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Vertebrate Intelligence: The Null Hypothesis [and Discussion]

E. M. Macphail and H. B. Barlow

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Vertebrate intelligence: the null hypothesis

BY E. M. MACPHAIL

Department of Psychology, University of York, Heslington, York YO1 5DD, U.K.

Human cognitive capacities have so evolved that man is able to solve an extensive range of problems having very different properties. Comparative psychologists have endeavoured to throw light on the evolution and nature of this general intellectual capacity by exploring performance of non-human vertebrates in a variety of learning tasks, in the expectation of demonstrating superior intelligence in species more closely related to man. It has, however, proved difficult to establish that any observed difference in performance is due to a difference in intellectual capacity rather than to a difference in such contextual variables as, for example, perception or motivation. Three hypotheses that might account for the lack of experimentally demonstrable differences in intelligence amongst non-humans are discussed. The first proposes that the data currently available may have been misinterpreted: that, for example, the potential role of contextual variables has been exaggerated. According to the second hypothesis, the questions posed by comparative psychologists have been inappropriate: learning mechanisms are adaptations evolved for life in a specific ecological niche, so that mechanisms available to species from different niches are not properly comparable. It is argued that neither of these two hypotheses receives convincing empirical support. A third hypothesis proposes that there are, in fact, neither quantitative nor qualitative differences among the intellects of non-human vertebrates. It is argued that this null hypothesis is currently to be preferred, and that man's intellectual superiority may be due solely to our possession of a species-specific language-acquisition device.

1. COMPARATIVE INVESTIGATIONS OF INTELLIGENCE

The human mind is capable of solving an essentially infinite variety of problems, problems that may be not only novel to the individual but novel also in the sense that they are problems of a type that have not been encountered until relatively recent times by any human being. The specific environmental pressures that shaped the development of the human intellect have, then, led to the evolution of a species of intelligence having very general application. Among the questions that psychologists with an interest in human intelligence seek to answer are, first, how did this general problem-solving capacity evolve, and second, what is the nature of this capacity? These two questions are not entirely independent: theories of the evolution of human intelligence must inevitably embody assumptions about its current nature and, similarly, evidence of the nature of the intellect at an earlier stage of development would carry implications for its nature at more advanced stages.

Since human beings can solve a far wider range of problems than any non-human species, humans are, in the sense in which I am using the word intelligent, more intelligent than non-human animals. It has also widely been supposed that differences in intelligence can be seen between non-human groups of animals, and that there is a ranking of species in intelligence, having humans at the highest point. Indeed some believe that there is good scientific support for this view. Jensen, for example, writes: 'in terms of measured learning and problem-solving capacities, the single-cell protozoans (for example, the amoeba) rank at the bottom of the scale, followed in order by the invertebrates, the lower vertebrates, the lower mammals, the primates, and man. The vertebrates have been studied most intensively and show fishes at the bottom of the capacity scale, followed by amphibians, reptiles, and birds. Then comes the mammals, with rodents at the bottom followed by the ungulates (cow, horse, pig, and elephant, in ascending order), then the carnivores (cats and dogs), and finally the primates, in order: new world monkeys, old world monkeys, the apes (gibbon, orangutan, gorilla, chimpanzee), and, at the pinnacle, humans' (Jensen 1980, p. 175). Now if such a ranking does exist (whether or not the ordering is that posited by Jensen), there is clearly an opportunity available to explore the evolution of intelligence: although no living species is an ancestor of man, some at least are, phylogenetically, close relatives, and it would not be unreasonable to hope to trace the evolution of the intellect by contrasting the intellectual capacities of species progressively less closely related to man. It seems inevitable that such an enquiry, if successful, would throw considerable light on the structure of the human intellect.

The widespread acceptance among non-specialists of the notion that some non-human animals (rhesus monkeys, say) are more intelligent than others (goldfish, for example) is, no doubt, based on relatively informal observations of their behaviour. For analytical studies, we turn to the work of those comparative psychologists who have attempted to deduce specific differences in intellectual function from controlled observation of performance of various species in problem-solving tasks. One broad distinction that may be made among their proposals for differences in intellect is that between qualitative and quantitative differences. By a qualitative difference between species is meant the possession by one species of a mechanism that is absent in another; *prima facie* evidence of a qualitative difference might be the observation that there was some task or set of tasks that could be solved by one species, but not by another. A quantitative difference between two species would mean that one species used a mechanism or mechanisms common to both species more efficiently than the other, and this might be reflected in a faster rate of solution or better asymptotic performance level by one species in some task solved by both.

The fact that the performance of two species in some learning task differs does not, of course, necessarily imply a difference in intelligence between the species. Before any such conclusion could be reached, plausible alternative accounts in terms of what Bitterman (for example, 1965) has called 'contextual variables' would have to be ruled out. It might, for example, be the case that the sensory or motor capacities of the species differed, or that the reward used was less effective in one species (perhaps due to a difference in motivation). It is clearly not possible to equate such variables across species, and Bitterman has recommended the use of the technique of systematic variation to rule out explanations in terms of contextual variables. This technique involves repeated tests of the species in a given task, using different levels of plausibly relevant variables: if one species, for example, mastered a food-rewarded task at any of a wide range of levels of food deprivation, and another failed at all levels, it might reasonably be assumed that the performance difference was not attributable to differences in deprivation.

What interspecies differences in intellect have, then, been proposed by comparative psychologists, and how well are these proposals supported by evidence? A survey of the literature on vertebrates (Macphail 1982) generated what were, to the author at least, somewhat unexpected answers to those questions. First, remarkably few specific proposals have been made concerning the nature of differences in intellect between vertebrate groups; second, none of the proposals applicable to vertebrates (excluding man) appears to enjoy convincing support. There have, of course, been many reports of differences between species in performance on a variety of learning tasks, and a number of these reports have indeed generated proposals for differences in intellect. My survey concluded, however, that in no case was it possible to rule out the possibility that the performance difference was due to effects of contextual variables. This may, at least in part, reflect the fact that despite the evident force of the argument for its use, the technique of systematic variation has rarely been used in practice, presumably because of its time-consuming nature.

If comparative psychology has failed to demonstrate the differences in intellect that were so confidently expected, the question that inevitably arises is, why have no differences been identified? This paper will consider three contrasting responses to that question.

2. THE ROLE OF CONTEXTUAL VARIABLES

One response to the question might, of course, simply be that my 1982 account misinterpreted the status of current proposals (or of some of them). It could be that the evidence in their support is stronger than was alleged, that some evidence was, perhaps, unreasonably dismissed, or that other evidence was overlooked entirely. Evidently it would not be possible fully to counter such possibilities without detailed discussion of individual issues. There is, however, one general objection to the approach adopted which may appropriately be discussed here. It might be argued that an exaggerated prominence was given to the role of contextual variables and that to adopt the position that any observed performance difference should be ascribed (unless proved otherwise) to differential effects of contextual variables, makes it systematically impossible that any performance difference would be interpreted as reflecting an intellectual difference. There is no finite catalogue of potentially relevant contextual variables: how, therefore, could their effects be conclusively ruled out?

As applied to proposals for qualitative differences, this objection has little force. Most such proposals have in fact been rejected because of the successful demonstration of some phenomenon in a species previously believed incapable of it. In many cases, it has been possible also to point to contextual variables critical to the appearance or not of a phenomenon in a species. For example, an extensive series of reports using various teleost species failed to observe any improvement (such as is seen in rats) in performance across a series of reversals of simultaneous discriminations, and this led Bitterman (1965) to propose that this task reflected a qualitative difference between the rat and the fish intellect. Many subsequent studies have, however, succeeded in showing significant serial reversal improvement in fish, and it is clear that one important factor favouring its appearance is proximity of choice and reward site (see, for example, Mackintosh & Cauty 1971; Engelhardt *et al.* 1973). In fact it appears (Macphail 1982) that there is currently no phenomenon of learning demonstrable in one (non-human) vertebrate species that has not been found in all other vertebrates in which it has been sought systematically: by which is meant, of course, sought in more than one or two isolated investigations. In other words, it is simply not the case that qualitative differences in performance have been 'explained away' by reference to contextual variables.

The argument is no more convincing when applied to the rejection of proposals for quantitative differences, proposals based on quantitative differences in learning rate or asymptotic performance levels. The principal difficulty with these proposals is that there is not, for any species, any unique or standard performance level in a given type of task. The performance of a species inevitably alters as contextual variables alter, and overlap between different species has been found at certain values of such variables in most of the tasks claimed to reflect quantitative differences; in the case of other tasks, it has been possible to point to some contextual variable known to affect performance in one species, and which has not been varied systematically for the other species concerned (Macphail 1982). Moreover, in some cases performance of some supposedly inefficient species has subsequently been observed at so high a level that no further appeal to contextual variables is necessary, there being, in effect, no difference to explain. Mackintosh, for example, has suggested (for example, Mackintosh 1970) that probability learning is a task in which pigeons perform less efficiently than rats, this inefficiency reflecting a lower stability of attention in birds than mammals. But Macphail & Reilly (1983) found that some pigeons achieved perfect performance (100% choice of the majority stimulus) in a conventional probability task in which the majority stimulus was rewarded on 70% of trials (the minority stimulus being rewarded on 30% of trials). The same birds achieved this optimal performance in both colour-relevant and position-relevant versions of the discrimination (so that in at least one version, a salient irrelevant stimulus may be assumed to have been present).

A further objection might also then be made to the dismissal of the many instances of species contrasts for which no evidence derived from the use of the technique of systematic variation is available. Given that that is the only decisive evidence, and that it is unavailable, it might be argued that it is equally valid to conclude that some given performance difference is due to an intellectual contrast as to some other contrast. But this argument is clearly unsound: there is ample evidence that contextual variables do affect performance levels within a species (and in an individual animal), so that parsimony clearly requires that differences should in the first place be ascribed to them rather than to intellectual differences of which, it is argued here, there is as yet no undisputed demonstration available. There will be an opportunity to judge a specific argument in which appeal is made to contextual variables in a later section of this paper, in which the maze-learning capacities of the pigeon are discussed.

3. Ecological considerations

A second response to the absence of demonstrations of interspecies intellectual differences might be that comparative psychologists have failed because they have made invalid theoretical assumptions in designing their experiments, so that those experiments have not been appropriate to the questions of central interest. Comparative psychologists have conducted laboratory experiments in the expectation of obtaining differences in performance from distantly related groups of animals. But each living species has evolved to cope with the specific demands of the type of environment, the ecological niche, that it occupies. Animals should be selected for comparison, not because they are distantly related, but because they occupy contrasting ecological niches; animals may be distantly related but have evolved, in parallel and independently, capacities that are adapted to some similar environmental demand. According to this view, general intelligence is a misleading concept: different problems in natural environments are solved by different, problem-specific, devices, and problems in artificial laboratory environments will be solved, if they are solved at all, by devices pressed into service in tasks that at best could only give a misleading view of the true capacities of an animal.

If most problems are solved by devices that are both species- (or niche-) and problem-specific, then it would clearly not be appropriate to compare intelligence across species, nor would it be sensible to attempt to trace the evolution of a general problem solving capacity (since none exists). It is therefore important to emphasize that the claim that problem solving is achieved by a number of specific devices is an empirical claim and not, for example, a necessary consequence of acceptance of the principle of evolution by natural selection. Many general process learning theorists (for example, Dickinson 1980) now incline to favour the view that association formation may properly be seen as a process of attributing causes to events. Since there are causal links between events in all environments, it is not at all unreasonable to expect that at least some learning mechanisms might be held in common by species from very different niches. Whether mechanisms of association formation might be all that are required for all non-human forms of problem solving is a large and important question, but not directly relevant to our interest in interspecies comparisons.

As a preliminary to discussion of the 'ecological' view, it should be pointed out that one difficulty is, of course, that it still does not explain why psychologists have failed to detect differences in capacity using their artificial tasks. Goldfish, pigeons, rats and monkeys appear, at least on the surface, to occupy very different niches: surely at least one of the tasks used should have engaged a very different device in one species from that used by some other: but the problem is that no such differences have been demonstrated.

Two specific predictions follow from the position under consideration. The first is that within one species, it should be possible to demonstrate that learning in one type of task proceeds in some way differently from that seen in some other types of task. The second prediction is that, by considering tasks that exploit specific differences in the environments of two species, it should be possible to demonstrate between-species differences in learning which can plausibly be attributed to differences in learning mechanisms.

(*a*) *Biological constraints*

The proposal that there should be within-species differences in learning according to the type of task encountered has been intensively investigated over recent years by psychologists interested in what have become known as 'biological constraints' on learning. Such constraints would, it was believed, undermine traditional general process theories, which had assumed an interchangeability of different categories of stimuli and reinforcers in the formulation of laws of learning. As examples of such proposed constraints, it may be constructive to consider two instances drawn from poison aversion learning. Garcia & Koelling (1966) found that rats showed better conditioning of internal (taste) stimuli as compared to external (auditory and visual) stimuli when illness was the reinforcer, but the opposite relationship when shock was the reinforcer. This experiment seemed to indicate that learning about audiovisual stimuli and taste stimuli depended on the motivational system engaged, and that such stimuli were not simply interchangeable as traditionally believed. Learning about poisoned food also appeared to be distinguished from other types of learning in that learning could occur even when long delays intervened between the taste stimulus and the induction of illness (for example, Garcia *et al.* 1966). These and other examples of biological constraints have attracted many investigators, and the resulting research has made substantial contributions to learning theory. As an excellent recent review (Domjan 1983) makes clear, however, research on biological constraints has not forced psychologists to abandon general process theories. Rather, proposals have been made for the accommodation of the findings within general process theories, and new experiments have been conducted, finding parallel results in tasks other than, say, poison-aversion learning. It has been proposed (for example, Testa & Ternes 1977) that one factor favouring the selective association of taste cues with poisoning might be similarity (in, for example, temporal pattern) between the conditional and the unconditional stimulus (c.s. and uc.s.). As indirect support for this view, there is now good evidence that similarity of c.s. and uc.s. does facilitate conditioning in tasks not involving poison aversion (for example, Testa 1975; Rescorla & Furrow 1977). Similarly, it has been suggested that long-delay learning in poison avoidance studies may occur because taste stimuli encounter few potentially interfering stimuli in the time intervening before uc.s. arrival (Revusky 1971). This proposal led to food-reinforced maze learning studies in which procedures were introduced to minimize intradelay sources of interference, and learning was indeed demonstrated despite delays of up to 1 h between choices and rewards (Lett 1975). Now it is far from proved that those two factors (c.s.–uc.s. similarity and interference-reduction) provide complete (or even partial) explanations of either selective association formation or long-delay learning in the poison-aversion paradigm. On the other hand, it is equally unclear (Domjan 1983) that there remain any examples of biological constraints that cannot be accommodated within general-process theory. Rather than posit special learning subsystems for each behavioural category, it would seem parsimonious at present to assume the reality of general processes of learning, applicable across many tasks.

Before leaving this topic, it should be added that discussion of it has been brief, partly because reports of 'biological constraints', while suggesting that there might be unexpected specificities between cues and reinforcers, did not in any case necessarily threaten the notion of general intelligence. It might well be the case that there exist some reinforcer-specific adaptations, knowledge of which would be a necessary adjunct to any general process theory, so that certain limitations to that theory's applicability could be understood. It would then be necessary to compile a catalogue of such constraints, but sensible, nevertheless, to continue the attempt to formulate a general theory. So that, while it is argued here that there is as yet no convincing demonstration of a selectivity in association formation which is not the consequence of a general principle applicable to all reinforcers, such a demonstration would not necessarily discredit the attempt to compare intelligence across species.

(*b*) *Optimal foraging strategies*

A further proposed type of reinforcer-specificity may pose a more systematic threat to general process theory since it suggests that different types of reinforcer engage different behavioural problem solving strategies. The proposal in question derives from optimal foraging theory. That theory proposes that the foraging behaviour of animal species has evolved so as to optimize the ratio of energy intake to energy expenditure, and generates predictions about, for example, prey or food type selection, and search patterns both between and within localities. Consideration of this theory inevitably invites speculation on the nature of the mechanisms that might be used in achieving optimal performance. For search patterns, two clear possibilities emerge. On the one hand, a species may assess the probability of food (for example) being in one place rather than another by using general mechanisms, used in the assessment of probabilities of co-occurrence of stimuli, responses and events of all kinds. On the other hand, individual species may have evolved foraging stragegies adapted to the specific type of distribution of the different resources within their niches, a particular strategy being engaged when foraging for one type of resource (for example, food) but not for another (for example, water) which might have a quite different distribution. This latter possibility would have important implications for the majority of investigations of intelligence carried out by comparative psychologists. For results of studies of problem solving motivated by food reward would be largely irrelevant to problem solving motivated by water reward, and so would not throw light on mechanisms of general intelligence (supposing that such mechanisms indeed exist independent of resource-specific strategies).

If there are foraging-specific learning mechanisms, then it should be possible to find species whose distribution of some natural resource differs systematically, and to show differences in their foraging behaviour related to the difference in resource distribution. Moreover it seems likely that such differences should be detectable in laboratory-based experiments as well as in natural environments. Given that animals do solve problems in artificial environments, it seems plausible that, if specific learning mechanisms are involved, then food-rewarded problems would be solved by engaging mechanisms adapted to foraging for food. Not only is it plausible, there is indeed evidence (for example, Lea 1979) that the pattern of both successful and unsuccessful predictions derived from optimal foraging theory found in natural environments is duplicated in laboratory tests.

The radial maze provides, according to some workers, an example of a task in which the performance of different species may reflect differences in foraging behaviour, evolved for contrasting types of food distribution. The radial maze consists of a set of arms (usually eight), each of which has a goal box at its end, radiating from a central platform. Each goal box contains a small, limited amount of food so that a food-deprived animal, starting from the central platform, optimizes its intake : effort ratio by entering each of the eight arms (and consuming the food in its goal box) once only in a series of eight choices. Olton & Samuelson (1976) found that rats performed with remarkable efficiency in the radial maze, averaging more than seven choices of different arms in a series of eight choices. Olton has since suggested (for example, Olton & Schlosberg 1978) that one factor contributing to the rats' success is their tendency, having found food in one place, to avoid that place. This tendency may be innate, since it is seen in young (immediately post-weaning) rats (Olton & Schlosberg 1978). A number of authors have followed Olton's suggestion that the 'win-shift' strategy is a foraging-specific adaptation, to be anticipated in animals whose 'food sources are dispersed or require time to be replenished so that obtaining some food in one area decreases the likelihood of finding additional food there' (Olton & Schlosberg 1978, p. 809).

Bond *et al.* (1981) compared the performance of rats and pigeons in a conventional eight-arm radial maze, using food reward. On the assumption that the natural food resources of the pigeon tend to be 'concentrated and dependable', in contrast to the 'diffusely distributed, irregularly available, and readily depleted' (p. 575) resources of the rat, Bond *et al.* predicted that pigeons would show poor 'spatial event memory', this latter prediction reflecting the notion that pigeons need only remember where food is normally available, not the series of places from which food has recently been obtained. However remarkable it may have been to suppose that homing pigeons, legendary navigators, should show poor spatial event memory, the results were in agreement with their predictions: pigeons made significantly more errors (re-selection of arms already visited) than rats. There is, however, good cause to doubt both the proposal that the difference observed reflects a difference in cognitive capacity and the explanation given for the difference.

The first response to the finding of Bond *et al.* is to ask whether the difference in performance might not have been due to contextual variables, rather than to intellectual differences. Mizumori *et al.* (1982), for example, reported a failure by mice to show spatial memory in a radial maze. The dimensions of the maze were smaller than those normally used, but juvenile rats tested in the identical maze showed efficient spatial memory. It might have been supposed, therefore, that the spatial memory of mice was inferior to that of rats. A recent report by Pico & Davis (1984) suggests, however, that despite the superficial comparability of the rat and mouse visual systems, the species difference in performance was largely due to perceptual factors: mice showed good spatial memory when the arms of the maze were made visually more discriminable. There is evidence also that the performance of rats in eight-arm radial mazes may differ significantly according to physical properties of the maze (for example, Markowska *et al.* 1983). There may, therefore, have been some property of the maze used by Bond *et al.* that made it less well adapted to pigeons than rats. Indeed, some support for this proposal is provided by the observation by Bond *et al.* that the pigeons showed little spontaneous exploration of their maze, so that on occasion the experimenters had to drive pigeons from an explored arm back to the central choice area.

Grounds for supposing that pigeons may be capable of better performance than that reported by Bond *et al.* are provided by a study by Wilkie *et al.* (1981), which used ring doves (*Streptopelia risoria*), birds that are closely related to pigeons (both species belong to the same order, Columbiformes) and that rely on similar food resources. The birds were tested in a 14-arm maze, which consisted of two banks of seven tubes, one above the other, radiating out from a central well. There was a perch at the entrance of each arm, and the doves flew from perch to perch, or from perch to floor or perch. Four birds were allowed to make 14 choices each day, and at asymptote the mean number of correct choices was approximately 11. There was considerable variation from day to day, and from bird to bird, one dove showing 13 correct choices (out of 14) on six of the final 20 sessions of testing. That same bird showed, over those final 20 sessions, no errors over the first six choices of each session, and this contrasts with the sharp fall in accuracy seen on the pigeons' sixth choices (a mean of approximately 60% correct) in the Bond *et al.* report. Wilkie & Summers (1982) note that the doves in the apparatus used by Wilkie *et al.* did not, unlike the pigeons of the Bond *et al.* study, show marked tendencies to visit adjacent arms, and suggest that this may have contributed to their superior performance. We may therefore note that ring-doves are capable of remarkably accurate performance in a 14-arm radial maze and reserve judgement on the question whether their relatives, the pigeons, which appear to face similar foraging demands, might not also possess a capacity superior to that suggested by the Bond *et al.* report. It appears unlikely, to say the least, that a real difference in radial maze capacity between the species could in any case be accounted for in terms of contrasts in distribution of food resources.

A further issue of relevance here is whether pigeons, as might be expected from the 'resource-distribution hypothesis' (Bond *et al.* 1981), in fact show a preference for win-stay as opposed to win-shift strategies in food-rewarded tasks. A clear answer to this question has been provided by Olson & Maki (1983), who explored pigeons' delayed alternation performance in a T-maze. Each trial consisted, first, of a rewarded forced choice to one or other goal box, followed, after a delay, by a free choice in which only the box not entered on the forced choice contained food. The pigeons rapidly mastered this 'win-shift', task, and also performed accurately despite long delays (up to 16 min) between the forced and the free choice. This latter finding indicates that, just as the 'spatial event' memory of the ring dove enjoys a large capacity in terms of the number of items that may be retained, the spatial event memory of the pigeon enjoys impressive capacity in terms of the duration for which information may be retained. Olson & Maki went on to test birds in a 'win-stay' version of the same task, in which the goal box rewarded in the free choice was the same as that entered in the forced choice; the pigeons performed very poorly in this task, averaging fewer than 50% correct choices throughout the period of testing, and this was true whether or not the goal-box food in the forced choice was wholly or only partly consumed by the pigeon. It appears that pigeons, like rats, have a strong tendency to adopt win-shift as opposed to win-stay strategies in certain food-rewarded tasks.

There is evidence (Roitblat *et al.* 1982) that Siamese fighting fish (*Betta splendens*) also have a predisposition to adopt win-shift, as opposed to win-stay strategies, and the evidently widespread occurrence of the strategy in vertebrates clearly raises doubts concerning the resource-distribution account of its origin. Gaffan & Davies (1981, 1982) go further, and argue that the label 'win-shift' is misleading, since it is not, it appears, reward that induces shifting in rats: rats, having explored one place tend to explore an alternative location, whether or not reward has been obtained. Gaffan & Davies (1982) show, moreover, that this tendency simply to shift from a location is in fact weakened by the obtaining of a reward in that place. It seems that we are seeing the operation of a tendency spontaneously to shift, which may reflect some information-gathering exploratory tendency. Such tendencies are seen not only with respect to places, but to other stimuli also: monkeys, for example, having been shown a novel object, show a strong preference, when that object is subsequently re-presented along with a new object, to select the new object, whether or not the original presentation had been rewarded (for example, Mishkin *et al.* 1962). The tendency to shift is not so strong, at least in rats, as to be ubiquitous: rats do not, for example, show spontaneous alternation in jumping stands, or in mazes in which they have to jump a gap to move from arm to arm (Jackson 1941). The tendency need not prevent the development of highly efficient win-stay performance: monkeys performing learning set tasks, despite an initial tendency to show 'win-shift' behaviour, do, as is well known, become highly proficient performers in that task, which, of course, requires adoption of a win-stay, lose-shift strategy with respect to objects.

We have considered cases in which different species have been contrasted according to differences in the distribution of their food supplies. Equally relevant is the search for contrasts within a species between behaviours motivated by types of reward having different 'natural' distributions. A number of authors have, for example, suggested that water is a resource that should, at least in the case of rats, be more dependably found repeatedly in the same place than food. Perhaps the earliest claim to have detected differences in learning that might reflect such a difference was made by Petrinovich & Bolles (1954), who reported that hungry rats rewarded for alternating choices in a T-maze performed more efficiently than thirsty rats in the same task, and suggested that the 'stereotypy' of thirst-motivated behaviour reflected the dependability of water resources. A subsequent report (Bolles & Petrinovich 1956) came, however, to a very different conclusion. The deprivation techniques used in the original report had resulted in loss of mass over the course of the experiment by the hungry rats, but in a gain in mass by the thirsty rats. The second study introduced deprivation techniques which allowed thirsty rats to lose mass, and hungry rats to gain mass, and showed that, irrespective of the type of motivation, rats that lost mass showed efficient alternation performance, while those that gained mass did not.

Subsequent experiments have also failed to find any weaker a tendency in thirsty than in hungry rats to adopt 'win-shift' strategies. Kraemer *et al.* (1983) found excellent performance in a radial maze by thirsty rats, and these authors describe an (unpublished) study by R. H. I. Dale and W. A. Roberts, in which rats were run in a radial maze either hungry or thirsty, and at either 100% or 85% of their *ad libitum* feeding masses. At both levels of body mass, the thirsty rats performed more accurately than the hungry rats. Kraemer *et al.* conclude: 'thus, the suspicion that accurate choice performance in the radial maze is dependent upon general behavioural characteristics associated with food foraging may not be entirely accurate' (p. 380). We can only agree: just as there does not seem to be evidence available to show that different species solve problems in which a common type of reinforcer is used in different ways, those ways reflecting contrasts in the distribution of that reinforcer type, there is, similarly, no evidence that a given species solves problems in which different reinforcers are used by engaging different mechanisms of learning.

4. The null hypothesis

The preceding sections have argued that the appeal to contextual variables as the preferred explanation of species differences in performance on learning tasks is justifiable, that there is as yet no convincing demonstration of a species-specific biological constraint on the associability of particular stimuli or reinforcers, and that species-specific foraging strategies do not appear to determine the course of learning in laboratory-based learning tasks. Discussion of those topics was motivated by their being sources of possible objection to the rationale and methodology of comparative psychologists' investigations of intelligence. If those objections are to be rejected, attention must return to the search for an explanation of the lack of demonstrations of differences in intelligence among vertebrate species.

The position advocated here is based on the proposition that the null hypothesis tested in comparative investigations of any behavioural trait must be that there are no differences among species in that trait. In the absence of experimental proof of any difference the scientist's conclusion should therefore be that there are no differences. In the present case we should, then, conclude that there are no differences, either qualitative or quantitative, among vertebrates (excluding man). In common with all scientific hypotheses this null hypotheses cannot be proved, only disproved; support for the hypothesis will grow as the number of failures to disprove it increases, and to the extent that those failures represent convincing disproofs of specific alternative hypotheses. There is, however, one interesting corollary of the hypothesis that merits particular attention, and that is, that the intellectual demands of any task that is solved by one (non-human) vertebrate may be met by any other vertebrate. So, all the intellectual achievements of chimpanzees should be, contextual variables apart, within the compass of other vertebrates, including, of course, non-mammals. One difficulty with this proposal is that many of the most impressive achievements of the chimpanzee have involved the use of its limbs, and this poses for comparative psychologists the challenge of devising for vertebrates without comparable limbs, tasks whose formal intellectual demands parallel those made in the tasks mastered by chimpanzees. Two recent examples of the use of such tasks, both involving avian subjects, will be discussed here.

The first is taken from a series of studies by Epstein and his colleagues (known as the Columban Simulation Project), each of which attempts to demonstrate in pigeons performance formally comparable to that seen in chimpanzees or other 'higher' vertebrates, performance widely assumed to reflect the superior intellectual capacity of those species. The experiment to be described is an investigation of 'insight' and was modelled on the famous report of Kohler (1925), which has been cited widely as a demonstration of the superior intellect of chimpanzees. In Kohler's original report, a banana was suspended from the ceiling of a room out of reach of a group of six chimpanzees. A wooden crate was available in the room, some distance from the banana. After vain efforts to leap for the banana, and after much pacing up and down, one of the chimpanzees, Sultan, suddenly moved the crate beneath the banana, climbed on it, and now successfully leaped to seize the banana. The novelty and abruptness of the solution convinced Kohler that a process of insight in the chimpanzee had been demonstrated.

Birch (1945) has shown that other apparently insightful solutions are not obtained from chimpanzees without previous manipulatory experience of the objects involved in the solution, and it is reasonable to suppose that Kohler's chimpanzees had indeed previously both moved and stood on boxes. Epstein *et al.* (1984) therefore carried out an experiment, the first phase of which involved training pigeons to move and to stand on, a small cardboard box. In some sessions, the pigeons were trained to move a cardboard box towards a green spot placed at some point at the foot of one of the walls of the apparatus (pushes in the appropriate direction being rewarded with food). In other sessions, pigeons were trained to peck a small toy banana suspended from the ceiling of the apparatus; the banana could be reached by standing on the cardboard box, now placed (by the experimenters) directly beneath it. The box and banana were in different locations in different sessions, there was no green spot, and pushing the box was not rewarded; flying up to peck the banana was also not rewarded, and so extinguished. These two habits, directional pushing, and standing on the box, were established after considerable training, and then a test session was carried out, in which the banana was suspended from the ceiling, the box was present in the chamber at some distance from the banana, and no green spot was presented. The pigeons behaved in essentially the same way as Sultan: they showed initial vain efforts to stretch up to reach the banana, restless pacing, and then 'each subject began rather suddenly to push the box in what was clearly the direction of the banana.... Each subject stopped pushing in the appropriate place, climbed, and pecked the banana' (Epstein *et al.* 1984, p. 61).

We are not concerned here to discuss the nature of the solutions of such problems, whether insight, for example, is a necessary or a useful concept, the key point of interest is the parallel between the chimpanzee and the pigeon performance. There is clearly every reason to suppose that the pigeons solved the problem in exactly the same way as the chimpanzee.

From one of the earliest examples of the supposed intellectual pre-eminence of apes, we may turn to a contemporary example, the series of experiments (for example, Gardner & Gardner 1969; Patterson 1978; Terrace *et al.* 1979) on teaching sign language to apes. Early attempts to teach chimpanzees to speak (for example, Hayes 1961; Kellogg 1968) found rather poor language acquisition, with production of very few words by the subjects. There are, however, reasons for supposing that the physical characteristics of the chimpanzee vocal tract render it incapable of producing the whole range of sounds used in human speech. Recent experiments have, therefore, attempted to teach language without involving speech, by using either American Sign Language, designed for the use of deaf humans (see, for example, Gardner & Gardner 1969; Patterson 1978) or wholly artificial languages (see Premack 1971). These investigators have been markedly more successful than the original speech-based studies, and have, for example, reported successful acquisition of vocabularies of more than 100 words (see Patterson 1978). Now if all vertebrates are capable of comparable intellectual attainment, it should be possible to carry out language-acquisition experiments by using species other than apes, with a comparable degree of success. Birds are clearly not suitable subjects for experiments on sign-language acquisition, but, equally clearly, in birds capable of imitating human speech we have subjects eminently suitable (as apes are not) for speech-based language-acquisition work. The question then is, are birds such as parrots or mynah birds capable of a comparable degree of language acquisition by using speech as are apes, who use sign language?

Mowrer (1950) attempted to train a number of birds of different species (including parrots, a mynah bird and parakeets) to talk, but his training procedures were not particularly systematic, and do not appear likely to have endowed sounds with meaning. Mowrer began by following the utterance (by the experimenter) of a given word with food; when this procedure succeeded in obtaining production of the same word by the bird, the bird was rewarded, again with food. In essence, the birds were taught to imitate sounds produced by their trainers, those sounds having no referent for the birds (except, perhaps, food). Mowrer did succeed in eliciting some words from his birds, but his results were unimpressive, and the method used allows little confidence in Mowrer's claim that birds seem wholly incapable of sentence-formation.

Recent results of an investigation with an African grey parrot (*Psittacus erithacus*) have been more encouraging (Pepperberg 1981, 1983). The parrot (Alex) has been trained by using a technique whereby he is shown an object of interest to him (not a food object) which he is given only if he produces its name; its name he learns originally from dialogue between two trainers. Although Alex has as yet a relatively small vocabulary, consisting of five colour adjectives, four phrases describing shape, and nine nouns, he can combine them appropriately to refer to more than 50 different objects (Pepperberg 1983). There is evidence also that Alex has not learned simply what sound or series of sounds is associated with what object. Alex can respond appropriately to the questions: 'what colour?' and 'what shape?', shown an object for which he has names for both its colour and shape (Pepperberg 1983). This is true for novel objects, and provides evidence for the possession by the parrot of relatively abstract concepts.

Pepperberg's parrot has not yet equalled the achievements of the various apes trained in sign language: his vocabulary, for example, is much smaller than those of the apes. But as the single avian subject yet exposed to an appropriate training schedule, he gives good support to the view that the parrot's talent for language acquisition may not be significantly different from the ape's.

5. Human intelligence

Introduction of experiments on language acquisition in birds and apes leads finally to a brief discussion of the issue which is, perhaps, of the most general significance, namely, the status of human intelligence. While it has been argued here that there are no differences among the intellects of non-human vertebrates, it was acknowledged that humans outstrip other vertebrates in problem-solving capacity. I have argued elsewhere (Macphail 1982) that this capacity cannot be divorced experimentally from the capacity for language, and that the essence of the problem is this: do humans acquire language because they are more intelligent than non-humans, or are humans more intelligent than non-humans because they do acquire language? Of direct relevance to this question is work on language acquisition in non-humans: if non-humans can acquire language, albeit less efficiently than humans, then perhaps the safest conclusion would be that humans acquire language more efficiently because they are (quantitatively) more intelligent. A review of relevant studies (Macphail 1982) concluded, first, that sentence production was the essential characteristic of human language, and, second, that apes do not produce sentences. The most economical account of the data appears, therefore, to be that humans possess a species-specific language-acquisition device, and that it is this qualitative difference alone that distinguishes their intelligence from that of non-human vertebrates.

Scientific hypotheses are commonly, and rightly, judged by two standards, those of parsimony and plausibility. The position outlined above has been argued throughout in terms of parsimony, and it may be thought that its principal weakness is found when it is judged by the criterion of plausibility. It seems likely that the plausibility of these notions as applied to non-humans will grow as demonstrations accrue of hitherto unsuspected capacities in non-mammals (the experiments of Epstein and Pepperberg serve as examples).

There are, however, consequences of this parsimonious account of human intelligence that may be more difficult to accept. For example, humans without language would, according to this view, be no more intelligent than non-human vertebrates. In other words, an otherwise normal human not exposed to language and not educated in a language-using society would be no more intelligent than a chimpanzee (and so, no more intelligent than a goldfish). This may seem extreme, but does invite interesting questions. What problems could the language-deprived human solve that the chimpanzee could not? How would a human intellect locked within a goldfish's body demonstrate its powers? Reflection on these questions may suggest novel ways of seeking to reject the null hypothesis as applied to non-humans, and efforts to reject that hypothesis, whether or not they succeed, are surely the best way to expose the nature of animal intelligence.

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Discussion

H. B. Barlow, F.R.S. (*University of Cambridge, U.K.*). There is another hypothesis that has already been alluded to by the previous speakers, and I would like to ask whether you think it has been excluded by the comparative learning studies you have reviewed. The hypothesis is that intelligence varies greatly between species, but is concerned primarily with the formation of a working model of the normal environment that an animal lives in. Do the learning tests you review exclude the possibility that the accuracy and completeness of this model varies greatly between species? And if the answer is 'no', might it not be a more fruitful hypothesis than your third – null – hypothesis?

Let me point out that if intelligence depends upon the accuracy and completeness of the cognitive model, this does not reduce the importance of language for intelligence, but rather offers an explanation for why it is so important: language makes it possible to share and spread the model among many members of a community, and (especially for written language) it allows this model to persist in time and to be successively improved. As Jerison said, a human utterance can communicate part of the speaker's model.

On this view, your null hypothesis may possibly hold for learning ability as tested by experimental psychologists, but does not hold for intelligence.

E. M. Macphail. Although it is difficult to see how differences in cognitive models might be measured, there can be no doubt that animals of different species do form very different models of their environments, and no doubt that these models play a role in the general adaptability of animals. But an important factor in the formation of such models must be the quality of sensory information available, and there is equally no doubt that sensory capacities vary widely. Unless it can be demonstrated that species differences in cognitive models are not a consequence of differences in sensory capacities, I see no need to accept the argument that differences in models reflect (or constitute) differences in intelligence. To put the case in a somewhat crude way: the environmental models formed by the blind must be very different from those formed by sighted individuals, and the range of problems soluble by a blind man is indeed much restricted compared with the range soluble by sighted humans, but we would not wish to argue in consequence that the blind are less intelligent than those with sight.