response hypotheses. It should be noted, however, that the tendency toward early response shifts contributed only in part to better reversal learning. Differences in error scores across trials and between strains were still significant when they were adjusted for the influence of trials-to-shift scores.

It might be argued that Strain DBA does not shift from incorrect to correct responding more quickly, but merely makes more response shifts than the C57 strain. This does not appear to be true since percent shift curves were identical for the two strains.

Slower swimming speeds have been related to decreased escape incentive

Fig. 2. Mean trials preceding the first response shift after a reversal.

(Waller et al, 1960). Consequently, decreased motivation to escape for the slower strain (C57) may have retarded error elimination on early reversals. This hypothesis is weakened by the observation that swimming speeds did not differ at R-2, where the largest differences in errors between the two strains were observed. Further, Es have reported either no relation between speed and errors (Waller et al, 1960) or increased errors for Ss with faster swimming speeds (Elias, 1969, 1970). Nevertheless, the possibility that general differences in emotionality, activity level, or motivation between the two strains is related to reversal learning ability is subject to further exploration. The fact that strain differences in reversal learning do occur emphasizes the role of genetic factors in reversal learning ability and suggests that generalizations concerning phyletic differences in reversal learning may be premature prior to testing of widely diverse strains within species.

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