Odour discrimination: a cognitive strategy or not?

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An animal that shows progressive improvement over the course of training on a series of related discrimination problems is sometimes described as having formed a learning-set. We could debate whether or not this is an appropriate use of the term, but the issue of real substance concerns the nature of the process or mechanism responsible for such an improvement when it occurs. In particular, how can we tell when the animal has adopted a 'higher order strategy', such as win–stay, lose–shift? Reid and Morris insist that improved performance is not in itself evidence for such a strategy and in this they are surely right. Indeed, in this respect, at least, they understate their case – even perfect performance (100% from trial 2 of each new problem) could be explained by simpler theories of discrimination learning.

According to such theories[1], an animal will choose correctly between alternatives when the difference between the approach strength governed by the positive and that governed by the negative exceeds some critical amount. In principle there is no reason why a single training trial should be insufficient to establish this critical difference and thus no reason why perfect trial 2 performance should be taken to reflect the operation of some 'cognitive' strategy. What needs explanation, if this view is adopted, is why performance should be rather poor on the early problems of a learning-set series. The usual assumption is that other disruptive factors are operating early on, but that these lose their effectiveness as training proceeds. There are a number of possibilities here, but perhaps the most obvious is that the change in approach strength generated by a reinforced trial might initially tend to accrue as much to irrelevant aspects of the situation (to the cues that define the position of the alternatives, for instance) as to the relevant cues themselves. Theories of discrimination learning[2] have been specifically designed to explain how this initial tendency comes to be eliminated and attention concentrated on the relevant stimulus dimension; these theories are thus quite capable of explaining the progressive improvement seen in learning-set studies, particularly those in which some well-defined dimension (such as odour) is relevant in all problems.

However, the availability of an alternative explanation does not exclude the possibility that the development of a win–stay, lose–shift strategy contributes to the improvement seen over a series of olfactory problems, and Reid and Morris would be wise to be cautious about pressing this stronger claim. They cite two lines of evidence from their own experimental work on olfactory discrimination learning[3], each of which is suggestive rather than conclusive. The first comes from the finding that extended training on a single problem produces transfer to a novel test problem every bit as substantial as that produced by prior learning-set training. The force of this observation depends on the assumption that extended training does not itself generate some higher order strategy, probably an acceptable view, but an assumption none the less. The second argument depends on the observation that serial reversal training also produces good transfer to a novel problem even when there is no observable improvement over the series of reversals, and hence no overt sign of the development of a win–stay, lose–shift strategy. The failure to find serial reversal improvement raises a number of issues, some of which will be taken up shortly. For our present purposes, however, it is enough to note that it is conceivable that a strategy that has begun to develop under serial reversal training might be able to show itself only under the rather different conditions of the transfer test.

The implication of what has been said, is that, on the basis of the evidence so far available, we cannot know whether the progressive improvement shown over a series of odour discriminations is the result of a win–stay, lose–shift strategy or not. The critical experiment remains to be done. What can distinguish performance based on this strategy from what might be achieved by very rapid but otherwise orthodox associative learning processes is the impermanence of the information held about the value of individual stimuli. Animals using the strategy know to approach the cue associated with reward (or to avoid the nonrewarded cue) but are assumed to hold information about this association only in the short term. In a few cases[4,5] evidence for this analysis has been provided by the demonstration that the performance of learning-set proficient subjects is severely disrupted when a longer than usual delay is imposed between one trial on a given problem and the next. We have no such demonstration for the case of odour discrimination in rats. Until one becomes available, it seems prudent to accept that the development of a higher order strategy has not yet been proved for odour discrimination in rats.

To accept this view begs a further question. If rapid improvement over a series of odour discriminations is not to be explained by the notion that olfactory cues have privileged access to higher cognitive processes, then what is its source? Perhaps the simplest way to deal with this question is to deny the validity of the premise that the improvement seen in olfactory learning is uniquely rapid. Learning-set procedures have not been much used with rats, presumably because our laboratories are equipped for auditory or visual discrimination tasks and it is difficult to obtain in these modalities the large numbers of discriminable cues that are required for a thorough study. However, occasionally the effort has been made, with results that appear to justify it. Kay and Oldfield-Box[6] constructed a large set of three-dimensional shapes and, using a procedure similar to that originally employed by Harlow[7] with primates, were able to show rapid acquisition by rats. In one of their experiments the rats were reliably scoring more than 70% correct on the first 20 trials of each problem after having learned no more than four such problems previously. Rapid progressive improvement is not a special feature of olfactory learning.

There remains one feature of olfactory learning that might prompt us to allow it some special status, and ironically this is found in the work of Reid and Morris[3] themselves. It is their finding that serial reversal improvement fails to occur. Such improvement emerges quite readily when rats are trained on an analogous visual discrimination[3]. One reason for this improvement, it has been suggested, is that the rats come to restrict attention to the relevant stimuli, to abandon position habits, and so on, an interpretation that makes Reid and Morris's failure to find the effect all the more puzzling since it is just these processes that they suggest might generate the improvement they observe in the olfactory learning-set procedure. I have no solution to this enigma. All I can do is express the hope that further research will clarify the issue of what conditions are necessary for serial reversal improvement in olfactory learning; also, given the current state of confusion on this issue, to urge caution about taking the Reid and Morris result as a convincing demonstration that olfactory learning is in some way special.

Selected references

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Odor-guided learning and memory in rats: is it 'special'?

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Unlike neocortical sensory modalities, the olfactory system is fully evolved in rodents, and olfactory projections reach hippocampal circuitry in as few as two synapses. So it seems worth asking whether such an anatomically defined 'privileged access' to hippocampal processing translates into anything extraordinary about the olfactory cognitive capacity in rodents. In commenting on the article by Reid and Morris, we will consider first the issue of the olfactory learning-set, and then the role of hippocampal processing in odor-guided learning and memory.

The rules guiding olfactory 'learning-set'

In our original report describing rapid improvement in odor discrimination[1] we used 'the phrase "learning-set" to refer to positive transfer across discrimination problems, without prejudice about the underlying mechanisms'. In the present analysis Reid and Morris begin admirably by setting out three criteria for demonstrating learning-set: one-trial learning, transfer across problems with the same rule, and sensitivity to inter-trial interval (ITI). However, in our view, their analyses fail to support the contention that olfactory learning-set does not occur and shed no new light on the mechanisms of positive transfer. First, Reid and Morris' study[2] assessed performance across only seven discrimination problems. Since monkeys require hundreds of problems to demonstrate errorless learning, an analysis based on only seven problems seems insufficient to draw a meaningful negative conclusion about the ultimate performance abilities of rats. In a closer approximation, Slotnick and Katz[3] described a rat given 56 problems; 11 of the last 20 were learned with one or no errors, suggesting rats might well demonstrate consistent one-trial learning with extended training. Second, in their attempts at transfer tests, Reid and Morris' observation of rapid initial improvement after a single problem is reminiscent of our own findings without overtraining[1], and pales by comparison to Slotnick's[4] description of a method for nearly errorless learning. Moreover, the results on reversal only provide compelling confirmation that it is difficult to get rats to contradict an odor association[1]. If, as Reid and Morris argue, improvement across successive problems is entirely due to learning general task procedures, why did performance differ in serial discrimination versus serial reversal, which involved the same procedures? Reid and Morris offer no explanation, but we argue below that rats come 'prepared' to learn new novel discriminations and resist a contradictory rule for serial reversal. Third, Reid and Morris admit that sensitivity to ITI has yet to be examined, although we have recently reported that odor memory is indeed affected by the length of the ITI in a different paradigm[5]. In sum, Reid and Morris' findings simply confirm previous indications that rats require little formal training to become proficient at learning new odor associations.

The superb performance of rats on serial odor discrimination can be reconciled with their failure in serial reversal by considering how the 'win–stay, lose–shift' rule might apply to associative learning with odors. Perhaps rats have an innate or developmentally acquired capacity for rapid and permanent odor associations, and do not require a new 'cognitive rule' for odor discrimination. Positive transfer across problems probably involves learning