

Immediate Response Strategy and Shift to Place Strategy in Submerged T-Maze

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A considerable amount of research has demonstrated that animals can use different strategies when learning about, and navigating within, their environment. Since the influential research of Packard and McGaugh (1996), it has been widely accepted that, early in learning, rats use a flexible dorsal hippocampal-dependent place strategy. As learning progresses, they switch to a less effortful and more automatic dorsolateral caudate-dependent response strategy. However, supporting literature is dominated by the use of appetitively motivated tasks, using food reward. Because motivation often plays a crucial role in guiding learning, memory, and behavior, we examined spatial learning strategies of rats in an escape-motivated submerged T-maze. In Experiment 1, we observed rapid learning and the opposite pattern as that reported in appetitively motivated tasks. Rats exhibited a response strategy early in learning before switching to a place strategy, which persisted over extensive training. In Experiment 2, we replicated Packard and McGaugh's (1996) observations, using the apparatus and procedures as in Experiment 1, but with food reward instead of water escape. Mechanisms for, and implications of, this motivational modulation of spatial learning strategy are considered.

Keywords: spatial strategy, place, response, aversive, motivation

In spatial navigation tasks, animals can attend to many sources of information. In particular, psychologists have long debated the extent to which animals use cues from either external location or internal movement to guide their behavior in maze learning tasks (Tolman, 1948, 1949). Does the animal learn to approach the location of reward or to make an appropriate series of turns?

It has been widely accepted that animals initially learn about relational information found in the configuration of environmental cues (place learning) and, subsequently, switch to a more automatic, and less cognitively effortful, response strategy over time (Restle, 1957, 1962). For example, in a commonly used “dual-choice” task that can be solved by either “place” or by “response” strategies (Tolman & Gleitman, 1949; Tolman, Ritchie, & Kalish, 1946), rats are trained to find a food reward in one arm (e.g., east) of a four-arm maze. Rats are started in the south arm, and the north arm is blocked.

Rats readily solve this task, exhibiting a decline in the latency to reach the goal location as well as in the number of errors. To assess the solution strategy used, probe tests, in which the south arm is blocked and the rats are started from the north arm, are inter-

persed throughout training. If a rat enters the originally rewarded arm, the use of place information is inferred, but if it enters the originally nonrewarded arm, a response strategy is inferred. In a highly influential study that used this task, Packard and McGaugh (1996) found that rats expressed a place strategy early in training, but a response strategy later in training. Moreover, the results of transient inactivation experiments indicated that the rats initially adopted a hippocampus-dependent place strategy, which, as training continued, was increasingly overlaid, but not replaced, by a caudate-dependent response strategy.

Demonstrations of these strategy shifts are dominated by appetitively motivated tasks, with food reinforcement. In Experiment 1, we examined performance in a similar, but aversively motivated task: rats escaped a submerged maze by swimming to a hidden platform. Remarkably, we observed a response strategy early in training followed by a switch to a place strategy, which persisted over extended training. This observation was opposite of the pattern of data described in the appetitive maze (Packard & McGaugh, 1996). In Experiment 2, we used the same protocol and apparatus, but with food reward rather than water escape, and replicated Packard and McGaugh's (1996) observation that normal rats initially displayed a place strategy followed by the adoption of a response strategy.

General Method

Subjects

Male Long Evans rats (275–325 g; Charles River Laboratories, Raleigh, North Carolina) were housed individually in a temperature-controlled room, with lights on from 7:00 a.m. to 7:00 p.m. Rats in Experiment 1 ($n = 34$) had free access to food (Teklad Chow 2018; Harlan Laboratories, Madison, Wisconsin) and water.

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The 16 rats in Experiment 2 were maintained at 85% of their *ad libitum* weights by limiting access to food.

The 10 rats in the single group in Experiment 1 previously received pairings of an 80-dB white noise with 45-mg sucrose pellets (Formula 5TUT; TestDiets; Richmond, Indiana) and presentations of the white noise without reinforcement while under food restriction; they were given 2 weeks to recover. All other rats were experimentally naive.

Apparatus

A white, circular, galvanized steel water tank (height = 57 cm, depth = 173 cm) was surrounded by a circular black curtain (height = 180 cm) with attached white shape cues. A four-arm plexiglass plus maze (arms: length = 72.5 cm, width = 20 cm), including removable plexiglass inserts to block access to the individual arms when necessary, was placed inside the tank.

Submerged maze. For Experiment 1, the tank was filled with water (depth = 52.5 cm; $M_{\text{temperature}} = 27^{\circ}\text{C}$, $SD = 1$) and nontoxic, white Premium Tempera paint (Blick Art Materials, Galesburg, Illinois) to obscure the escape platform's location (height = 50 cm, depth = 12 cm), positioned 5 cm from the side of the tank and 1.5 cm below the water's surface.

Dry maze. For Experiment 2, the water was removed from the tank, and a plexiglass floor was added to the maze, giving it walls of 12 cm height. An aluminum reward cup (height = 2 cm, depth = 6 cm) was secured at the ends of the east and west arms.

Experiment 1

Method

Habituation. Rats were first placed in the south (start) arm for two 2-min habituation trials. Access to the north arm was blocked during habituation and training trials.

Training. The rats then received two training trials each day, on which they were placed in south arm, facing the wall, and trained to locate the hidden platform in either the east or west arm (counterbalanced). A correction procedure was applied such that rats making an error were allowed to subsequently locate the platform. Errors included entries into the nonrewarded arm and reentries into the start arm.

Rats were required to remain on the escape platform for 10 s before being removed, towel-dried, and placed in a holding cage. Rats were run in squads of four such that each rat received its first trial before the second trial was administered (McDonald & White, 1994). The two remaining rats in the single group were run in an additional squad. Thus, the intertrial interval (intertribal interval) depended on the performance of all rats in a squad (range: 2–5 min).

Rats in all groups received two training sessions followed by a probe test. The single group ($n = 10$) received no further training or testing. The extended group ($n = 24$) was divided into two subgroups (matched by performance over the first two training sessions), and received additional probe tests after every two (frequent, $n = 12$) or four (infrequent, $n = 2$) training sessions. We varied probe frequency because we were uncertain about the rate of learning and the likelihood of counterconditioning or extinction on probe tests.

Probe tests. On single-trial probe tests, there was no escape platform and access to the south arm was blocked. Rats were placed in the north arm and allowed to choose between the normally rewarded or the nonrewarded arm. We reported the first arm entered by each rat. Rats approaching the reinforced extramaze cues and entering the normally rewarded arm were designated as “place learners,” whereas rats producing the reinforced response and entering the normally nonrewarded arm were designated as “response learners.” On reaching the end of the arm, rats were removed from the maze and towel-dried, beginning the next training session after approximately 30 min.

Data Analysis. An overhead camera and computer-assisted tracking system recorded each rat's position in the maze. During training, an experimenter recorded each rat's latency to reach the platform as well as errors accrued. For the single group, measures were analyzed with Goal Arm (Correct Arm [East or West]) \times Session mixed-design analyses of variance (ANOVAs). Data from the extended groups in Experiment 1 were subjected to Group (Frequent or Infrequent in Experiment 1; Infrequent or Rare in Experiment 2) \times Goal Arm \times Session mixed-design ANOVAs. If main effects and all interactions involving the goal arm counterbalancing variable were nonsignificant, we omitted that variable in subsequent analyses. All ANOVAs used the Greenhouse-Geisser correction for violations of sphericity. For each probe test, we determined the probability of observing the recorded number of “response learners” in each group, based on the binomial distribution. We also analyzed the change in probe test performance over training using ANOVAs, as described above (except in the single group, which was only tested once).

Experiment 2

Method

In Experiment 2, we used the same apparatus and training procedures as in Experiment 1, but with food reward rather than water escape contingencies.

Habituation. Habituation was conducted as in Experiment 1, except that 45-mg sucrose pellets (Formula 5TUT) were distributed throughout the south, east, and west arms and in the secured aluminum reward cups.

Training. Training was conducted as in Experiment 1, except that the reward was four 45-mg sucrose pellets placed in one of the aluminum cups (counterbalanced). If a rat failed to complete the task in 5 min, it was removed, without reward, and assigned a latency of 300 s.

Probe tests. Rats were probed either after every four (infrequent, $n = 8$) or eight (rare, $n = 8$) training sessions. We reduced the frequency of probe tests relative to Experiment 1 because a preliminary experiment suggested slower learning in the food-rewarded maze and some evidence of counterconditioning with frequent probe tests. No sucrose reward was available on probe tests.

Data analysis. Data analyses were conducted as in Experiment 1. Data were subjected to Group (Infrequent or Rare) \times Goal Arm \times Session mixed-design ANOVAs. If main effects and all interactions involving the goal arm counterbalancing variable were nonsignificant, we omitted that variable in subsequent analyses. All ANOVAs used the Greenhouse-Geisser correction for violations of sphericity.

Experiment 1: Submerged Maze

Results

In the single group, we observed nonsignificant decreases in latency to reach the platform, from a mean of 29.94 s ($SEM = 5.14$) on the first trial to 15.86 s ($SEM = 3.00$) on the second trial, $F(1, 9) = 4.090$, $p = .074$, and in the number of errors, from 1.50 errors ($SEM = 0.48$) to 0.75 errors ($SEM = 0.24$), $F(1, 9) = 1.833$, $p = .209$. On the probe trial, eight of 10 rats entered the normally nonrewarded arm, suggesting the rapid acquisition of the escape-reinforced motor response (binomial test, $p = .055$).

We also observed rapid acquisition during training of the two extended subgroups, evidenced by asymptotic mean latency and number of errors to the platform after Day 3 (see Figures 1a–b). Group \times Goal Arm \times Session ANOVAs showed a significant effect of session for both latency, $F(19, 380) = 20.125$, $p < .001$, and number of errors, $F(19, 380) = 14.705$, $p < .001$.

Although we were concerned that counterconditioning or extinction from probe tests would affect subsequent training performance, there were no significant effects of group on either latency, $F(1, 20) = 0.267$, $p = .610$, or number of errors, $F(1, 20) = 0.170$, $p = .684$. Additionally, no interactions were significant for latency ($ps > .344$) or number of errors ($ps > .741$), except a marginally significant Goal Arm \times Session interaction for errors, $F(19, 380) = 2.446$, $p = .088$.

The frequent group was first probed after two training sessions (see Figure 1c). On this probe, eight of 12 rats entered the nonrewarded arm and were designated as response learners. Although this proportion of response learners did not differ significantly from chance ($p = .193$), combined with the 10 rats in the single group, which were also probed after two training sessions, 18 of 24 rats exhibited a response strategy ($p = .011$). By contrast, on the final probe test, only one rat in the frequent group ($p = .003$) and two rats in the infrequent group ($p = .019$) entered the normally nonrewarded arm, indicating that, by the end of training, a significantly greater than chance number of rats were place learners (21 of 24 overall, $p < .001$).

We then evaluated the change in solution strategy over the course of the experiment. A Group \times Test ANOVA of responding on the probe tests common to both groups (even-numbered probe tests in Figure 1c) showed significant effects of test, $F(4, 88) = 4.29$, $p = .003$, but no effect of group, $F(1, 22) = 1.15$, $p = .294$. Analysis of the decreasing linear trend in using the “response” strategy over these probe tests was significant for the two groups combined, $F(1, 22) = 15.45$, $p < .001$, and for the frequent group alone, $F(1, 22) = 13.73$, $p = .001$, and marginally significant for infrequent group alone, $F(1, 22) = 3.43$, $p = .077$. ANOVA of responding over all 10 probe tests of the frequent group also showed significant effects of test, $F(9, 99) = 2.55$, $p = .011$, and decreasing linear trend, $F(1, 11) = 10.98$, $p = .007$.

Despite this change in solution strategy, the rats showed no significant change in their latencies to reach the escape platform on probe trials over the course of testing. ANOVA showed no significant main effects or interactions ($ps > .295$). These latencies were comparable to those observed on contemporaneous training sessions.

In conclusion, in the submerged maze, rats exhibited a response strategy at the beginning of training and switched to a place

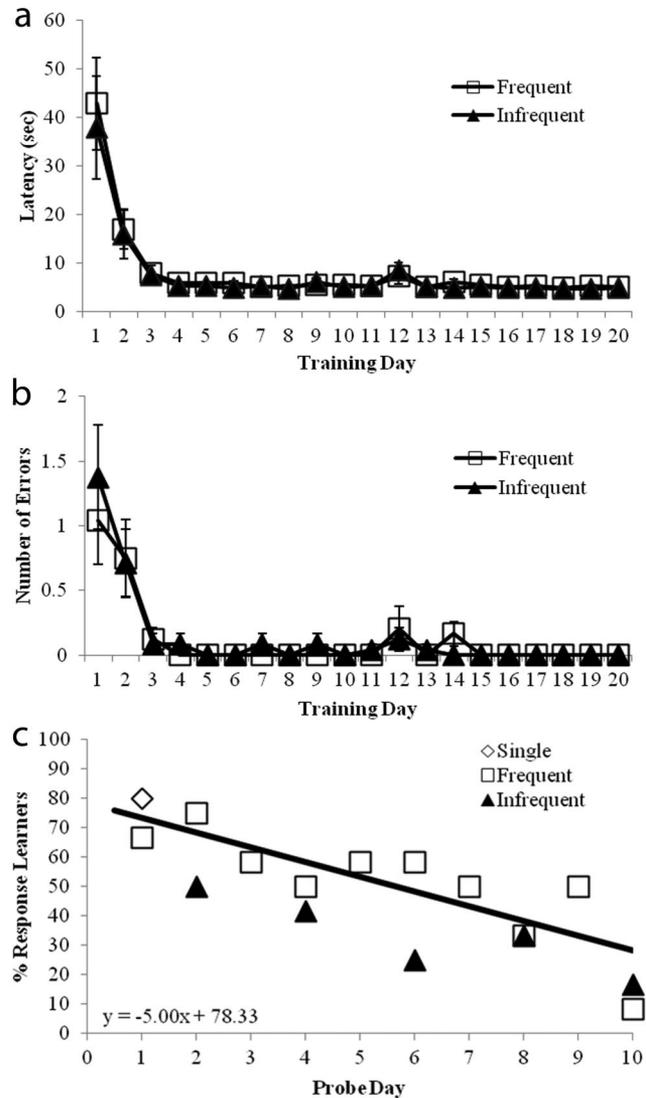


Figure 1. Mean latency to reach the escape platform (a) and mean number of errors during acquisition in the extended groups of Experiment 1 (b). Rats received two training trials per day. Error bars denote standard error of the mean. Percentage of response learners in Experiment 1 (c). Rats in the single group received a single probe trial after the second training session and rats in the frequent and infrequent groups received a single probe trial after every 2 or 4 training sessions, respectively. Trend line (equation shown) is based on frequent group data points.

strategy by the end of training, a pattern opposite to that reported with food-rewarded procedures (e.g., Packard & McGaugh, 1996).

Experiment 2: Dry Maze

Results

During training, we observed gradual acquisition of maze performance, with asymptotic mean latency to the reward cup and number of errors after Day 14 (see Figures 2a–b). ANOVAs showed significant effects of session for both latency, $F(39,$

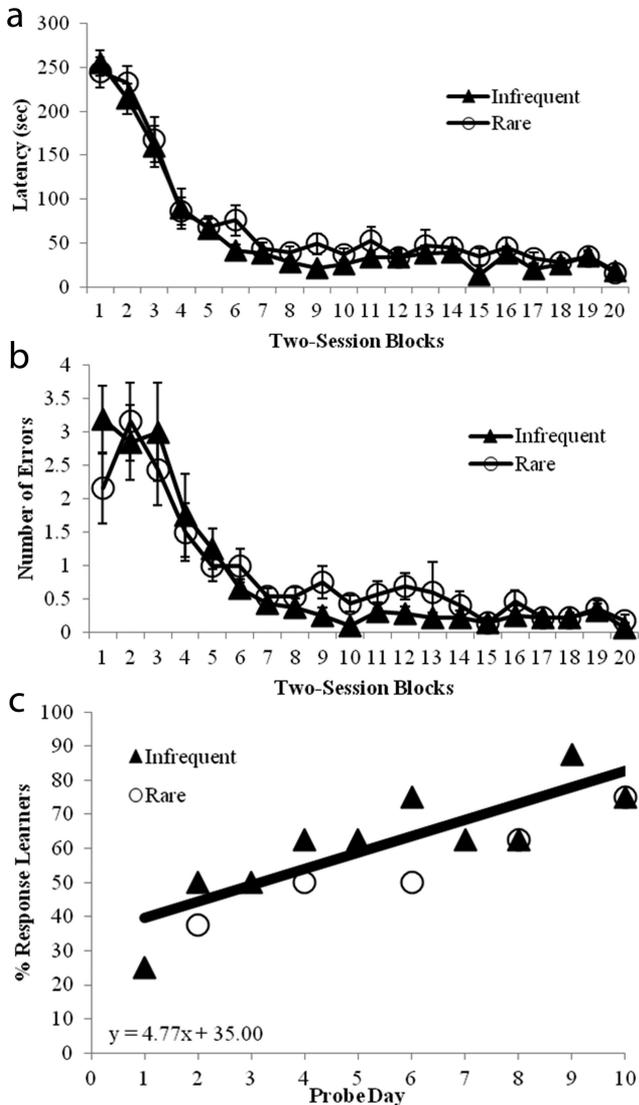


Figure 2. Mean latency to reach the reward cup (a) and mean number of errors during acquisition in Experiment 2 (b). Rats received two training trials per day. Error bars denote standard error of the mean. Percentage of response learners in Experiment 2 (c). Rats in the infrequent and rare groups received a single probe trial after every 2 or 4 blocks of two training sessions, respectively. Trend line (equation shown) is based on infrequent group data points.

468) = 48.189, $p < .001$, and errors, $F(39, 468) = 12.245$, $p < .001$. However, as in Experiment 1, there were no significant effects of group (probe test frequency) for either latency, $F(1, 12) = .636$, $p = .441$, or number of errors, $F(1, 12) = .156$, $p = .700$. The main effect of the goal arm counterbalancing variable was significant for number of errors, $F(1, 12) = 5.969$, $p = .031$, but not latency, $F(1, 12) = 3.186$, $p = .100$. Finally, the Goal Arm \times Session interaction was significant for latency, $F(39, 468) = 2.595$, $p = .038$, but no other interactions were significant for either latency ($ps > .435$) or number of errors ($ps > .160$).

After 4 days of training, the infrequent group received its first probe test (see Figure 2c). Two of eight rats entered the nonre-

warded arm, suggesting that the majority of rats were place learners (but not significantly, $p = .109$). The rats in the rare group exhibited a similar tendency in their first probe test (which occurred after eight training sessions): two of eight rats entered the previously nonrewarded arm ($p = .109$). Thus, combined over the two groups, 12 of 16 rats were place learners on their initial probe trial ($p = .028$). By contrast, on the final probe test, six of eight rats in the infrequent group ($p = .109$) and seven of eight rats in the rare group ($p = .035$) entered the previously nonrewarded arm. Thus, combined over the two groups, 13 of 16 rats were response learners on their final probe trial ($p = .011$).

We then evaluated the change in solution strategy over the course of training. A Group \times Test ANOVA of responding on the probe tests common to both groups (even-numbered probe tests in Figure 2c) showed no significant effects of test, $F(4, 56) = 2.00$, $p = .108$, or group, $F(1, 14) = 1.571$, $p = .231$, and no Group \times Test interaction, $F(4, 56) = .71$, $p = .591$. Nevertheless, analysis of the increasing linear trend over these probe tests was significant for the two groups combined, $F(1, 14) = 7.06$, $p = .019$, and for the rare group alone, $F(1, 14) = 7.60$, $p = .015$, but not for the infrequent group alone, $F(1, 14) = 1.00$, $p = .333$.

Thus, rats initially used a place learning strategy, but switched to a response strategy with further training, the same pattern as found by Packard and McGaugh (1996), but the opposite to that found in the submerged maze in Experiment 1. We directly compared the changes in solution strategies over the courses of training in Experiments 1 and 2 by conducting an Experiment \times Group \times Test ANOVA on probe test performance (see Figures 1c and 2c). This ANOVA showed a significant Experiment \times Test interaction, $F(4, 144) = 5.76$, $p < .001$, and a significant difference in the linear trends in the two experiments, $F(1, 36) = 20.67$, $p < .001$. No other effect or interaction was significant.

General Discussion

Rats rapidly learned to escape to a hidden platform in a submerged maze task. Probe tests indicated that the rats initially adopted a response strategy, but switched to a place strategy as training continued. By contrast, with the same apparatus and similar procedures, rats rewarded by food began as place learners and switched to a response strategy, as described previously by Packard and McGaugh (1996).

Previous investigations using the submerged dual-choice maze task (Elliot & Packard, 2008; Packard & Wingard, 2004) focused on rats' early use of a place strategy. In those experiments, the only probe test was administered after 12 training trials. The proportion of untreated rats that displayed a place strategy in that probe (~60%) was similar to that observed here after 12 trials. By testing throughout training, the present study provides a more complete description of the course of strategy selection in the submerged "dual-choice" maze. Although it is possible that, after more training, rats in the submerged maze would revert to a response strategy, our Experiment 1 involved extensive postasymptotic training without such a return. Thus, we conclude that the nature of reinforcement or motivation substantially affected spatial learning strategy selection and progression in this task.

Our results differ from those obtained in the submerged maze when rats are started from both north and south arms throughout training. Packard and Gabriele (2009) found that rats learn more

rapidly in such “dual-start” tasks when they are required to approach the same location than when required to make the same response. Perhaps the changing stimulus situation in the dual-start task favors earlier selection of a place strategy.

The shift from a place to a response strategy in the food-rewarded maze has been described as a shift from an initial tendency to use relatively complex allocentric information to locate food resources, which are naturally distributed widely in space, to a cognitively more economical (and perhaps automatic) strategy of using egocentric response information to obtain reward efficiently. By contrast, the escape-motivated submerged maze may immediately provoke a fight-or-flight response, including automatic motor movements, anxiety, and the release of stress hormones. These movements may be reinforced by escape and therefore rapidly conditioned. Notably, in both our and Packard's studies, learning was considerably more rapid in the submerged maze than in the food-rewarded maze.

Packard and colleagues (Elliot & Packard, 2008; Packard & Wingard, 2004) found that administration of anxiogenic drugs biased rats toward using a response strategy in the submerged maze: Although, after 12 training trials, control rats tended to use a place strategy, drug-treated rats showed significantly greater use of a response strategy. Of note, these effects were apparently mediated by the basolateral amygdala (BLA): Infusions of anxiogenic drugs directly into the BLA mimicked the effects of intraperitoneal injections, and, in dual-start versions of the task, inactivation of the BLA blocked the effects of intraperitoneal injections.

Other evidence has indicated that rodents show increased switching from spatial to response-related strategies after chronic stress (Schwabe, Dalm, Schächinger, & Oitzl, 2008), acute stress induced by restraint or exogenous administration of corticosterone (Schwabe, Schächinger, de Kloet, & Oitzl, 2010), or by the reactivation of an adverse memory (Hawley, Grissom, Patel, Hodges, & Dohanich, 2013). Similarly, chronic (Schwabe et al., 2008) or acute (Schwabe et al., 2007) stress increased the use of stimulus-response over spatial strategies in humans. Furthermore, in devaluation experiments, stress has been shown to modulate the nature of instrumental learning, prompting use of a stimulus-response or habit strategy over more cognitive goal-directed action (e.g., Schwabe & Wolf, 2009; Schwabe, Hoffken, Tegenthoff, & Wolf, 2011).

Reinforcement of escape responses and their exacerbation by stress might easily account for the immediate expression of a response strategy in the submerged maze, but does not address the subsequent shift to a place strategy. However, repeated exposure to the maze and availability of a coping (escape) response might lead to habituation of its anxiogenic properties, hence, reducing expression of a response strategy and favoring expression of a place strategy. Indeed, in more conventional escape-avoidance settings, rats often show reduced stress levels as learning continues, despite sustained performance on the task (e.g., Seligman & Johnston, 1973).

Neural systems often compete in the control of performance, such that the elimination of one system results in greater control by another system. For example, inactivation of hippocampus impairs acquisition of a spatial strategy, but facilitates learning of a response strategy in both dry and submerged mazes (Chang & Gold, 2003; Schroeder, Wingard, & Packard, 2002). Stress, which com-

promises hippocampal function (Kim & Diamond, 2002), might encourage striatal control over initial behavior in the submerged maze. As rats habituate to anxiogenic properties of the maze, decreased stress hormone levels may release the animal to encode and use place information. Thus, under some circumstances, perhaps spatial learning performance is mediated by more gradual hippocampal learning that occurs after rapid engagement of striatal, amygdalar, or other learning systems.

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