



## Rule Learning by Rats

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D and E)]. Another potential consequence of electrodiffusion is that local postsynaptic depolarization, by extending the dwell time of intracellular glutamate (Fig. 1D), may enhance activation of NMDARs. This is likely to interact synergistically with the depolarization-dependent attenuation of postsynaptic glutamate transport and relief of Mg<sup>2+</sup> block, thus potentially facilitating induction of NMDAR-dependent synaptic plasticity.

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Supporting Online Material

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 Materials and Methods  
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# Rule Learning by Rats

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Using rules extracted from experience to solve problems in novel situations involves cognitions such as analogical reasoning and language learning and is considered a keystone of humans' unique abilities. Nonprimates, it has been argued, lack such rule transfer. We report that *Rattus norvegicus* can learn simple rules and apply them to new situations. Rats learned that sequences of stimuli consistent with a rule (such as XYX) were different from other sequences (such as XXY or YXX). When novel stimuli were used to construct sequences that did or did not obey the previously learned rule, rats transferred their learning. Therefore, rats, like humans, can transfer structural knowledge from sequential experiences.

The ability to extract generalizable rules from specific experiences is a fundamental attribute of human higher cognitive functioning (1, 2). For instance, human language learning relies on learning grammatical rules that allow the English speaker to discriminate “the dog bit the woman” (subject-verb-object) from “bit the woman the dog” (verb-object-subject). Rules can also be transferred to newly encountered items, contributing to the understanding and production of new sentences. Cross-linguistic differences in grammatical rules serve to highlight the challenge facing the developing child: that phrase structure rules must be learned. Language is only one of many cognitive domains where problems of this type are present, raising the issue of the nature of the underlying cognitive substrates supporting rule learning in general.

Rule learning has been investigated in different species and stages of human development (3, 4). Pre-linguistic infants (5), primates (6), and even some birds (7, 8) can learn rule-like temporal structures. Starlings, for example, are able to learn sequential structures made up of segments of birdsong and can recognize

whether patterns are consistent with those in a training set. Although the question of whether the birds use recursion to solve the discrimination is controversial, they do appear to use a form of rule (8, 9).

We studied the ability of rats to learn and transfer rules. We developed a procedure to test rule-transfer learning in the rat, an animal that, it has been argued, might have limited or perhaps even no ability parallel to that used by humans (3, 5). Rats were trained with three-element sequences (such as ABA or BAB) paired with food. We asked whether they would learn something about the overall pattern of cues (such as XYX). At least three cognitive abilities are required in order to learn this rule and apply it in novel situations. The first is an ability to learn that a sequence of cues signals food (10, 11). Second, animals need to discriminate sequences paired with food from those that are not. Rats can learn two-element sequences, A followed by B rather than B

**Table 1.** Illustration of the three rules and mean rate (per minute) of food tray entries in each group in response to both reinforced (RF) and nonreinforced (NRF) rules on the first and last block of training. Each group received food after one of the three rules (XYX, XXY, or YXX) and no food after the other two rules. Although no differences were found between the three groups or between reinforced and nonreinforced rules during the first two blocks of training trials [*F* values (2,12) < 1], by the last block of training trials the main effect of reinforced versus nonreinforced rule was statistically significant in all three groups [*F*(1,12) = 8.21, *P* < 0.01], although neither the main effect for the different groups or the interaction were statistically significant [*F* values (2,12) < 1] suggesting that the effect was similar with all three rules.

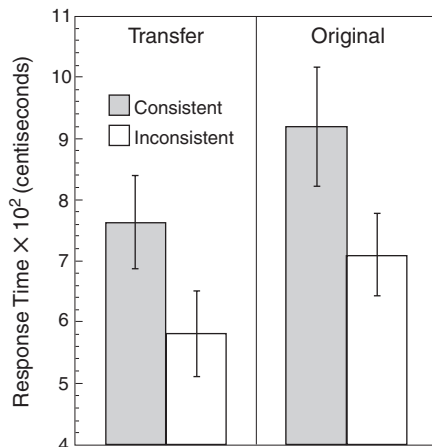
Block of learning trials	Group 1 Rule 1 (XYX) ABA, BAB		Group 2 Rule 2 (XXY) BBA, AAB		Group 3 Rule 3 (YXX) BAA, ABB	
	RF	NRF	RF	NRF	RF	NRF
First	12.66	12.58	9.14	9.81	13.94	13.97
Last	25.97	24.18	24.47	22.97	32.08	29.06

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followed by A (12), as signals for food. The third is the ability to transfer a rule to novel instances. We tested whether the rats learned a generalized rule rather than simply the trained instances. The transfer involved novel sequences that were either consistent or inconsistent with a previously trained rule but used stimuli that rats had never been exposed to or trained with.

Discrimination between stimuli is not a fixed ability, because animals usually show some generalization to novel items. For example, to the extent that a new stimulus C has more perceptual similarity to A than to B, animals will treat C like it is A (10, 13). Furthermore, similarity is not restricted to perceptual features. Animals will treat two different cues with the same consequences (for instance, being paired with food) as similar (14). Finally, animals will sometimes treat stimuli that have the same relative position on a stimulus dimension (such as being greater than or brighter than) as similar (15). In our experiment, the stimulus changes within and between sequences were not monotonically distributed along a dimension. There were no stimulus-specific perceptual cues or common consequences that previous research might have predicted could have allowed generalization of behavior.

The rules were based on experiments that have shown that prelinguistic human infants behave as if they learn rules embedded in sequences created from auditory phonemic cues (5, 16). We used patterns of visual (experiment 1) and auditory (experiment 2) stimuli that obeyed a similar rule.



**Fig. 1.** Mean time (in centiseconds) with head in the food trough during the final 10 s of a sequence, subtracting the 10-s prestimulus interval for that trial. Response rates are shown separately for consistent sequences and inconsistent sequences, and the analysis confirmed that there was more responding to consistent than inconsistent sequences during the transfer test in the absence of food [ $F(1,13) = 5.35, P < 0.05$ ] and during a test of the original stimuli [ $F(1,13) = 4.87, P < 0.05$ ].

The cues in experiment 1 consisted of three-element sequences composed of short 10-s exposures to two visual cues: a bright light (A), or darkness (B) presented in a dimly lit environment. The rats were divided into three groups, with each group receiving Pavlovian conditioning for food after sequences that obeyed one of three rules. One group received food with the *YXX* rule (ABA and BAB), another group with the *XXY* rule (AAB and BBA), and finally a third group with the *YXX* rule (BAA and ABB). Each group also received trials with the other two sequences but without food. Would each group learn their rule for food and discriminate reinforced from nonreinforced sequences? We compared the rats' anticipatory responding for food during the third element of each sequence but before the food was available. The animals were able to discriminate among the sequences by the end of the experiment (Table 1). They came to respond more at the end of sequences that signaled food than to trials of either of the other two rules, and there was no evidence for differential responding to these two nonreinforced rules (17). Because A and B immediately preceded both food delivery and the absence of food, animals could not use the identity of the final stimulus to solve the discrimination. One possible solution involves the rats using unique pairs of stimuli that might have differentially signaled reinforced from nonreinforced sequences. Rats trained with *XXY* as the reinforced sequence might only have used the first pair of stimuli as a unique cue, whereas those trained with *YXX* might have used the final pair of stimuli; finally, the group whose reinforced sequence was *YXX* could have learned to use a pair formed by the first and third stimuli. However, if animals did make use of different stimulus combinations in each group we would expect discrimination levels to differ because each of these discriminations would have involved quite different levels of difficulty. For instance, using a strategy based on the first two stimuli to discriminate *XXY* from the other patterns would imply that the third stimulus is uninformative. The third stimulus would effectively delay reinforcement, and weaken the discrimination, relative to reinforcement after *YXX*, in which food was contiguous with the unique stimulus pair. Overall, the notion that only stimulus pairs were crucial for learning does not account for the similar learning observed in all three groups. Discrimination performance did not differ among groups (17), suggesting that animals were anticipating food delivery by learning the whole triplet stimulus pattern. Rats had to use all three stimuli and their position in the sequence, a form of rule learning, to solve the discrimination.

These results demonstrate that rats can learn three-element sequences, but it is possible that one method of solving the task involved memorizing the two sequences paired with

food. Perhaps multiple instances of the rule (such as ABA and BAB) were treated as behaviorally similar but not perceived as examples from a broader category.

In a second experiment, we used a transfer test to explore this possibility. We tested whether rats could generalize learning of a rule to novel stimuli that were either consistent or inconsistent with the trained rule. We used a procedure similar to that in experiment 1, but because there were no differences in learning the three rules in experiment 1, we trained all subjects with rule 1 (*YXX*) using two auditory pure tones (A = 3.2 kHz and B = 9 kHz). Auditory cues were used because they allow a wider range of cues for the transfer test. Animals received food at the end of ABA and BAB sequences, but not after BBA, AAB, BAA, or ABB. After acquisition, we presented them with transfer stimuli composed of two novel pure tones (C = 12.5 kHz and D = 17.5 kHz). The stimuli were counterbalanced so that the stimuli in the roles of A, B and C, D were reversed for half of the animals and were chosen to ensure that no common frequency relation was present between the pairs. If rats had simply learned something specific about the reinforced elements ABA, they should have been unable to choose CDC and DCD over CCD, DDC, CDD, and DCC. The amount of time that the rats kept their heads in the food trough during the final element of the sequence was used as a measure of learning. The results of the transfer test are presented in Fig. 1, excluding two rats that failed to learn the initial discrimination. More anticipatory behavior for food was exhibited during sequences that were consistent with the previously learned rule, even though the rats had never been presented with these particular instances and there was no food presented during the test. As with experiment 1, animals responded more to the rule-consistent sequences than to both inconsistent sequences. There were no differences in responding to the two inconsistent rules (17). To test whether the rats remembered the trained sequences, we presented the original stimuli again, without any food reinforcement or any retraining, and found that they could still apply the rule to the original stimuli and consequently respond more to the previously reinforced sequences (Fig. 1).

The design of these experiments rules out a number of simple explanations of the rats' behavior. They could not have solved this discrimination simply by learning the final element of the sequences, because these elements were the same for both reinforced and nonreinforced sequences. Similarly, they could not use pairs of stimuli embedded in the sequences to solve the discrimination, because this would lead to differing levels of performance in experiment 1. The result of experiment 1 could be explained by the animals memorizing the sequential configuration of

the reinforced triplets. Experiment 2 showed that the rats transferred what they had learned about the sequences to novel instances. This transfer could not be achieved by memorizing the specific patterns. The counterbalancing of the exemplars of each rule prevented learning of a particular pitch or timbre pattern instead of the sequence pattern. Animals were trained with both high-low-high and low-high-low frequency changes and therefore no simple pitch change can account for the original or transfer results. Pitch changes along the frequency dimension were not fixed and did not follow a continuum, and the transfer cues were outside of the training range. Transfer had to be based on the entire relational sequence, resulting in rule-based behavior.

Finally, it remains possible that the animals learned the relational sequences as two separate but unrelated relational patterns and not as instances of the same category. However, during transfer, rats treated both patterns in the same way and equally different from all other instances belonging to a different category (17). Hence, an account that integrates both patterns as instances of the same category

is parsimonious and in line with data suggesting rule-governed performance.

These experiments show that rats can learn simplified rules and apply these rules to novel stimuli. Even if the cognitive mechanism that allows the rats' behavior is found to be dissimilar to that found in humans, it does seem that both species have evolved means of solving similar information problems, in this case the transfer of overall sequence relations [see also (5, 6, 9)]. These experiments suggest that some rule-governed behavior is present in rats and that well-understood principles of conditioning provide a perspective on what we think of as our most human of cognitive abilities.

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