PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Differences in Mechanisms of Intelligence Among Vertebrates [and Discussion]

N. J. Mackintosh, B. Wilson, R. A. Boakes and H. B. Barlow

Phil. Trans. R. Soc. Lond. B 1985 **308**, 53-65
doi: 10.1098/rstb.1985.0009

Phil. Trans. R. Soc. Lond. B **308**, 53–65 (1985)
Printed in Great Britain

Differences in mechanisms of intelligence among vertebrates

By N. J. Mackintosh[1], B. Wilson and R. A. Boakes[2]

[1] *Department of Experimental Psychology, University of Cambridge,*
Downing Street, Cambridge CB2 3EB, U.K.
[2] *Laboratory of Experimental Psychology, University of Sussex, Brighton BN1 9QG, U.K.*

Much comparative research aimed at establishing differences in intelligence among vertebrates has failed to convince the sceptic, because it has concentrated on a single experimental paradigm (such as learning sets), while employing a diverse array of species in the hope of establishing a rank ordering of intelligence. The sceptic can insist that such research has not even established that there are any differences in mechanisms of intelligence between any pair of vertebrate species, let alone elucidated the nature of the difference, and even the unsceptical will doubt that such research is ever likely to establish a rank order of intelligence.

It is more informative to concentrate on fewer species, but a broader range of experimental paradigms. Thus, studies of serial reversal learning have consistently suggested that goldfish do not show such rapid improvement as do rats. One explanation of this might be that rats learn more effectively than goldfish to use the outcome of one trial to predict the outcome of the next. The suggestion is supported by finding other experimental paradigms, such as alternation learning, which must also tap such a process, and where rats again learn more rapidly than goldfish.

Efficient learning-set performance may also depend on this process, but must in addition require the subject to transfer this rule across changes of stimuli. There is reason to believe that not all vertebrates are equally adept at such transfer, and this possibility is explored in a series of experiments studying the transfer of matching-to-sample in pigeons and corvids. The corvids display significantly better transfer and the close similarity in training procedures possible with these subjects makes it unlikely that this is due to differences in these training procedures.

1. Introduction

Comparative psychologists have spent about 100 years in the more or less serious scientific study of animal intelligence. It cannot be claimed that they have very much to show for their pains. They have discovered a great deal about the processes underlying conditioning and simple associative learning, and have established that some of these processes are of great generality, to be found in most vertebrates and almost certainly in numerous invertebrates also. But there is a persistent belief that simple conditioning is not the only form that animal intelligence can take, and that intelligence should not be so widely and uniformly distributed. If these beliefs are justified, then there is rather little else that animal psychology can point to in the way of solid achievement. Macphail (1982), for example, is able to conclude a painstaking analysis of comparative studies of intelligence with the suggestion that, for all we know of the matter, there is no good reason to assume that there are any differences, either quantitative or qualitative, in the mechanisms of intelligence of non-human vertebrates. Have 100 years of research really produced no evidence one way or other to answer this question? And if not, why not?

In partial defence it is important to acknowledge that there are formidable difficulties in the way of good comparative research. But some have been of psychologists' own making. The history of research on learning sets provides a good example. Harlow (1949) had discovered that although, if trained on a simple discrimination problem (where choice of one alternative is rewarded and choice of the other is not), rhesus monkeys might learn to choose the correct alternative no faster than rats, if they were trained on a whole series of such problems, in each of which a new pair of stimuli was used, the monkeys would show a remarkable improvement and eventually learn each new problem in a single trial. In no time at all, there were studies of learning-set formation in primates ranging from human children to marmosets, and in other mammals from cats to squirrels to rats, and a rank-order of mammalian intelligence, based on this one task, was constructed (for example, Warren 1965; Passingham 1982).

It is quite possible that the differences in performance observed in these learning-set experiments do indeed reflect some differences in mechanisms of learning or intelligence. But such data alone will never be sufficient to establish this conclusion, nor will it greatly help to add yet more species to the list, or to correlate differences in learning-set performance with differences in some notional phyletic status or relative brain size. What is needed is first a realistic acknowledgement of alternative explanations, for example the trivially uninteresting possibility that primates are likely to learn a series of visual discrimination problems more rapidly than rats because they have a more elaborate visual system. But, above all, we need a theory of the nature of these putative differences in learning mechanisms, and we need to test that theory by examining its predictions in other experimental situations.

2. Serial reversal

It will be easier to start with a possibly simpler task – one at which rats at any rate are quite proficient. It has long been known that if rats are trained on a series of reversals of a single discrimination problem, where choice of first one alternative and then of the other is rewarded, the speed at which they learn each new reversal will rapidly increase. Some such improvement is probably the norm in vertebrates: although it was once thought that some teleost fish were unable to learn later reversals any faster than earlier ones, it is now clear that under some conditions of training they can. But, despite suggestions to the contrary, this hardly proves that there are no differences between, say, rats and goldfish in the processes of reversal learning. Figure 1 provides some illustrative examples of the performance of these two groups on visual (brightness or colour) and spatial reversals. It is apparent that the goldfish are notably less proficient than the rats. What is not so immediately apparent, but should be emphasized, is that figure 1 provides a very conservative estimate of this difference. The data for the goldfish have been selected as the two clearest examples available of improvement over a series of reversals.† Those for the rat are by no means so highly selected: although they show one characteristic feature of the rat's performance, namely that later reversals are learned reliably

---

† An experiment by Setterington & Bishop (1967) has provided clear evidence of improvement over a series of spatial reversals by another species of teleost fish, African mouth breeders. Although the published data are presented in a manner which makes comparison with the data shown in figure 1 impossible, Dr Setterington has kindly provided his original data, from which it is possible to calculate that the fish averaged 9.1 errors per reversal over reversals 1–10, 9.1 over reversals 11–20, and 8.6 over reversals 21–30. After 70 reversals the average number of errors per reversal had dropped to 6.6. The improvement is significant but not obviously any more rapid than that shown by goldfish in figure 1, and, by rat standards, slow.

faster than the original discrimination, there are numerous experiments in which rats have learned later reversals with only a single error.

Figure 1 suggests, therefore, that there are significant differences in the performance of rats and goldfish on a series of discrimination reversals, but it leaves open the possibility that these differences are due to uninteresting differences in experimental procedure. The fact that rats learn visual reversals very much faster than goldfish even though taking just as long to learn the original discrimination makes it unlikely that differences in sensory capacity are involved, but speed of reversal is affected by numerous other factors. How could we prove that variations in the contribution of one or more of these factors were not responsible for the difference in performance? It is not at all obvious that any further study of reversal learning by rats or goldfish could ever do this. For, as a matter of fact, just as there are conditions of training under which goldfish show no improvement over a series of reversals, so are there for rats (for example if they are trained at the rate of only one trial per day, Clayton 1962). This hardly proves that the differences shown in figure 1 are artefacts of differences in conditions of training; but it does mean that without some independent criterion for deciding what were functionally comparable conditions, further experiments on reversal learning may never be able to disprove this. And what could that independent criterion be?

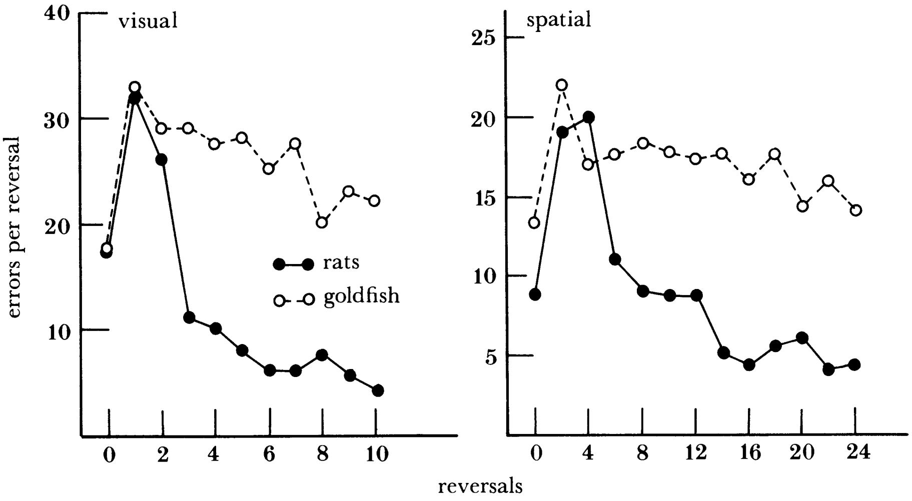

Figure 1. Errors per reversal over series of visual or spatial reversals by rats and goldfish (O = original discrimination). The visual reversal data for the rats are from Mackintosh & Holgate (1969) and for the goldfish from Engelhardt *et al.* (1973). The spatial reversal data for both animals are from Mackintosh & Cauty (1971).

Perhaps we should try a different approach. If the difference in reversal performance is due to a difference in learning mechanism, what might this be? One simple possibility is that the highly efficient reversal performance of rats reflects their ability to use a set of cues whose relation to reward stays constant throughout the experiment. The difficulty in reversal learning is that now one stimulus, now the other, predicts reward, and reliance on the physical attributes of these stimuli to predict the outcome of a trial means that each new reversal requires the unlearning of an old predictive relationship and the learning of a new one. But, with the exception of the first trial of each new reversal, there is a consistent relationship between the outcome of one trial and the animal's choice on the preceding trial and the outcome of that choice. On any given trial (but the first), of the two alternatives A and B, A will be rewarded either if A was chosen on the preceding trial and that choice was rewarded, or if B was chosen and that choice was not rewarded.

If rats become proficient at reversal learning because they learn that choice and outcome of choice on one trial predict the outcome of the next trial, and if goldfish are less efficient at detecting or using this relationship, we should expect to see differences in other experimental paradigms. One task that requires an animal to use the outcome of one trial to predict the outcome of the next is alternation learning. In the simplest case, a response such as pressing a lever or panel is rewarded only on every alternate trial. Rats rapidly detect this pattern and learn to respond on rewarded trials following non-reward, but to slow down or refrain from responding on non-rewarded trials following reward. Goldfish, by contrast, find this an extraordinarily difficult task, as figure 2 shows.

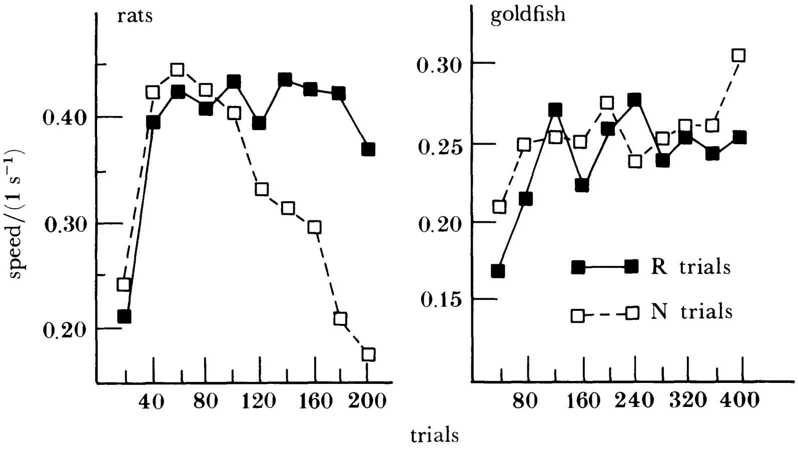

FIGURE 2. Speed of responding on rewarded (R) and non-rewarded (N) trials by rats and goldfish in experiments on alternation learning. The rat data are from Bloom & Malone (1968) and the goldfish data from Mackintosh (1971).

3. TRANSFER OF REVERSAL LEARNING

There are several other experimental paradigms where differences between the behaviour of rats and goldfish are readily understood as differences in the extent to which they detect these sorts of regularities (Mackintosh 1974; Macphail 1982). It does not seem too fanciful to suggest that the ability to track sequential variations and dependencies in the occurrence of food or other events of consequence might be an important component of intelligence. Certainly, it seems demanded by other tasks beloved of comparative psychologists, such as the discrimination learning-set task. The most plausible account of the experienced rhesus monkey's one-trial learning of any new discrimination problem is that he has learned the consistent predictive relationship between choice and outcome on one trial and outcome of the next. But in this case, unlike that of serial reversal, another process would seem to be required. One-trial reversal learning requires that the animal learn that choice of a specific stimulus, A, will be rewarded if, on the previous trial, he either chose A and was rewarded or chose B and was not. In the learning-set task, he must learn that this is true of *any* pair of stimuli, A and B. The rule must be generalized across changes in physical stimuli.

Evidence of such generalization in primates has been obtained from two variants of the serial reversal experiment. In one, the animal is trained on a discrimination between A and B and then on a single reversal of A–B; then on C versus D and its reversal; then on E versus F and so on. Rhesus monkeys, it is well established, rapidly increase their speed of learning new reversals (Warren 1960*a*). Cats have shown some evidence of such generalized improvement at reversal, but without matching the rhesus monkey's ability to reverse any new problem after a single error (Warren 1960*b*). The second variant involves training animals on a series of reversals of a single discrimination and then transferring them to a new problem, for example to a series of new discriminations in the standard learning-set procedure. Chimpanzees and macaque monkeys show excellent transfer under these circumstances (Schusterman 1964; Schrier 1966; Warren 1966). But in the only published study with another mammal, Warren (1966) found no evidence of transfer in cats, even though they had been trained on more than three times as many reversals, to a point where they were making half as many errors per reversal, as monkeys who have shown excellent transfer (Schrier 1966).

An alternative transfer task is learning a series of reversals of a new discrimination. Staddon & Frank (1974) trained pigeons for up to 134 reversals of one discrimination, by using a standard free-operant multiple schedule, before transferring them to a new discrimination and its reversals. Although by the end of training on the original series, all birds consistently made more than 90% of their responses to the correct stimulus on the first day of each new reversal, the change of stimulus markedly disrupted their performance, and it took more than 20 reversals before they were performing at this level of accuracy again. The two birds who were treated identically during their original and transfer reversal series performed no more accurately over the first half dozen reversals of their second problem than they had on the first. Paula Durlach has been undertaking a rather more systematic experiment along these lines. Her preliminary results confirm that pigeons, although showing a progressive reduction in the number of errors per reversal of one discrimination, are disrupted by a change in stimuli. Although there is clear evidence of some transfer from one pair of colours to another, there seems to be little or no transfer if birds are initially trained on reversals of a line orientation discrimination before being transferred to colour reversals. The most plausible interpretation is that the positive transfer in the former case reflects an increase in attention to colour cues, but that there is rather little transfer of any more general process responsible for reversal improvement. This is entirely consistent with the pigeon's relatively inefficient performance on standard learning-set tasks. Wilson (1978) trained pigeons on a series of 1000 visual discrimination problems. By the end of training they were averaging less than 55% correct on trial 2 of each new problem.

The question still remains whether the differences in behaviour suggested by all these experiments imply genuine differences in processes of learning or whether they are uninteresting consequences of some unspecified differences in experimental procedures. The diversity of results we have considered may make this latter alternative seem less plausible, but it cannot easily be ruled out. The experimental arrangements used to study reversal learning in goldfish or learning-set formation in pigeons differ markedly from those used for rats and primates. And even if the apparatus and training procedures were identical, we could not be sure that they were making equivalent demands on, say, the sensory or motivational systems of such diverse animals. It would make more sense to compare the behaviour of animals that did not differ so grossly in bodily structure or phyletic position. Different groups of birds promise to provide suitable material for such comparisons, for Kamil and his colleagues have shown that American blue jays, members of the corvid family, can perform very efficiently on the standard learning-set task, and will show significant transfer from serial reversal of one discrimination to a series of new problems (Kamil *et al.* 1973, 1977).

4. Transfer of matching and oddity in pigeons and corvids

We shall describe a set of experiments studying the transfer of matching and oddity learning in pigeons and European corvids (jackdaws, jays, rooks). Matching and oddity are types of conditional discrimination: animals are required to choose between two 'comparison' stimuli (for example, red versus yellow); which alternative is correct depends on the colour (red or yellow) of the 'sample' stimulus displayed at the outset of the trial. In matching, the correct comparison stimulus is the same as the sample; in oddity the comparison stimulus that is different from the sample is correct. Pigeons and corvids have no difficulty learning matching and oddity discriminations; the question is how they do it, and whether they can transfer the solution across a change of stimuli. Transfer of matching and oddity by pigeons was first studied by Cumming & Berryman (1965); they initially trained pigeons with three colours as stimuli; red, green and blue, and found that when they substituted yellow for blue the birds' performance dropped to chance. Zentall & Hogan (1974, 1975, 1978) adopted a potentially more sensitive, savings measure of transfer. Having trained pigeons on matching or oddity with one pair of stimuli, they transferred them to a new pair, with half the birds continuing on the same kind of problem as before (matching to matching or oddity to oddity) and half reversed to the opposite problem. Zentall and Hogan have consistently reported that the birds continuing on the same kind of problem learn their transfer task faster than those shifted to the opposite problem, and have taken this to mean that pigeons solve matching and oddity discriminations by learning that reward is predicted by the relation (of similarity or difference) between sample and comparison stimulus, and that they can transfer this rule across a change in stimuli.

There are two aspects of Zentall & Hogan's data that should give one slight pause. First, in several of their experiments they have studied transfer between red and green lights in one problem and yellow and blue in the other. But another of their own experiments (Zentall *et al.* 1981) establishes rather clearly that pigeons show substantial sensory generalization between red and yellow and between green and blue lights. The question at issue is certainly not whether transfer can occur when animals treat one pair of stimuli as similar to another. Secondly, in their other studies there was a consistent and striking asymmetry in the transfer found. Although pigeons learned a second discrimination, when it was matching, faster if their first discrimination had also been a matching problem, when the second task was oddity it did not matter whether the first was matching or oddity. Independent replication of their procedures confirms exactly this pattern of results as can be seen in the left-hand panel of figure 3 (Wilson *et al.* 1985*a*). It is only in the case of birds tested on matching, therefore, that there is any reason to postulate transfer of the relational rule. But there is also a reliable asymmetry to the way in which pigeons learn matching and oddity discriminations in the first place, which suggests an alternative explanation even of this apparent transfer. Pigeons have an initial preference for oddity, but may actually take longer to learn oddity to a high level of accuracy than to learn matching (Cumming & Berryman 1965; Wilson 1978). Because their initial preference is so often rewarded when they are trained on oddity, perhaps they learn less and perhaps this explains why they take so long to solve a second problem when it requires something more than responding in accordance with their natural preference. The suggestion is that prior training on oddity produces negative transfer when pigeons are subsequently trained on matching. The suggestion is supported by an experiment (Wilson *et al.* 1985*a*) in which pigeons were trained on a matching discrimination, having previously been trained either on matching or on oddity with a different pair of stimuli, or on a conditional discrimination whose solution did not involve any relation between sample and comparison stimuli (the problem was of the following form: there were two sample stimuli, A or B, and two different comparison stimuli, X and Y. The solution required birds to learn the quite arbitrary rule: if the sample is A, then X is rewarded; if the sample is B, then Y is rewarded). The performance of these three groups of pigeons on transfer to matching is shown in the right-hand panel of figure 3. It is clear that although birds previously trained on matching learned faster than those previously trained on oddity, they did not learn any faster than those trained on the conditional discrimination. If there is no difference between matching- and conditional-trained birds, the opportunity available to the former, but not to the latter, to learn the matching relation between sample and comparison stimuli cannot have benefited subsequent matching learning. The difference between matching- and oddity-trained birds must have been due to negative transfer from oddity rather than to positive transfer from matching.

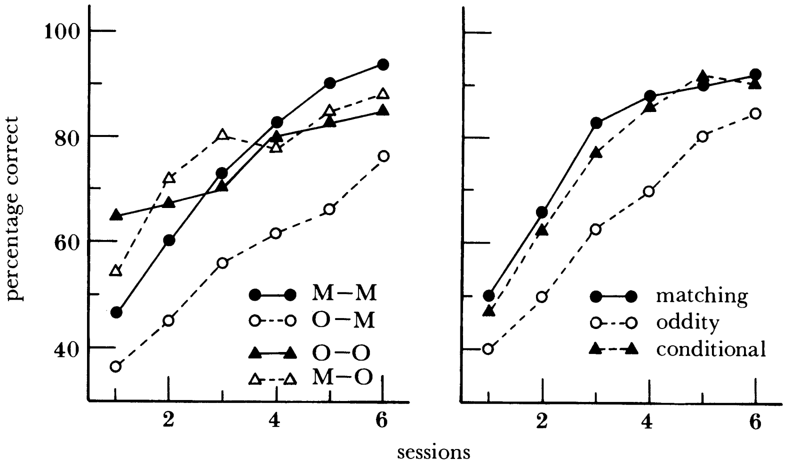

FIGURE 3. Transfer of matching and oddity learning by pigeons. The left panel shows the course of learning matching or oddity to red and yellow stimuli after prior training, on matching or oddity, to blue and green. Group M–M was trained on matching with both sets of stimuli, group O–M on oddity and then transferred to matching, while groups O–O and M–O were transferred to oddity after prior training on oddity or matching respectively. The right panel shows the course of learning matching to red and yellow stimuli after prior training on matching, oddity or conditional discriminations with different colours. Data from Wilson *et al.* (1985*a*).

There is thus remarkably little evidence for the transfer of matching in pigeons. There are two possible explanations: either pigeons do not, under the conditions of training used so far, solve matching and oddity discriminations in terms of the relation between sample and comparison stimuli; or, although they do learn this relationship, they do not transfer it across a change of stimuli. Three observations suggest that the second alternative is the more likely. First, it is hard to see how the asymmetry between matching and oddity problems alluded to above (for example, the initial preference for oddity) is to be explained without supposing that the pigeon detects the fact that the relation between sample and correct comparison stimulus differs in the two cases. Secondly, there is some evidence that pigeons may, under some circumstances, learn a matching discrimination faster than a non-relational conditional discrimination, suggesting that the presence of the relational cue may facilitate learning (Zentall *et al.* 1984). Thirdly, Zentall *et al.* (1981) have shown that whereas pigeons' performance on a well-trained matching task may be disrupted by changing the correct comparison stimulus, but not by changing the incorrect stimulus, performance on oddity is disrupted by changing the incorrect comparison stimulus, but not by changing the correct one. In each case, performance is disrupted only when the comparison stimulus that is the same as the sample is changed, and the implication must be that this relationship is used in the solution of these problems.

If this is accepted, then the pigeon's apparent failure to transfer matching or oddity to new sets of stimuli is a failure of transfer not of learning. They detect the relationship, but cannot apply it to new stimuli, and their poor performance is consistent with their poor performance on learning sets and the relative lack of transfer following serial reversal training. But how poor is their performance? Is there any reason to believe that any other animal would behave any differently? It is, in fact, well established that both primates and dolphins can solve generalized matching or oddity problems, where the stimuli change on every trial and only the relation between sample and comparison stimuli is available to predict reward (Mishkin *et al.* 1962; Herman & Gordon 1974). But the procedures of these experiments are so different from those used with pigeons that it is difficult to specify the cause of any apparent difference in outcome (see, however, D'Amato & Salmon 1984). What is needed is a comparison of the performance of pigeons and other birds, trained with exactly the same procedures, stimuli and apparatus.

Such a comparison reveals clear and striking differences between pigeons and corvids. Where the pigeons show at best only marginal signs of transfer, evident if at all only from differences in rate of learning, transfer in the corvids is relatively unambiguous and evidenced by significant deviations from chance on the first day of testing (Wilson *et al.* 1985*b*). In one experiment, pigeons and jackdaws were initially trained on either a matching or a non-relational conditional discrimination. Although the procedure was nominally identical for both species, the jackdaws took rather longer to learn these problems than the pigeons, showing for example an even more marked preference for the odd (incorrect) stimulus in the matching problem. In spite of this, when all birds were tested on a new matching problem with a different set of stimuli, it was only the jackdaws that provided evidence of differential transfer. The left panel of figure 4 shows the performance of the pigeons: although learning quite rapidly, the nature of their prior experience had no effect on their performance and both groups scored at chance on the first day. The jackdaws, however, although again learning matching slowly, were affected by their earlier training. Those that had previously learning matching scored above chance on the first day, while those trained on the conditional discrimination scored well below chance (indicating their natural preference for oddity) and the difference between the two groups was maintained for the remainder of the experiment.

To increase the chances that pigeons might show positive transfer, in a second experiment pigeons and European jays were trained on a series of three different matching (or oddity) discriminations, each with a new pair of colours, before a final test problem, where the stimuli were horizontal and vertical lines, on which they were trained either with the same conditions of reward (that is, matching if they had so far learned matching, and oddity if they had so far learned oddity) or reversed. The results, collapsed across matching and oddity, are shown

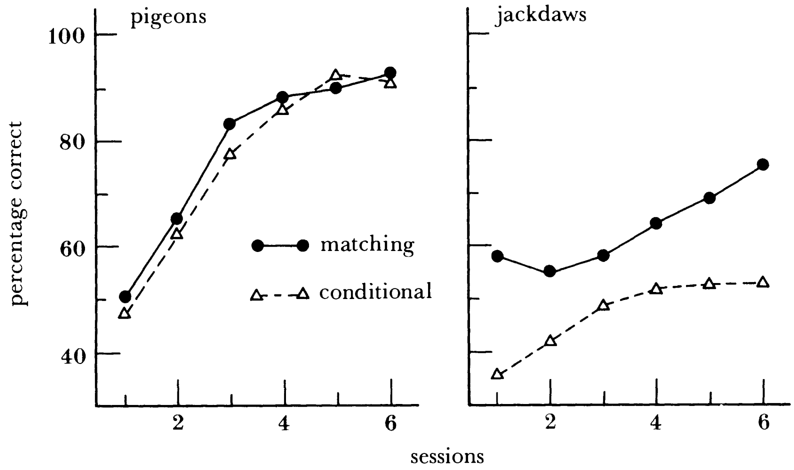

FIGURE 4. Transfer to matching after prior training on either matching or conditional discriminations with different stimuli in pigeons and jackdaws. Data for pigeons from Wilson *et al.* 1985*a* (as shown in figure 3); data for jackdaws from Wilson *et al.* (1985*b*).

in figure 5. Consider first performance on the three colour problems. Although there was no difference between pigeons and jays on the first discrimination, by the time they reached their third problem with the same rule, the jays were learning very much faster than the pigeons, and were performing well above chance on the first day of the problem. On the final problem, both pigeons and jays performed less accurately if they were shifted to the reverse conditions, but whereas this difference was reliable and persisted in jays, in the pigeons it was small, not significant, and was not maintained on subsequent days of testing.

A third experiment used a rather different paradigm for testing transfer across a change in

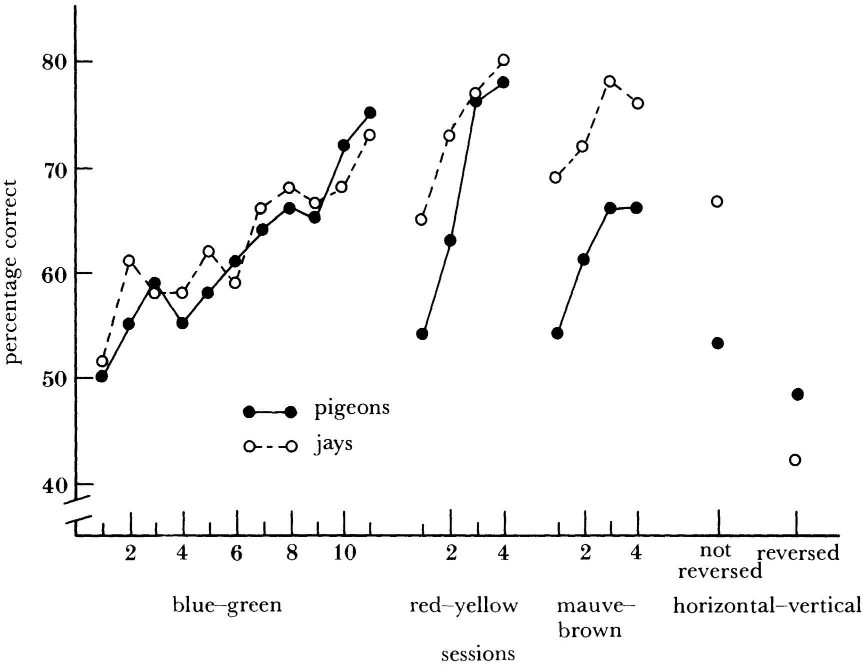

FIGURE 5. Course of learning three consecutive matching or oddity colour discriminations by pigeons and jays, together with transfer to a horizontal-vertical discrimination with reward assignments not reversed or reversed. Data from Wilson *et al.* (1985*b*).

stimuli. Pigeons and rooks were trained to choose between two illuminated panels. If they were the same colour (both blue or both mauve) then a response to the right-hand panel was rewarded; if they were different (one blue and one mauve), a response to the left-hand panel was rewarded. Once they had learned this discrimination (which proved very much harder than ordinary matching or oddity) they were transferred to a new pair of colours, red and yellow, either with the same or with the reversed rule. On the first day of this new problem, rooks scored well above chance (68% correct) if the rule stayed the same, and below chance (40%) if the rule was reversed. Pigeons scored exactly at chance (50%) in both conditions, and there was no reliable difference between reversed and non-reversed groups over ten sessions of training on the new problem.

The results of these experiments show some rather clear differences between the behaviour of pigeons and corvids trained under comparable conditions. It is always possible to insist that unsuspected differences in the impact of these training procedures on the two groups of birds were in fact responsible for these differences in behaviour. But there comes a point at which this argument starts to lose its force. We know of no plausible candidate for such a critical factor, and if recourse is always to be made to the possibility of such an effect, the position it seeks to defend will become irrefutable in principle, and hence vacuous.

What should be acknowledged, of course, is that these results do not, and could not, prove that pigeons are incapable of transferring a rule across a change in stimuli. There are occasional hints of such transfer in the published data, and it is always possible that other training procedures might succeed more clearly where those tried so far have failed. The history of comparative psychology is replete with categorical, but subsequently recanted, assertions about the limits to a particular animal's capacities. What the present results do suggest is that there is a real difference between pigeons and some other birds (and by extension, therefore, probably a difference between pigeons and, say, some primates) in the extent to which such rules are readily transferred.

5. Conclusions

Our conclusion is that it is possible to identify two processes, use of the outcome of one trial to predict the outcome of another, and transfer of this or other rules across a change in physical stimuli, both of which seem required, for example, for efficient learning-set performance, and neither of which is uniformly distributed among vertebrates. It is possible that differences in these processes may underlie some observed differences in learning-set performance. This is a fairly modest conclusion. We are not advancing a general account of the evolution of intelligence in vertebrates; and we have not even addressed the question why such differences might appear between the rather haphazardly selected animals under discussion. There is little point in considering such larger issues until we have done a great deal more to establish that there are any differences to talk about.

Finally, it is worth stressing that part of our conclusion was not about differences between animals at all, it concerned the identification of certain processes of learning and intelligence. The real interest of the comparison between pigeons and corvids, for example, is not to prove that pigeons are stupid, but rather to take advantage of the pigeon's apparent failure to transfer say, the matching rule to new stimuli, to establish the point that such transfer is not an automatic consequence of teaching an organism a matching discrimination. When transfer does occur, therefore, this is precisely something that demands explanation; it requires the postulation of a process or set of processes that probably lies outside the scope of our simple theories of conditioning or associative learning.

REFERENCES

Bloom, J. M. & Malone, P. 1968 Single alternation patterning without a trace for blame. *Psychon. Sci.* **11**, 335–336.

Clayton, K. N. 1962 The relative effects of forced reward and forced nonreward during widely spaced successive discrimination reversal. *J. comp. Physiol. Psychol.* **55**, 992–997.

Cumming, W. W. & Berryman, R. 1965 The complex discriminated operant: studies of matching-to-sample and related problems. In *Stimulus generalization* (ed. D. Mostofsky), pp. 284–330. Stanford: University Press.

D'Amato, M. R. & Salmon, D. P. 1984 Cognitive processes in cebus monkeys. In *Animal cognition* (ed. H. L. Roitblat, T. G. Bever & H. S. Terrace), pp. 149–168. Hillsdale, N. J.: Lawrence Erlbaum Associates.

Engelhardt, F., Woodard, W. T. & Bitterman, M. E. 1973 Discrimination reversal in the goldfish as a function of training conditions. *J. comp. Physiol. Psychol.* **85**, 144–150.

Harlow, H. F. 1949 The formation of learning sets. *Psychol. Rev.* **56**, 51–65.

Herman, L. M. & Gordon, J. A. 1974 Auditory delayed matching in the bottlenose dolphin. *J. exp. analyt. Behav.* **21**, 19–29.

Kamil, A. C., Jones, T. B., Pietrewicz, A. & Mauldin, J. E. 1977 Positive transfer from successive reversal training to learning set in blue jays. *J. comp. Physiol. Psychol.* **91**, 79–86.

Kamil, A. C., Lougee, M. & Shulman, R. J. 1973 Learning-set behaviour in the learning-set experienced bluejay. *J. comp. Physiol. Psychol.* **82**, 394–405.

Mackintosh, N. J. 1971 Reward and aftereffects of reward in the learning of goldfish. *J. comp. Physiol. Psychol.* **76**, 225–232.

Mackintosh, N. J. 1974 *The psychology of animal learning*. London: Academic Press.

Mackintosh, N. J. & Cauty, A. 1971 Spatial reversal learning in rats, pigeons and goldfish. *Psychon. Sci.* **22**, 281–282.

Mackintosh, N. J. & Holgate, V. 1969 Serial reversal training and nonreversal shift learning. *J. comp. Physiol. Psychol.* **67**, 89–93.

Macphail, E. M. 1982 *Brain and intelligence in vertebrates*. Oxford: University Press.

Mishkin, M., Prockop, E. S. & Rosvold, H. E. 1962 One-trial object-discrimination learning in monkeys with frontal lesions. *J. comp. Physiol. Psychol.* **55**, 178–181.

Passingham, R. W. 1982 *The human primate*. W. H. Freeman: San Francisco.

Schrier, A. M. 1966 Transfer by macaque monkeys between learning-set and repeated-reversal tasks. *Percept. mot. Skills* **23**, 787–792.

Schusterman, R. J. 1964 Successive discrimination-reversal training and multiple discrimination training in one-trial learning by chimpanzees. *J. comp. Physiol. Psychol.* **58**, 153–156.

Setterington, R. G. & Bishop, H. E. 1967 Habit reversal improvement in the fish. *Psychon. Sci.* **7**, 41–42.

Staddon, J. E. R. & Frank, J. 1974 Mechanisms of discrimination reversal. *Anim. Behav.* **22**, 808–828.

Warren, J. M. 1960*a* Supplementary report: effectiveness of food and nonfood signs in reversal learning by monkeys. *J. exp. Psychol.* **60**, 263–264.

Warren, J. M. 1960*b* Discrimination reversal learning by cats. *J. genet. Psychol.* **97**, 317–327.

Warren, J. M. 1965 Primate learning in comparative perspective. In *Behavior of nonhuman primates: modern research trends* (ed. A. M. Schrier, H. F. Harlow & F. Stollnitz), pp. 249–282. New York: Academic Press.

Warren, J. M. 1966 Reversal learning and the formation of learning sets by cats and rhesus monkeys. *J. comp. Physiol. Psychol.* **61**, 421–428.

Wilson, B. 1978 Complex learning in birds. Unpublished D.Phil. Thesis, University of Sussex.

Wilson, B., Mackintosh, N. J. & Boakes, R. A. 1985*a* Matching and oddity learning in the pigeon: transfer effects and the absence of relational learning. (In preparation.)

Wilson, B., Mackintosh, N. J. & Boakes, R. A. 1985*b* Transfer of relational rules in matching and oddity learning by pigeons and corvids. (In preparation.)

Zentall, T. R., Edwards, C. A., Moore, B. S. & Hogan, D. E. 1981 Identity: the basis for both matching and oddity learning in pigeons. *J. exp. Psychol: Anim. Behav. Proc.* **7**, 70–86.

Zentall, T. R. & Hogan, D. 1974 Abstract concept learning in the pigeon. *J. exp. Psychol.* **102**, 393–398.

Zentall, T. R. & Hogan, D. E. 1975 Concept learning in the pigeon: transfer to new matching and nonmatching stimuli. *Am. J. Psychol.* **88**, 233–244.

Zentall, T. R. & Hogan, D. E. 1978 Same/different concept learning in the pigeon: the effect of negative instances and prior adaptation to transfer stimuli. *J. exp. analyt. Behav.* **30**, 177–186.

Zentall, T. R., Hogan, D. E. & Edwards, C. A. 1984 Cognitive factors in conditional learning by pigeons. In *Animal cognition* (ed. H. L. Roitblat, T. G. Bever & H. S. Terrace), pp. 389–405. Hillsdale, N.J.: Lawrence Erlbaum Associates.

H. B. Barlow, F.R.S. (*University of Cambridge, U.K.*). My first question is, again, whether you think the learning tests you describe really test intelligence. If intelligence determines the knowledge and understanding an animal has of its normal environment (that is, the accuracy and completeness of its 'cognitive model'), would this have been tested in your experiments, or would your careful control of the conditions of your tests have more or less excluded the possibility of an animal using such background knowledge, acquired outside the learning situation?

My second question is methodological. For 40 years or so psychologists of sensation and perception have recognized that thresholds are statistical in nature and that when a human subject, or an animal, detects a weak signal he is often making remarkably efficient use of the information available. It is, furthermore, possible to express this efficiency quantitatively on an absolute scale (Rose 1944; Barlow 1980), and this makes possible valid comparisons between sensory performance at different tasks, between the performance of different species, and even between the performance of a single neuron and that of an intact whole animal.

Now learning is surely also a statistical task: some particular correlation, covariation, or association between two events has to be identified among all the possible such correlations, and this identification must be based on the statistical evidence the animal receives. It should be possible to apply the efficiency measure of statistical decision theory to this problem, and this would make comparisons across species and across tasks much more valid. Has this been done? I am aware that signal detection theory has been applied to measure the *sensory* capacities of animals, but has it been applied to their *learning* capacities?

To put the question another way, *rapid* learning is often equated with *better* learning, but this is not necessarily the case – the animal may be jumping to an incautious conclusion, just as a rash individual may achieve sensitivity by adopting a low criterion that leads to many false positive responses: have these considerations been taken into account by learning theorists?

References

Barlow, H. B. 1980 The absolute efficiency of perceptual decisions. *Phil. Trans. R. Soc. Lond.* B **290**, 71–82.
Rose, A. 1948 The sensitivity performance of the human eye on an absolute scale. *J. opt. Soc. Am.* **38**, 196–208.

N. J. Mackintosh. I suspect that there is no single process called 'intelligence'. Our argument was that one possibly important component of intelligence, and one that may differ between different animals, is the extent to which an animal can transfer an abstract rule across a change in physical stimuli. Our paradigm for studying this involves training animals on a task whose solution could be based on a general rule and testing them in a new situation to see how well they apply it. Although Professor Barlow is, I think, correct in suggesting that we try to control for or exclude the possibility of animals using knowledge acquired outside the learning situation, there is also a sense in which we are measuring precisely what he is asking us to. We are providing animals the opportunity to form a model of a particular environment, albeit an artificial one (that is, to learn that a particular rule describes what happens in it), and we are measuring the adequacy of that model to cope with a change in the environment. And our measures are certainly not equating rapid learning with better learning. Jackdaws, for example, learning matching discriminations very much more slowly than pigeons; and all corvids transferred to a new problem with a reversal of rule persisted in performing much less accurately than pigeons for hundreds of trials.

I do not know of attempts to apply signal detection theory specifically to learning capacities. The experimental paradigm which, as far as I can see, most clearly requires an animal to detect one imperfect correlation out of a variety of other correlations is 'probability learning'. An animal is trained on a discrimination between two alternatives, A and B, where choice of A is rewarded on, say 70% of trials and choice B on the remaining 30%. Even consistent choice of A will mean that only 70% of the animal's first choices are rewarded, while purely random choice, or consistent choice of, say, the left-hand alternative, regardless of whether it is A or B, will ensure that 50% of first choices are rewarded. The available evidence (Mackintosh 1974) suggests that pigeons are at least as efficient at this sort of task as rats, both animals eventually coming to select the most favourable alternative, A, on more than 90% of trials (the question of whether they learn at the same speed has not been addressed). The task could obviously be made more difficult by arranging that one stimulus predicted reward on 70% of trials, another on 65%, a third on 60% etc. It might be interesting to see whether this affected the outcome, but I know of no data that would answer this question.

Reference

Mackintosh, N. J. 1974 *The psychology of animal learning*. London: Academic Press.