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The comparative psychology of intelligence

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Abstract: Recent decades have seen a number of influential attacks on the comparative psychology of learning and intelligence. Two specific charges have been that the use of distantly related species has prevented us from making valid evolutionary inferences and that learning mechanisms are species-specific adaptations to ecological niches and hence not properly comparable between species. It is argued here that work using distantly related species may yield valuable insights into the structure of intelligence and that the question of whether or not learning mechanisms are niche-specific is one which can only be answered by comparative work in "nonnatural" situations. The problems involved in defining and assessing intelligence are discussed. Experimental work has not succeeded in demonstrating differences in intellect among nonhuman vertebrates. Hence the null hypothesis – that there *are* no differences in intellect among nonhuman vertebrates – should be adopted; the superiority of human intelligence stems from our possessing a species-specific language-acquisition device. One implication of the null hypothesis is that general problem-solving capacity is independent of niche-specific adaptations. A second implication is that problem-solving may involve relatively simple mechanisms; association formation in particular may play a central role in nonhuman intelligence, allowing the successful detection of causal links between events. Causality is a constraint common to all ecological niches.

Keywords: anagenesis; association formation; biological constraints; comparative psychology; ecology; intelligence; language-acquisition device; learning, optimal foraging theory; species differences

1. Contemporary criticisms of comparative psychology

Charles Darwin provided the original impetus for the discipline of comparative psychology, since his theory of evolution made it clear that a degree of continuity should be expected between the mental life of animals (nonhuman animals, that is) and man. One area in which evidence for this continuity was sought by the early psychologists was that of intelligence. It was – as it still is – generally accepted that man is the most intelligent of organisms, and it was as widely believed that some of the different stages through which man's intellect had passed in the course of its evolution could be seen manifested in animals. The early decades of this century saw a rapid growth in the number of studies of learning in animals, and a growth also in the academic prestige of animal learning as an area of investigation (Boakes 1984).

The last three or four decades have seen a sharp decline in the standing of comparative psychology, a decline marked by the publication of a number of influential articles which have been highly critical of the field. The first of these (Beach 1950) documented two facts: (1) Although there had been a rise in the number of papers reporting studies using animals as subjects, there had in fact been a marked drop in the range of species used, so that the albino rat had become the dominant subject, and (2) the interests of comparative psychologists appeared to have narrowed sharply, resulting in a concentration on learning and conditioning at the expense of the study of "unlearned" behavior.

Although Beach noted that there were certain advantages to be gained by concentrating on one species, he argued that no sensible comparative psychology would emerge from comparisons between only two species, rat and man. This particular objection can be taken further. The great majority of the reports of studies using rats contained (then as now) no explicit comparisons of their performance with that of any other species, including man; such studies hardly warrant the term "comparative." It would seem better to restrict that term to work in which there is a clear attempt to compare and contrast the performance of subjects from two or more species, and to adopt Hodos and Campbell's (1969) suggestion that studies confined to the analysis of one (nonhuman) species should be classified as simply "animal psychology."

The years following the publication of Beach's paper saw a steady increase in interest in ethology – reflecting a shift from the concentration on learning as a topic – and at least some increase in the number of papers in which attempts were made to compare different species. The most influential of these comparative studies were conducted by Bitterman, Gonzalez, and their colleagues, whose subjects included goldfish, turtles, pigeons, rats, and monkeys. These studies became the target of yet another critical review, however (Hodos & Campbell 1969).

Bitterman (e.g., 1965a) reported two contrasting modes of performance in each of two experimental paradigms (serial reversal learning and probability learning), and characterized the performance of all the species used in those problems as either "ratlike" or "fishlike." There

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were both spatial and visual versions of the tasks, and Bitterman noted that whereas ratlike behavior was found in spatial problems in monkeys, rats, pigeons, and turtles, fishlike behavior was seen in visual problems in turtles and (in probability learning) in pigeons. "As we ascend the phyletic scale," Bitterman concluded, "new modes of adjustment appear earlier in spatial than in visual contexts." (Bitterman 1965a, p. 408).

Hodos and Campbell (1969) objected forcefully to statements that emanated from a number of contemporary comparative psychologists. The principal focus of these objections was based on their respective authors' apparent assumption that there was a phylogenetic scale along which living animals could properly be arranged. Hodos and Campbell pointed out that the notion of such a scale is a relic of the *Scala naturae*, introduced into Western thought by Aristotle and not finally abandoned until the acceptance of Darwinism. The notion of a phylogenetic scale has been replaced by that of the phylogenetic tree; living species are at the tips of the branches of the tree, and no living species is considered as higher or lower than any other. There is, then, no scale to ascend, and rats are not (phylogenetically) higher animals than goldfish.

Hodos and Campbell went on to argue that contrasts between the behavior of distantly related species, such as those selected by Bitterman, "do not permit generalizations to be made about the evolution of intelligence or any other characteristic of these organisms since they are not representative of a common evolutionary lineage." (Hodos & Campbell 1969, p. 345). In fact, according to Hodos and Campbell, the absence of a firm grasp of evolutionary theory resulted in there being, in 1969, *no* theory in comparative psychology.

It is clear that Hodos and Campbell's criticisms were justified. For example, any series of reports on the performance of subjects of one species from each of, say, four of the extant vertebrate classes could not conceivably pretend to track the evolution of the behavior concerned. However, it is not entirely clear that there was no theory underpinning the work of comparative psychologists in 1969. It will be instructive in this context to see what Bitterman gave as the theoretical justification in his 1965(a) article for embarking on his comparative work.

According to Bitterman (1965a), one possible reason for the concentration – so deplored by Beach – by animal psychologists on a very few species, and on the rat in particular, was a widespread acceptance among psychologists of the view that there were no qualitative differences in intellect among animals. This view, derived from Thorndike, was based on the observed similarity in performance on learning tasks of a variety of animals. Bitterman's investigations were inspired by the conviction "that [Thorndike's] hypothesis had not yet received the critical scrutiny it seemed to warrant, and that it was much too important to be taken any longer on faith" (Bitterman 1965a, p. 397). In contrast to earlier investigators, however, Bitterman proposed to compare species not in terms of numerical scores such as trials or errors to a criterion of mastery, but in terms of "*functional relations* – to find out whether their performance would be affected in the same way by the same variables" (Bitterman 1965a, p. 398).

It is not difficult to show that Bitterman was justified in claiming the prevalence of the assumption that there were no major qualitative differences in intelligence among animals. Both Hull and Skinner, major luminaries of behaviorism some four decades ago, made such an assumption explicit. Hull, for example, wrote: "The natural-science theory of behavior being developed by the present author and his associates assumes that all behavior of the individuals of a given species, and that of all species of mammals, including man, occurs according to the same set of primary laws" (Hull 1945, p. 56). And Skinner wrote: "The only differences I expect to see revealed between the behavior of rat and man (aside from enormous differences of complexity) lie in the field of verbal behavior" (Skinner 1938, p. 442). Although both of these authors confined their generalizations to mammals, it can be seen that Bitterman's assertion is well supported, and there can also be little doubt that such an assumption contributed to the narrowing of interest down to the single species *Rattus norvegicus*. Bitterman was surely also right both in suggesting that this assumption required exploration, and in introducing novel techniques in an effort to uncover species differences.

If accordingly we put aside Bitterman's evolutionary speculations – speculations which were generated by his results – we see that there was a sound theoretical basis underlying his enterprise. Moreover, his selection of species makes sense in the light of that theoretical position; his object was to see whether *any* (qualitative) differences in intellect could be demonstrated among animals, any such difference between any two species being sufficient to achieve that object. If there are species differences, they would seem most likely in distantly related species occupying very different environments. Fish, reptiles, birds, and mammals are, from that perspective, obvious candidates. The final selection of individual species was presumably governed, as in most biological research, by such mundane considerations as cost, availability, and general suitability for the training procedures envisaged.

2. Goals of comparative psychology

It might be objected that the theoretical basis attributed here to Bitterman is, if sound, very limited, that in effect it still comes down to what Hodos and Campbell (1969) described as research "without any goal other than the comparison of animals for the sake of comparison" (p. 337). If the successful demonstration of a difference in intelligence between two distantly related species would not permit valid evolutionary inferences, is the sole goal of such research to demonstrate that there are indeed some such differences to be found *somewhere* in the animal kingdom? Other than discrediting the "traditional" theory, what theoretical advantage is to be gained by uncovering differences in intellectual function between two species?

There are a number of potential advantages to analyzing differences between species, however remotely related those species might be. One advantage is that successful analyses may provide insights into the mechanisms underlying learning. Consider first Bitterman's original results, and grant for the moment his (now retracted) conclusion that goldfish never show serial reversal improvement, whereas rats almost always do. If we make the not unreasonable assumption that goldfish and rats use comparable mechanisms in that wide range of tasks (such as "simple" association formation) in which their performance is similar, the implication is that rats have some mechanism unavailable to goldfish, one that allows serial reversal improvement. Now this conclusion does have important theoretical implications for the analysis of the intelligence of the rat. It implies that the rat uses mechanisms in serial reversal learning that are not involved in simple association formation, and that any theory of learning which attempts to "reduce" serial reversal learning to association formation is unlikely to be valid. Thus any species difference in learning which demonstrates the existence of a mechanism in one species that is not present in another would be likely to yield important insights into the organization of intellectual activity in the species possessing the "extra" device.

A similar rationale for comparative psychology has been made by Sutherland and Mackintosh (1971), who point out that if (as is not uncommon in theories of animal learning) some hypothesis explains a set of diverse behavioral phenomena as all being due to the operation of a common mechanism, then a species that shows any one of the phenomena should show them all, and any exceptions would constitute grave prima facie difficulties for the hypothesis. In more general terms, comparative research using a variety of behavioral paradigms might be expected to show which sets of phenomena invariably go together and so constitute syndromes each of which may call for a unitary explanation in terms of mechanisms not involved in other syndromes.

The potential benefits of comparative psychology advanced above depend on there being differences between species in the complement of mechanisms of intelligence. Now whether there actually exist any such qualitative differences between species, and whether such differences can be demonstrated by the tests devised to date are, of course, empirical questions. Suppose, then, that research succeeds in demonstrating not qualitative but only quantitative differences between species – could quantitative differences yield theoretical insights?

There are two ways quantitative differences in intellect might manifest themselves. One species might be found quantitatively inferior to another in the solution of some problems, but not others. One prima facie implication of such a pattern of results would be the following; solving the set of problems that differentiate between the species draws upon a mechanism not involved in the problems both species solve at similar rates. This in turn, as was argued in the context of qualitative differences, might yield valuable insights into the structure of intelligence.

On the other hand, one species might be inferior to another across the entire range of problems used, although capable (eventually) of solving any problem solved by the "superior" species. Such an outcome would lend force to the view that at least some mechanisms of intelligence are common to the solution of virtually all problems, thus supporting "general process" theories of learning (e.g., Revusky 1985).

I shall close this section on goals by returning to look again at what was, after all, originally the main goal of comparative psychologists: establishing the course of evolution of intelligence. Suppose that differences in intellectual capacity emerge experimentally. It has been argued (Gottlieb 1984; Yarczower & Hazlett 1977) that the analysis of such differences could generate hypotheses about the evolution of intelligence even in cases in which the species involved were not closely related.

Suppose, for example, that as a consequence of some (currently unknown) constraints, intelligence inevitably evolved within every phylogenetic sequence in the same systematic way, through the addition of novel devices to the previous complement, and that the evolution of each additional device in the series depended upon the preexistence of all the earlier devices. Suppose also that these constraints resulted in the parallel occurrence of the same progression in the complement in a number of independent phylogenetic groups. Two consequences would follow. First, we could properly speak of the intelligence of some species being more advanced than that of others; second, we could detect steps in the course of the evolution of intelligence by finding animals – from whatever lineage – that were at different stages of that progressive evolution. If two species at different stages *were* found to be closely related, then, of course, the notion that the less advanced species did represent a stage through which the ancestors of the more advanced species had passed would gain plausibility.

Such an account of the detection of stages in evolution has much in common with the notion of "anagenesis," a concept which denotes "the progressive evolution of adaptive behavior, learning ability or intelligence" (Gottlieb 1984, p. 449). Some have argued that comparative psychologists have quite properly used this notion to guide their research (e.g., Gottlieb 1984; Yarczower & Hazlett 1977). Proponents of this view agree that the concept of a unitary phylogenetic scale is to be rejected, but they claim that it can be replaced by the notion that there are for biological characters (and for intelligence in particular) levels of evolutionary progress, so that different groups of animals can correctly be described as being at "lower" or "higher" grades or levels of intelligence.

Although it is clear that if, as in the hypothetical scenario sketched above, the evolution of intelligence was similar in all lineages, the present account would agree with the "anagenetic" approach, it is not clear (to this writer at least) whether the applicability of the notion of anagenesis is universally taken to depend on such assumptions. Clearly two species might differ in intellect so that one was capable of solving a wider range of problems than the other, and in such a case it would be reasonable to speak of the more successful species as more intelligent than the other. The intelligence of the two species could also have evolved along quite different paths, however, and unless that possibility could be ruled out, there would be little virtue in the claim that the two species exhibited different grades in the evolution of intelligence. Such a claim would, moreover, be seriously misleading if the type of intelligence shown by the "less advanced" species was interpreted as one which would have been shown by ancestors of the "more advanced" species.

This discussion of the notion of anagenesis has two implications:

First, in order to know whether one type of intelligence might reasonably be interpreted as representative of a stage of intelligence in ancestors of another species with a different type of intelligence, it will be necessary to analyze the nature of the intelligence shown in the extant species. To the extent that there appears to be a significant overlap in capacities, the "advanced" species being superior by virtue of possessing extra capacities, support will accrue for the notion that the two species might manifest two steps in the evolution of intelligence. The key to understanding the evolution of intelligence will accordingly lie in the valid analysis of intelligence in extant species, in understanding *how* animals solve problems. In the absence of fossil evidence of the evolution of intelligence, the goal of understanding the course of that evolution must inevitably become secondary to that of analyzing the nature of intelligence in living animals, since an understanding of the latter is a necessary prerequisite for an understanding of the former.

Second, unless intelligence has evolved in a similar manner in different phylogenetic lineages, an understanding of its evolution is most likely to be gained by the study of closely related species (provided those species exhibit differences in intellectual capacity).

The latter conclusion should not, however, obscure the fact that, as argued at the beginning of this section, there are other goals of comparative psychology which may be achieved using distantly related species even if intelligence has not evolved in such a highly constrained way.

3. General versus specific capacities

The discussion of potential advantages of comparative research embodied two assumptions which should be made explicit. The first is that there are differences of some kind among the intellects of at least some species, differences which might be exploited to yield insights. This is not an assumption which should arouse too much controversy – at the very least, most psychologists would grant that human intelligence differs from that of any nonhuman, and in fact most psychologists would probably also expect to find many differences among nonhuman species. A second assumption is that there are at least some mechanisms of intelligence common to species which may usefully be compared. If, for example, two species solve all problems in qualitatively different ways, then nothing would be gained by considering as a syndrome the set of problems that one species alone could solve. The "successful" species could perfectly well use the same mechanism to solve those problems (or some of them) as was used in some other problems both species could solve.

This last assumption is somewhat more controversial. Lockard, in yet another widely cited attack on comparative psychology wrote: "The century-old linkage between comparative psychology and animal intelligence is disconnected. What we used to call intelligence and tested as problem-solving ability now appears to be an aggregate of special abilities, each one evolved as a response to ecological factors posing problems" (Lockard 1971, p. 173). This is a view clearly not shared by Bitterman, who writes: "Some rather unlikely prophets armed with a few half-digested findings have in recent years been successfully promoting the belief that learning is a set of specialized adaptations about which we can make no general statements at all" (Bitterman 1984a, p. 60).

One uncontroversial point may surely be made concerning this issue: It is an empirical matter, a question of fact rather than of logic, whether there do exist mechanisms involved in problem-solving that are common to different species. The fact that two species occupy different ecological niches does not necessarily imply that *all* of their problem-solving devices differ. (It does not, of course, necessarily imply even that *any* of their devices differ.) Moreover, whichever assumption is held, the course of action to be recommended appears to be similar: The modes of problem-solving used by different species should be explored, and that course will inevitably provide valuable data for comparative psychologists, even if the data do point to the conclusion that the goals some comparative psychologists have set for themselves – the goals set out here – cannot be attained.

4. Definition of intelligence

The emphasis of much of the preceding discussion has been on the use of comparative investigations to uncover the mechanisms of intelligence – to establish how animals solve problems – rather than on such questions as whether one animal is more or less intelligent than another, or how intelligence has evolved. This parallels Sternberg's (e.g., 1979) approach to human intelligence, with the term mechanism (or device) being used here very much the way that Sternberg uses the phrase "information-processing component." It is in the light of such an approach that the definition of intelligence will be considered. [See also Sternberg: "Sketch of a Subcomponential Subtheory of Human Intelligence" *BBS* 3(4) 1980 and "Toward a Triarchic Theory of Human Intelligence" *BBS* 7(2) 1984.]

There are many formal definitions of intelligence, and I do not intend to add to that collection here, for two reasons. First, we all – as speakers of English, rather than as psychologists – know what "intelligence" means; second, there are disadvantages in attempting a formal definition. There is a good precedent for the former argument. Darwin, in his chapter on instinct in *The Origin of Species,* wrote: "I will not attempt any definition of instinct. It would be easy to show that several distinct mental actions are commonly embraced by this term: but every one understands what is meant, when it is said that instinct impels the cuckoo to migrate and to lay her eggs in other birds' nests" (Darwin 1866, p. 148). The point is not trivial; a conventional understanding of the term "intelligence" *is* sufficient to delineate our general area of interest. The dangers of attempting a more specific definition constitute a further argument. Suppose that we adopt some definition of intelligence such as, say, "the ability to solve problems." We might as a consequence narrow our consideration of evidence to the problem-solving literature. We would then exclude the literature on habituation. But it may be that the mechanisms of habituation are also involved in problem-solving; we shall not know whether this is true until we understand both problem-solving and habituation. And until we understand these issues we should not exclude any potentially relevant body of data from consideration.

One of the reasons for the plethora of definitions of intelligence is that definitions vary according to the use to be made of them. In the present context, a definition is required only to provide a focus for an analysis of literature, to determine what work is (or might be) relevant. One of the goals of the inquiry is to make progress toward understanding the nature of intelligence and so to provide a formal definition of intelligence, one which will state in what intelligence consists. To attempt such a definition before examining the evidence is to put the cart before the horse.

I propose to use the word "intelligence" as it is generally used and to base the selection of relevant areas of interest on two salient characteristics of human intelligence – characteristics which are not, I believe, controversial. The first characteristic is that human intellectual capacity appears to be very general in its range of application. Human beings can solve an essentially infinite range of problems, many of which have never previously been encountered by earlier generations; it is not currently possible to predict which problems are soluble, and which insoluble, by humans. The second characteristic of human intelligence is the evident reliance of intellectual activity on previous experience, learning, and memory. Human beings are general problem-solvers who rely heavily on knowledge acquired through experience in their solution of problems.

This distinctly coarse view of human intelligence is nevertheless sufficient to guide the selection of tasks likely to be relevant to comparative psychologists interested in intelligence. They should study tasks with an eye to their general, formal demands on information-processing devices independent of such task-specific characteristics of the problems as the nature of the stimuli used, or of the response required.

It might seem that this notion of intelligence simply ignores the arguments of those, such as Lockard (1971), who claim that all learning mechanisms are species- and task-specific adaptations, by declining to consider evidence from ecologically based species- and niche-specific paradigms. But this is clearly not so, for no amount of investigation of a given species-specific adaptation will show whether that species is capable of general problem-solving. The only way to show that animals possess nothing more than task-specific adaptations is to explore their capabilities in arbitrary environments. If some species, for example, were shown to be an efficient forager for food in its natural environment, a forager which modified its pattern of behavior in the light of experience gained in the recent and not-so-recent past, that would not tell us whether it could solve arbitrary, nonnatural, food-rewarded problems. But if that same species proved quite incapable of solving "unnatural" problems, we might then begin seriously to consider the possibility that the learning mechanisms revealed in its foraging behavior were indeed specific to its natural environment, and that the species possessed only niche-specific foraging devices. If this example has an air of unreality, it is because we already know that a large variety of species are quite capable of learning in arbitrary tasks. How is this achieved, if not by the use of a general device?

One answer is that the capacity revealed in the "unnatural" situation is a fortuitous byproduct of some task-specific mechanism. Johnston, for example, claims that it is "characteristic of complex systems, well known to computer programmers, that they often respond to input other than that for which they were designed" (Johnston 1985, p. 15), he goes on to contrast "ecologically relevant learning abilities" with "ecologically surplus abilities." Perhaps any apparently general problem-solving ability a given species possesses (including, presumably, man) is a "surplus" ability conferred by the possession of some other device whose primary function is task-specific. (See also Johnston: "Contrasting Approaches to a Theory of Learning." *BBS* 4(1) 1981]

The "surplus" view of general problem-solving ability might give rise to (at least) two specific programs of action. The first would be to analyze some behavioral adaptation in its natural setting and from that analysis to predict performance in some other, nonnatural, setting. The second possibility would be to analyze some capacity in a nonnatural setting, and then seek its explanation as a byproduct of a task-specific device. Each course of action has been followed, but the results obtained have not given unequivocal support to the specialized adaptations view (Macphail 1985a). A consideration of each of these specific programs points also to the value of a more general program, for animals from different niches will possess different task-specific devices and hence different surplus abilities. In other words: "Different specific adaptations should not all yield a similar epiphenomenon" (Revusky 1985, p. 427). The first step in establishing the proposition that general problem-solving capacity is a surplus capacity must clearly be to show that that capacity, measured in nonnatural tasks, differs among species.

Before we leave the topic of definition, one final issue will be considered. Suppose that a psychologist conducts an extensive series of laboratory investigations on two species of birds, one a songbird, the other not, and that those investigations fail to reveal any differences in the performance of the two species. The psychologist might then conclude that there is no evidence of a difference in the intellectual capacity, or problem-solving ability, of the two species (and that is the conclusion I would draw). It is clear, however, that there is at least one type of learning (song learning) that does discriminate between the species. Is the comparative psychologist wrong, then, or at best severely distorting the truth? Not according to the case made out here. The pattern of results outlined would suggest that song-learning capacity was not relevant to the species' general capacity, which must in turn appear to be genuinely general, and hence in that sense comparable to the human capacity which lies at the heart of our notion of intelligence.

5. Assessment of contrasts in performance

This section will consider some general issues that arise in the assessment and interpretation of performance differences in comparative studies. One important issue in this context is the elimination of "contextual variables" (Bitterman 1965b) as potential causes of performance differences between species. Suppose two species are tested in identical versions of a given problem and that one species solves it and the other fails. Such a result *could* be due to some intellectual advantage of one species over the other, but other less interesting possibilities clearly exist. One species might find the reward less motivating than the other, or there might be sensory or motor demands in the problem that were satisfied more easily by one species because of a more developed visual system or the possession of hands rather than wings. Moreover, there is no way such variables can be "equated" between species – it simply makes no sense to compare, for example, the levels of hunger of two different species. If the effects of such variables cannot be ruled out, however, no assumption of intellectual difference can be made. It is, after all, clear that different species *do* vary in such factors as perceptual capacity, whereas the existence or otherwise of intellectual differences is precisely what is at issue.

Bitterman (e.g., 1965a; 1965b) has suggested that the potential role of contextual variables can be explored through "systematic variation." Suppose we wish to test whether some species fails to solve a food-rewarded problem because it is insufficiently hungry. We could then run that species in the same problem at a number of different levels of food-deprivation. If the species failed at all levels tested, and if a species which solved the problem succeeded across a wide range of deprivation conditions, it would be reasonable to conclude that the performance difference did not arise from a difference in motivation. Other potential contextual variables could be eliminated in the same way until the only plausible account remaining was a difference in intellect.

Systematic variation is a time-consuming technique requiring the rerunning of an experiment under many different conditions, and as a result, the technique has rarely been used. Instead, investigators have relied on covert appeals to potential outcomes of systematic variation studies: It is assumed that the task is such that, within a reasonable range, variations in contextual variables would not have a significant effect. For example, if a large number of experiments have shown that some phenomenon is reliably obtained in rats, then a single experiment, using goldfish, which fails to obtain the effect may appear to have considerable significance. But this would be a dangerously premature conclusion, since the history of comparative psychology is largely one of demonstrating in various species capacities previously denied them because of some earlier performance failure (Macphail 1982).

These caveats apply even more clearly to the notion that it is possible to do comparative psychology by looking at one species alone. If it were possible, for example, to demonstrate that a chimpanzee is capable of language acquisition, that would be of considerable relevance to the comparison of chimpanzee and man, but would not speak directly to the issue of intellectual contrasts between chimpanzees and, say, pigeons. One cannot deny to pigeons capacities attributed to chimpanzees unless a convincing search has been made for such capacities in the pigeon. Different training methods would be clearly required, so that some analogue of the chimp training procedure, suitable for pigeons, might be developed. The analogue might not be very close to the original procedure but – provided the pigeon mastered the analogue – this would not give grounds to doubt the bird's capacity. Only failures to master a task are grounds for positing intellectual contrasts; no amount of success by one species will demonstrate its superiority over another species which has not been tested.

There have been a number of reports of successful performance by pigeons in analogues of tasks originally mastered by such "higher" mammals as chimpanzees and dolphins. These include: (1) analogues of studies of interanimal communication between chimpanzees (Savage-Rumbaugh et al. 1978) and dolphins (Bastian 1967), the pigeon studies reported by Epstein, Lanza, and Skinner (1980) and by Boakes and Gaertner (1977); (2) a study by Epstein, Kirshnit, Lanza, and Rubin (1984) of problem-solving, involving standing on a box to reach a banana, the problem being an analogue of one originally solved by chimpanzees and taken to indicate "insight" in chimpanzees (Koehler 1925); and (3) a study of self-recognition in pigeons (Epstein, Lanza & Skinner 1981), the procedure being designed as an analogue of one used with chimpanzees and taken to reflect self-awareness in chimpanzees (Gallup 1970).

Although I (Macphail 1982; 1985a) have used some of these reports as support for the view that pigeons may indeed master problems supposed by many to indicate "higher" processes others have, very reasonably, drawn attention to differences between the analogues and their originals (e.g., Gallup, 1982; Savage-Rumbaugh, 1984). The point is that the (inevitable) differences between the analogues and their originals do not show that pigeons cannot do what chimpanzees can do; this could only be demonstrated by pigeons' failure to perform adequately in an analogue.

6. Experimental studies of species differences

I turn now to the major empirical question: What species differences in intelligence have been demonstrated by experimental investigations? The conclusion of my survey (Macphail 1982) of the literature on vertebrates was that no difference, either qualitative or quantitative, had yet been demonstrated among nonhuman vertebrates. I sorted the tests used into four classes, the first three being "simple" (habituation, classical conditioning, and instrumental conditioning), the fourth "complex" – a class having no unifying theme and defined by exclusion to refer to all those tasks which were not "simple." It should be noted that although the general definition of intelligence advocated here points to problem-solving as an important aspect of intelligent behavior, very little attention was paid to the literature on that topic in animals, because that literature is not comparative. Reports on problem-solving in animals (e.g., Ellen et al. 1984; Koehler 1925; Kummer & Goodall 1985; Maier 1932) have generally used only one species, and have drawn no explicit comparisons between its performance and that of others.

As far as simple tasks are concerned, there is probably a good measure of agreement that vertebrates have not been shown to differ (e.g., Dewsbury 1978; Warren 1965). But there is likely to be much less agreement about my conclusion from the analysis of complex task performance. This is not the place to recapitulate the various tasks considered, and the reasons for concluding that the observed performance differences were not due to differences in intellect. I shall, however, briefly review one topic, since important new work has appeared since 1982, and it will be possible to show in general how my survey reached the conclusions it did.

Bitterman (e.g., 1975) proposed that a major qualitative difference between fish and rats was that rats, unlike fish, could form "expectancies." Evidence to support this notion came from a number of paradigms using reactions to changes in reward, one example of which involved the shift from a large to a small reward. Crespi (1942) found that when rats running in an alley for a large reward (256 food pellets) were abruptly shifted to a small reward (16 pellets), their running speeds dropped rapidly, falling below those of rats which had been run throughout for the small reward (the successive negative contrast effect, or SNCE). Lowes and Bitterman (1967), however, found that when goldfish swimming for a large reward (40 worms) were shifted to a low reward (4 worms), their swimming speeds did not slow at all, despite the fact that fish swimming throughout for the small reward swam significantly more slowly than those swimming for the large reward.

Bitterman argued that the abrupt drop in the rats' running speeds – and in particular the depression in speed below that of controls – should be attributed to their disappointed expectancies. The absence of a similar reaction in goldfish could then be due to their not forming expectancies. Bitterman went on to specify what was meant by expectancies, arguing that fish were "pure S–R [stimulus–response] animals" whereas rats had an additional capacity for forming interstimulus associations (S–S associations, or expectancies).

More recently, however, Bitterman has reported (Bitterman 1984b) the results of a study of compound conditioning in goldfish which showed that they did form within-compound associations. Most investigators would agree that these are indeed S–S associations and, perhaps more to the point, Bitterman himself argues that within-compound associations provide "what is perhaps the clearest example of S–S association in vertebrates" (Bitterman 1984a, p. 63). The study that Bitterman describes consisted of three stages. In Stage 1, fish were trained to nose a target for food reward, the target displaying a compound of two stimuli – a white line (horizontal or vertical) on a colored (red or green) background. Each fish experienced two of the four possible combinations of stimuli (say horizontal on red, and vertical on green). In Stage 1, each color was experienced along with a particular line orientation; the object of Stages 2 and 3 was to determine whether an association had been formed between colors and orientations in Stage 1. In Stage 2, the fish learned a discrimination, either between a horizontal and a vertical line (on a black background) or between red and green (with no lines superimposed). In Stage 3, each fish learned a discrimination between the stimuli from the dimension not used for that fish in Stage 2. Consider the positive stimulus of Stage 3. That stimulus had been paired in Stage 1 with a stimulus that had gone on to become either the positive or the negative stimulus in Stage 2. Now if an association was formed in Stage 1, the Stage 3 discrimination should be learned faster if the Stage 3 positive stimulus had been paired (in Stage 1) with the Stage 2 positive stimulus rather than with the Stage 2 negative stimulus – and that is how the results came out. Goldfish form within-compound associations and are hence capable of forming S–S associations; they should, like rats, be capable of forming expectancies.

The demonstration that fish form expectancies does not alter the fact that the SNCE is elusive in goldfish. Bitterman (e.g., 1984b) now uses the absence of the effect as support for another proposal, namely, that in fish instrumental responding is not controlled by its remembered consequences (or by "associatively reinstated representations of past events"; Couvillon & Bitterman 1985, p. 437). There are good reasons, however, to suppose that the failure to obtain an SNCE in goldfish may be due to contextual variables. Rats do not invariably show the effect. It has been found in a number of studies that when rats in a runway are shifted from a high-concentration sucrose solution to a (less-preferred) low-concentration solution, they do not show the SNCE (Flaherty 1982); the same outcome is obtained when rats are shifted from immediate to delayed reward (Mackintosh & Lord 1973). Similarly, Chen et al. (1981) found that young (24–25 day old) rats running in an alley for milk reward showed a large and reliable SNCE, but for food pellet rewards they showed only a marginal SNCE. Older rats showed a clear SNCE when either type of reward was used.

Another important factor in the SNCE in rats is the response measure used. Although shifts in sucrose solution do not obtain the SNCE in runways, they do when a consummatory response measure is used (Flaherty 1982). A downward shift in sucrose concentration obtains an SNCE when an operant (bar-pressing) response measure is used (Weinstein 1970a; 1970b). Stanton et al. (1984) have shown that 17-day old rat pups shifted from a high (milk suckling) to a low (dry suckling) reward show SNCE on one measure (nipple attachment latency) but not on another (runway speed).

The effects of reward reduction in rats vary with type of reward, response measure, and age. Failures to obtain the SNCE are not yet well understood (Flaherty 1982): Until they are, it will be premature to rest theoretical speculation on failures to obtain the SNCE in goldfish, since such failures could very well be due to inappropriateness of one of the contextual variables critical to the appearance of the effect.

It should be added here that there have been two reports (Breuning & Wolach 1977; 1979) of the SNCE in goldfish. Both studies used an unconventional (classical conditioning) procedure with general activity as the response measure. A relatively short (mean 55 sec) intertrial interval was used, and Bitterman has argued that massed trials may allow the operation of nonassociative factors, such as sensory carry-over (Bitterman 1976; Gonzalez & Bitterman 1969). Moreover, both the recording technique used and the statistical analyses leave much to be desired. These studies clearly warrant careful replication, however, given the significance attached to the notion that the SNCE cannot be obtained in goldfish.

The demise of the notion that fish cannot form expectancies illustrates two important points about the negative results of my survey of the vertebrate literature. The first is that the apparent failure of fish to form expectancies has not been explained away as the effect of some unspecified contextual variable. It has been demonstrated that fish are *not* "pure S–R" animals and that, like rats, they too form S–S associations. Specific contextual variables are also known to be critical to the appearance or otherwise of the SNCE in rats and there exist claims in the literature for the successful demonstration of an SNCE in goldfish.

The second point to emerge from consideration of expectancies in goldfish is that it has been possible to conduct comparative research quite successfully using very distantly related species. Some writers (e.g., Hodos 1982; Mackintosh et al. 1985) have suggested that the difficulties associated with attempts to rule out effects of contextual variables are so forbidding that it would be more meaningful to pursue comparative work with species that are closely related and have similar bodily structures. Whereas this would be an entirely reasonable response to the endless appeals to contextual variables in attempts to dismiss evidence of potential intellectual contrasts, one must also note the force of demonstrating comparable phenomena in widely disparate species.

A final point harks back to the earlier discussion of the goals of comparative psychology. Although the proposal that goldfish are pure S–R animals has been rejected, it is clear that had it been upheld, it would have had profound theoretical implications. It would have indicated that the formation of S–R and of S–S associations represents different types of learning, using different mechanisms and having different evolutionary histories. All that would have been true, despite the fact that no generalizations could safely have been made from the comparison of goldfish and rats concerning either the course of evolution of the two types of conditioning or the existence of S–S association formation in fish in general. Since the proposal was rejected, of course, no such dramatic inferences can be made. However, some less striking implications for theory did arise from the body of experiments carried out. For example, although successive negative contrast is an elusive phenomenon in goldfish, simultaneous negative contrast is readily obtained (Gonzalez & Powers 1973). This suggests that the causes of those two NCEs are different; this implication has been drawn by workers concerned with the genesis of contrast effects in rats (e.g., Flaherty 1982). In other words, it is possible to gain insights into the organization of behavior in one species by studying that behavior in another species, however distantly related.

This section should not end without acknowledging that there are currently a number of specific proposals for species differences in intellect which enjoy experimental support (e.g., Shishimi 1985; Wilson et al. 1985). This is not the place to go into the details of those proposals, but one general point may be made: Their experimental support inevitably consists of reports of failures by a species to master some problem. Before any proposal can be accepted, it must be backed up by a series of such failures, a series involving systematic variation. Leaving aside reservations specific to particular proposals, I am not convinced that any proposal is yet supported by a sufficient body of such failures to warrant confidence in it.

Similar considerations apply *a fortiori* to proposals about how intelligence may have evolved and about methods that might be used to detect differences in intellect (e.g., Barlow 1983; Bullock 1986; Thomas 1980). Such schemes are valuable in providing specific hypotheses that can be subjected to experimental investigation, but they cannot be accepted until experiments consistently report failures by certain species to master specific tasks.

7. Human intelligence

Although the central concern of this target article is with the intelligence of nonhuman vertebrates, a brief digression into human intelligence is appropriate, if only for the sake of completeness. It is clear that humans can solve a much wider range of problems than any nonhuman: Human intelligence is therefore either qualitatively or quantitatively superior to nonhuman intelligence. It is equally clear that language contributes in an important way to problem-solving by humans, and that this is probably so even for problems which do not explicitly require language for their solution. Two possibilities arise. On the one hand, only humans might acquire language because they possess a higher level of general intelligence than nonhumans; on the other hand, humans might enjoy the same level of general intelligence as nonhumans but possess in addition a species-specific language-acquisition device. Humans, that is, may learn to talk because they are more intelligent than nonhumans (a quantitative difference) or may be more intelligent than nonhumans because they learn to talk (a qualitative difference). There are, of course, numerous other possibilities, but this simplified account may serve to highlight the central issue.

If humans acquire language because they are (quantitatively) more intelligent than nonhumans, and not because of any qualitative distinction, it should be possible to teach a nonhuman at least the rudiments of language. The question of whether nonhumans can acquire language is therefore critical to the issue of distinguishing between human and nonhuman intelligence. As is well known, recent years have seen a number of programs designed to explore this question; most of these have used one or another of the great apes as subjects (e.g., Gardner & Gardner 1969; Patterson 1978; Premack 1971; Rumbaugh 1977; Terrace et al. 1979). It is equally well known that the interpretation of the results of these studies has been highly controversial [See also *BBS* special issue on Cognition and Consciousness in Nonhuman Species, *BBS* 1(4) 1978 and Premack "The Codes of Man and Beasts" *BBS* 6(1) 1983.]

One major issue is: What does an animal have to achieve in order to demonstrate the rudiments of language acquisition? Is it, for example, sufficient to show parallels between the performance of an animal and that of a child in the early stages of language acquisition (e.g., Gardner & Gardner 1978)? There are in the present context two major difficulties facing the adoption of such a proposal.

One difficulty is that young children may not have progressed to the stage at which their language is of service in general problem-solving. In other words, children capable of, say, mere babbling or of one-word utterances, and who show no clear evidence of the use of the rules of grammar, may not enhance their intelligence through that capacity. We know that adult intellectual performance is strongly influenced by the capacity for language, but we do not know at precisely what stage language comes to be used in general problem-solving.

A second difficulty concerns the interpretation of the results obtained from studies of "naming" in nonhumans. All of the ape language-learning programs cited above have succeeded in establishing wide "vocabularies" of symbolic representations for agents, objects, qualities, and actions. It is not clear, however, that these vocabularies reflect anything more than the formation of associations between stimuli and those responses (or stimuli) used as "words" in the training programs. It is equally clear that all vertebrates are capable of forming formally similar associations, and it is not clear that such association-formation is all that occurs when a human learns the meaning of a word. Savage-Rumbaugh et al. (1983) have brought similar arguments to bear on the results reported by, among others, Gardner and Gardner (e.g., 1978), Premack (1976), and Terrace et al. (1979) but the effort by Savage-Rumbaugh et al. (1983) to demonstrate "representational" as opposed to "associative" naming has itself been questioned (e.g., Ristau 1983; Sugarman 1983).

One candidate which may be used as a specific criterion for language acquisition is the ability to form sentences. There are a number of reasons for adopting this criterion. The linguistic theories that have had the most influence on psychology agree that grammar is the most important aspect of human language (Garnham 1985); the production and comprehension of sentences is the safest proof of grasp of grammar. Many of Chomsky's influential arguments for the existence in humans of an innate, species-specific language-acquisition device apply specifically to grammar. For example, Chomsky's opposition to the notion that a general learning system could master any human language centers on the impossibility of any such system deducing the rules of grammar (e.g., Chomsky 1972). [See also Chomsky: "Rules and Representations" *BBS* 3(1) 1980.] Thus the most convincing rebuttal of Chomsky's claim that the human language-acquisition device is species-specific would be to demonstrate acquisition of grammar in nonhumans. A further reason for adopting the mastery of sentences as a criterion in this context is that it is plausible that a child who has advanced to that stage should then be able to use language to organize its problem-solving behavior in ways which may not previously have been possible.

The critical question here is: Can nonhumans form sentences? Unfortunately, if inevitably, it is precisely in this area that most controversy exists. A consideration of alternative accounts of the various claims for successful acquisition of grammar (that is, of accounts that do not appeal to linguistic concepts) requires a detailed analysis of experimental procedures and results; the fact that so many different techniques have been used means that each program requires separate analysis. I shall restrict myself here to two points about the language-acquisition programs.

First, no program has yet succeeded in gaining overwhelming support from the psychological community for the proposition that syntactic competence has been demonstrated. This applies equally to the much more restricted community of psychologists actively involved in these programs. Herman et al. (1984), for example, begin their report with a summary of the criticisms that have been directed at work on sentence-processing in apes; some of the most trenchant of the criticisms derive from workers who are themselves involved in language-acquisition programs. Herman et al.'s own work on sentence comprehension in bottlenosed dolphins is severely criticized by Premack (1985), the originator of the first chimpanzee training program of the modern era.

The second point is that language-acquisition programs are underway that use animals other than the great apes: Besides the work by Herman and his colleagues on dolphins, studies on language acquisition in Californian sea lions (Schusterman & Krieger 1984) and in an African Grey parrot (Pepperberg 1981; 1983) have been reported. Although these studies, like those in which apes are subjects, may not receive uncontroversial interpretations, they do point to the fact that there is as yet no reason to suppose that the capacities shown in these programs by apes are peculiar to primates.

Unless and until proof of language acquisition in nonhumans is available, we should assume that nonhumans are not capable of language acquisition – this is the hypothesis which those programs are designed to test, and until disproved, it should be accepted. If nonhumans cannot acquire the rudiments of language, then the most economical account of the distinction between the human and the nonhuman intellect may be that it is a qualitative distinction, and that humans possess the same "basic" general intelligence as nonhumans, plus a species-specific language-acquisition device which, when it becomes operational, also has very general application and so raises the level of general intellectual capacity far above that of nonhumans.

8. The null hypothesis and its implications

The case made out for comparative work in the first part of this target article rested on the assumption that contrasts between species would emerge. But my survey has found only one contrast – that man does acquire language, and nonhumans do not. It is naturally possible that I have wrongly dismissed (or ignored) some evidence, and that future work will reveal uncontroversial evidence of intellectual differences between nonhuman species. The latter possibility can never be dismissed, but suppose no species-difference in intellect among nonhuman vertebrates has been demonstrated – what does this signify? One straightforward implication (Macphail 1985a) of finding no significant differences would be, as in any scientific enterprise, that the null hypothesis should be accepted, and the appropriate null hypothesis here is surely that there are no differences, either quantitative or qualitative, among the intellects of nonhuman vertebrates.

One immediate and obvious implication of the rejection of intellectual differences among vertebrates is that vertebrate learning mechanisms are not a collection of specialized adaptations to ecological niches. There are two considerable bodies of experimental and theoretical work which stand opposed to such a conclusion; research on "biological constraints" and on "optimal foraging theory." [See Fantino & Abarca "Choice, Optimal Foraging and the Delay Reduction Hypothesis" *BBS* 8(2) 1985.]

The biological constraints literature is concerned primarily with the possibility that there are selective affinities between certain classes of stimuli (e.g., tastes, sounds) and specific reinforcers (e.g., illness, aversive shocks), and that these specific affinities have evolved in accordance with the ecological niches of species. A number of difficulties face these proposals. First, it is not clear that the affinities demonstrated to date cannot be interpreted in terms of "general process" theories (Domjan 1983). Second, the biological constraints hypothesis makes very few specific predictions, and some of those have been invalidated (Galef 1984; Kalat 1985). Third, there has not yet been any convincing attempt to relate those affinities that have been found to the natural ecology of the species concerned (Kalat 1985). It may finally be added that even if such species-specific affinities were in the end confirmed, they need not affect the case for general mechanisms of learning common to vertebrates (see Revusky 1985, for a similar conclusion). To characterize fully the learning capacities of a species, one might need to catalogue a number of biological constraints which would apply in relatively few specific conditions; but that catalogue would be an addendum to the principal mechanisms of learning used, those mechanisms being quite general in their application (and, according to the present point of view, common to all vertebrates).

Optimal foraging theory proposes that animals adopt foraging strategies which maximize net energy gain, and that different ecological niches will encourage the development of different strategies. The theory does not specify the proximal behavioral mechanisms by which such strategies will be achieved, and so does not necessarily rule out the possibility that mechanisms of learning are common to a variety of species and that the differing environmental experiences of those species will result in the development – through learning – of different foraging strategies. Some workers, however, have made predictions from the theory which clearly imply that the strategies differ systematically between species, and not as a result of learning. One strategy which has been cited frequently as an instance of an unlearned, niche-specific mechanism is the win-shift strategy. Olton and Schlosberg (1978), for example, attribute the remarkable efficiency of rats in the radial maze to a tendency in rats to shift to a place other than that in which they have recently been rewarded. This tendency is in turn explained by appealing to the notion that food is, in the natural habitat of rats, a rapidly depleted resource not reliably found in the same place on successive visits. Since such considerations do not apply to laboratory-reared rats, the implication is that such a strategy is an unlearned specialization, and clearly relevant to the solution of (at least some) food-rewarded problems.

I have discussed the "resource distribution hypothesis" in some detail (Macphail 1985a) and found it unsatisfactory in a number of ways. For rats, if some resource could be discovered which was reliably found in the same place in their natural habitat, then a win-stay strategy should have evolved for that resource. Such a proposal was originally made by Petrinovich and Bolles (1954), with respect to water. Subsequent work has shown, however, that rats shift just as readily after water deprivation as after food deprivation (Bolles & Petrinovich 1956), and, in particular, that rats are as efficient in radial mazes motivated by water reward as in those motivated by food reward (Kraemer et al. 1983). Moreover, species other than rats whose food distribution differs, so that food is reliably found in a given place, should exhibit win-stay strategies for food reward. Bond et al. (1981) claimed that this was the case for pigeons, and reported inferior learning in pigeons as compared to rats in a food-rewarded radial maze, arguing that this difference reflected a poorly developed spatial event memory in pigeons. I was able (Macphail 1985a) to point to the fact that, at least in some food-rewarded tasks, pigeons show a strong win-shift tendency (Olson & Maki 1983); I also pointed out that ring-doves, close relatives of pigeons and having similar food distributions, are efficient performers in a (modified) radial maze (Wilkie et al. 1981). I concluded that the relatively poor performance of pigeons in the Bond et al. maze was probably due to contextual variables and that we should "reserve judgement on the question whether . . . pigeons might not . . . possess a capacity superior to that suggested by the Bond et al. report" (Macphail 1985a, p. 44). It was with some satisfaction, therefore, that I noted the report of Roberts and Van Veldhuizen (1985) on the performance of pigeons in a radial maze. These investigators made relatively minor changes in training technique and in the maze itself; they found that, using a range of measures, their pigeons "performed the same as Bond et al.'s rats and far better than their pigeons" (Roberts & Van Veldhuizen 1985, p. 255).

The foregoing discussion of optimal foraging theory brings to mind a earlier conclusion. The multiplication of examples of achievement by one species does not in itself serve as evidence of superiority over some other species in which evidence of such capacities has not been sought; similarly, evidence of congruence between some behavioral pattern and a feature of the ecology of a species does not demonstrate a causal link between that behavior and the ecological feature. What must be shown is that different ecological features obtain different behavioral patterns (both within and between species). To date, no such demonstration pertinent to intelligence is available.

9. The role of association formation

The discussion so far has tended to treat the results of comparative investigations as negative, emphasizing failure to demonstrate differences. It is time now to adjust that attitude and to emphasize instead the positive aspect of comparative work, namely, the clear demonstration that so many learning phenomena appear consistently in groups of widely differing ecology and phylogeny. The notion that animal intelligence is a collection of adaptive specializations ought to be rejected, not simply because psychologists can find no between-species differences in learning, but because it is implausible to claim that the extensive range of phenomena seen in very different species is an accidental "surplus" epiphenomenon generated independently by idiosyncratic niche- and species-specific devices. The widespread distribution of similar learning phenomena is positive evidence of the equally widespread distribution of identical underlying mechanisms. This may in turn support the view that the mechanisms of learning are relatively simple.

One specific possibility worth exploring is that association formation lies at the core of problem-solving in nonhumans. Before discussing this possibility, I should emphasize that the proposal is *not* that all learning consists of association formation; there are important learning phenomena – such as habituation and latent learning – which do not involve association formation (or, at least, not overtly), and the processes involved in such phenomena may well play a role in tasks which would not be classified as "simple."

Association formation is a critical aspect of many of the "simple" tasks used by comparative psychologists. If notions of what elements may enter into associations are liberalized to include what Restle (1958) has called "Type A" cues, then association formation may be a sufficient explanatory principle to encompass what are, superficially at least, complex types of learning. Type A cues are those abstract and conditional aspects of a task which may remain constant when physical features (such as the particular stimuli used) of a task change. They allow a conceptualization of rule-governed behavior in terms of association formation. Restle's notions have clear application to such problems as concept formation and learning-set formation, and could presumably be used to reinterpret in terms of association formation many, if not all, tasks which involve the consistent use of one rule across different physical versions of the task. In other words, the essential requirement for the establishment of rule-governed behavior is the detection of a contingency between performance according to that rule and the occurrence of reinforcement. Association formation has to do with the detection of contingencies and there is no reason why the same device that detects contingencies between, say, buzzers and shocks should not also detect the contingency (in a learning set task) between reward and a Type A cue such as the compound comprising the after effect of reward and the memory trace of the object recently chosen.

The emphasis on the wide potential of an association-formation device is intended to pave the way for the introduction of one further positive aspect of the results of comparative work. For although it has been argued here that vertebrate learning mechanisms are of general applicability and have not evolved to meet specific demands of various ecological niches, it is not to be supposed that these mechanisms evolved independently of environmental demands. The implication is that the mechanisms evolved to meet some demand (or set of demands) that was common to a wide range of environments. This notion in turn agrees nicely with a conclusion reached by a number of psychologists, namely, that association formation is a process which evolved to detect causal links between events, or, in rather grander language, to detect the causal structure of the universe (e.g., Dickinson 1980; Revusky 1985; Testa 1974). Detection of causal links is a necessary prerequisite of useful prediction in all environments, so it makes good sense to suppose that the universality (in vertebrates at least) of a wide range of learning phenomena reflects the widespread distribution of devices concerned with the formation of associations through the experience of events which are contingent on each other owing to a causal link between them.

Contemporary learning theorists have been concentrating their energies on the rules governing association formation in relatively simple testing paradigms, using rats and pigeons almost exclusively as subjects. They are attempting to answer questions such as: What are the conditions for the formation of an association between two events? What is the nature of the representation of an event that forms a term in an association? A number of rival theories have emerged (e.g., Mackintosh 1975; Pearce & Hall 1980; Rescorla & Wagner 1972), and it will clearly be difficult to achieve a universally acceptable account of the supposedly simple processes involved in association formation. But the present interpretation of comparative research suggests both that concentration on a few species is justified and that a successful analysis of association formation may be very generally applicable to the intellectual activities of vertebrates.

Differences between species in association formation tasks will arise when the events – stimuli or responses – which serve as terms in associations are differentially available to the processing devices concerned with association formation. Some stimuli may be highly salient to one species, but detected only with difficulty, or not at all, by another; some responses may occur freely in one species, but be physically difficult or impossible for another. Species with highly developed sensory systems and sophisticated motor systems may therefore learn associations and adopt novel, adaptive modes of behavior not seen in species with less complex perceptual and motor systems. But the evidence currently available suggests that when events are equally detectable, all vertebrate species are equally adept at detecting contingencies between them. There is accordingly no need to suppose any difference between the species in those mechanisms specifically concerned with association formation, treated here as the central process of intelligence.

To return briefly to the subject of anagenesis: I argued (Section 2) that the notion of grades of intelligence made little sense unless it was assumed that the course of evolution of intelligence in different phylogenetic lineages had, owing to some unspecified constraint, been similar. The position reached here suggests that one constraint – causality – has indeed shaped the evolution of intelligence so that all nonhuman vertebrates have attained the same grade; a second grade is seen in humans alone. Whether there are other, lower, grades and whether such grades are exhibited in any living species of animal is as yet unknown.

10. Conclusions

The primary conclusion, assumed rather than argued in this article, is that comparative psychologists have not yet succeeded in finding a difference in performance between nonhuman vertebrate species that is to be attributed to a difference in intellect between the species, rather than to a difference in some contextual variable concerned with perception, motivation, or motor skill.

The secondary conclusions are as follows:

1. There are neither qualitative nor quantitative intellectual differences among nonhuman vertebrates.
2. Mechanisms of learning are of general applicability, and did not evolve as species-specific specializations to meet the demands of particular ecological niches.
3. Intelligent behavior in nonhuman vertebrates is dominated by association formation, a process which successfully uncovers causal links between events.
4. Human intelligence is differentiated from nonhuman intelligence by the existence of a species-specific language-acquisition device which incorporates processes other than association formation.

It can readily be seen that the present emphasis on association formation is hardly justified by the evidence discussed earlier. I have not attempted to show that all complex nonhuman learning performance can be "reduced" to association formation; nor have I produced any evidence for the assertion that language acquisition cannot be so reduced. The principal ground for this emphasis is one of economy. A coherent account of the universality of learning processes can be erected by pointing to the link between association formation and causality. The failure of nonhumans to acquire grammar can also be accommodated economically on the assumption that the rules of grammar could not be acquired by a device whose function was to detect contingencies between environmental events.

A further ground for the emphasis on association formation is that it provides a specific guide for future comparative research. One reason for the failure to detect species differences in intelligence may be that psychologists have used tasks which can be solved in terms of association formation. There may indeed be universal association-formation devices, but some species may possess additional devices – just as humans possess a language-acquisition device. Many authors have noted the potential importance for comparative work of tasks which are not associative in nature (e.g., Mackintosh et al. 1985; Rumbaugh & Pate 1984), but it is not yet clear that such a task is available. Restle's successful reanalysis of tasks such as learning-set formation and concept formation in terms of association formation shows that it will be peculiarly difficult to devise tasks which cannot be similarly reduced.

I shall end with some remarks on plausibility, raising one further implication of the null hypothesis in this context. It seems unlikely that if all nonhuman vertebrate species possess the same intellectual capacity there are genetically controlled variations in that capacity within species. Intelligence is a capacity of adaptive significance, so if within-species endemic variation were available, there would exist a selective pressure in favor of those possessing higher intelligence. If this were so, some ecological niches might create a stronger selection pressure than others, so that between-species differences would emerge. But we find no between-species differences; there is no convincing evidence for within-species variations in general intelligence in nonhumans either. Tryon (e.g., 1940) did develop two inbred strains of rats which had been selected on the basis of their performance in a food-rewarded maze, and at that time it was generally believed that maze performance was an index of general intellectual ability. But when Searle (1949) compared descendants of Tyron's maze-bright and maze-dull strains on a variety of learning tasks, the maze-dull rats were the equal of or superior to the maze-bright rats on more than half of the tasks. Searle found evidence for differences between the strains in motivation and activity, but he concluded: "No evidence was found that a difference exists between the Brights and the Dulls in the learning capacity *per se*" (Searle 1949, p. 323). In a review of a large number of studies involving selective breeding and strain comparisons, Wahlsten (1978) came to a similar conclusion with regard to the search for evidence of genetically controlled variation in general intelligence. Wahlsten's analysis of the literature provided him with no "reasons to expect that experimental results obtained with one piece of apparatus will generalize to another task, especially if it entails different motivation, response, or sensory modality" (Wahlsten 1978, p. 89). "Consequently," according to Wahlsten, "there are no grounds for speaking of rat or mouse "intelligence" (Wahlsten 1978, p. 89). Although that is not the position adopted here, it can be seen that it is entirely consonant with the proposal that the ("innate") intelligence of all individuals within a species is the same. Now if there are no innate individual differences in intelligence in nonhuman vertebrates, it would be odd to find such differences in humans – why should so conservative a trait abruptly develop variants? (Macphail 1985b). (It should be noted that these considerations apply only to the intelligence that man shares with nonhumans; there could, of course, be individual differences in the efficiency of the language-acquisition device, and these could in turn give rise to differences in intellectual capacity).

The position adopted here agrees, then, with the view that there may be no innate, unlearned differences in intellectual capacity among humans. This is a view that has likewise suffered considerably from a prima facie implausibility. One consequence of the predisposition to accept that "innate" differences in intelligence do exist is that unreliable evidence is too easily accepted. Kamin (1974) has shown that at least one widely cited source of support for innate differences in intelligence was actually fraudulent; he argues (1986) that even today evidence which supports the view that there are innate differences in a range of important behavioral traits, including intelligence, is still uncritically and carelessly assessed and relied upon by some authorities.

Arguments about between-species differences in nonhumans are – fortunately – not as emotionally loaded as those concerning within-species differences in man, but a similar issue arises. There is a natural tendency to regard a moneky as being more intelligent than a frog, and so to accept as genuine tests of intelligence tasks in which the monkey outperforms the frog. But other, admittedly less interesting, explanations must be conclusively ruled out, and in my view, such alternative explanations have been too easily dismissed in the past. I hardly expect my reviews of this area to lead to the widespread adoption of the null hypothesis – and I concede in any case that there is still far too little evidence to allow its confident adoption. But I do not think it overly optimistic to hope that the null hypothesis should receive serious consideration, and I take encouragement from the reflection that what has seemed implausible in one generation has not infrequently seemed common sense in the next.

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Intelligence and human language

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As I understand Macphail's presentation of the case for the null hypothesis, most (if not all) observed differences in learning performance among nonhuman vertebrates reflect some aspect of species differences in sensory, motor, or motivational systems. Given the dearth of positive evidence for performance differences that cannot be attributed to these contextual variables, the most appropriate assumption is that nonhuman vertebrates do not differ in their capacity to learn. By drawing attention to an important corollary of the null hypothesis, that *any* difference which cannot be explained by contextual variables counts against the null hypothesis, Macphail virtually guarantees an energetic search for that difference.

Although Macphail carefully develops the logic of the case for the null hypothesis, he does not appear to apply the same care to his choice of words and of the domain to which the null hypothesis applies. Differences in behavior become differences in learning; differences in learning become differences in problem-solving, and even intelligence. Learning is considered synonymous with problem-solving, and problem-solving is considered synonymous with intelligence. The proposal of no differences in the capacity to learn turns into a proposal of no differences, either quantitatively or qualitatively, among the intellectual capacities of nonhuman vertebrates.

To be fair, Macphail points out that the key to understanding the evolution of intelligence depends on a valid analysis of intelligence in living animals, which in turn requires an understanding of *how* animals solve problems. And, of course, flexible, adaptive behavior depends upon the ability to learn. Although learning, problem-solving, and intelligence may be intimately related, they are surely different. Equating complex concepts will not further our understanding of intelligence; blurred distinctions serve only to create a conceptual morass that cannot be subjected to experimental verification or falsification.

The concept of intelligence varies widely across people and cultures (see the volume edited by Sternberg and Detterman, 1986, for a wide range of contemporary perspectives on human intelligence). Most theorists, however, would agree that neither problem-solving nor intelligence can or should be treated as a unitary concept or ability. For instance, a cognitive theorist would argue that intelligent behavior results from the operation of a number of highly coordinated and finely tuned component processes and knowledge structures that function within a given organism–environment context. From this perspective, the key to understanding any form of intelligent behavior is to focus on the operating characteristics of the component processes and structures that support the behavior in question. Comparative studies of information processing in various domains can provide valid evidence relevant to the null hypothesis; they can also facilitate our understanding of intelligence. Understanding *how* animals solve problems demands a clearer specification of the multiple factors that support intelligent behavior, not a broader definition of intelligence.

Consider next the difference between human and nonhuman intellect. Macphail argues that the critical difference is human language. This conclusion is based on two observations – that humans can solve a wider range of problems than nonhumans and that only humans acquire human language – and from one assumption: that the capacity for human language contributes importantly to human intellectual superiority. I welcome this bold assertion. Although human language is often assumed to be critical to higher cognitive functioning, the assumption is seldom clearly articulated and hence rarely examined (Anderson 1987). In fact, the role of language in human problem-solving and other nonverbal intellectual behaviors is not clear. Good research is needed, not unexamined assumptions.

Macphail considers the simplified accounts of why only humans possess human language. Humans may have human language because either they alone have sufficient intellectual capacity (a quantitative difference) or because they have a species-specific (human) language-acquisition device that enhances the intellectual capacity they share with other vertebrates (a qualitative difference). From this perspective, Macphail argues that the ability of nonhumans to acquire the rudiments of a humanlike language system would provide support for a quantitative, but not a qualitative, difference between human and nonhuman intellect. I have two main difficulties with this position. First, the acquisition of a variant of a species-typical behavior by a member of another species seems to be explicable in a number of ways. For instance, nonhumans may acquire some humanlike communication skills either because they have sufficient intellectual capacity, because they are able to apply some aspect of a species-specific device to the task of acquiring a new communication system (cf. Rozin 1976), or because of some combination thereof. Second, our understanding of human language, its relation to the communication systems of other species, and its role in thought is still limited. If we don't know what counts as good evidence of human language ability, how can the acquisition of an arbitrary system based on human language be critical to anything? Although "animal language" research continues to raise questions that enhance our understanding of human language in its many guises, the results are not relevant to Macphail's thesis.

In fact, acquisition per se does not seem to be the critical issue. A true test of Macphail's position requires a demonstration of how human language enhances the intellect (cf. Premack 1986). What can an organism do with human language that it cannot do without if? More generally, we need to determine how the species-specific device(s) of any species influence the intellectual capacities of that species. In all cases, care must be taken to distinguish between abilities that depend upon those devices and abilities that are most clearly realized through those devices. By focusing attention on the presumed centrality of human language in intelligence, Macphail serves the cause of human and nonhuman cognition well by stimulating thoughtful comparative research on language, cognition, and intelligence.

Efficiency, versatility, cognitive maps, and language

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Macphail's stimulating target article evokes the following responses from one who is interested in the function of the cerebral cortex and other so-called higher centres.

Efficiency. It doesn't make sense to conclude that there are no "quantitative intellectual differences amongst nonhuman vertebrates" because there is not yet any generally agreed upon definition of intelligence that enables a quantitative scale to be defined for it; therefore it cannot justifiably be said that quantitative differences either do, or do not, exist. Perhaps Macphail means that quantitative intellectual differences have not been demonstrated, but that would be a substantially different conclusion.

Unlike his book (Macphail 1982), Macphail's target article has a welcome new emphasis on association formation and the reason for its central importance, namely, that it can uncover the causal links in the environment. This not only reduces the gap between his views and those of other writers on learning (e.g., Dickinson 1980; Mackintosh 1983), but it also fits some current views on the function of the cerebral cortex (Barlow 1983, 1986; Phillips, Zeki & Barlow 1984), and furthermore it leads to a quantitative scale for one aspect of intelligence, though it is a scale that has not yet been used. [See also Smolensky: "On the Proper Treatment of Connectionism" *BBS* 11(1) 1988.]

Since the decision whether two events are associated is a definable statistical task, the Fisherian measure of efficiency (Fisher 1925) can be applied to it. The principle is to find how many instances are needed to establish the association with a known degree of reliability, and to compare this with the minimum number of instances that would theoretically be required; the nearer the first figure is to the second, the higher is the efficiency with which the brain uses the evidence available about the association. Since Tanner and Birdsall (1958) introduced the measure to psychology it has been applied to many aspects of sensation and perception, including the detection of symmetry (Barlow & Reeves 1979), which is in a sense an associative task, but I do not think it has yet been used for assessing the ability to detect associations in a learning experiment. Surely it is potentially a big step forward to be able to reduce this one aspect of intelligence to a definable, objectively measurable operation.

Versatility. It is easy to talk associationism, but hard to come to grips with the "numbers explosion" that associationism leads to. There are so many possibilities to be considered by any association-detecting system handling the large range of events used in psychological experiments that there are certain to be limitations; some of the possible associations will not be detectable. Hence versatility is bound to be at least as important a criterion for intelligence as the efficiency defined above, and it is less easily quantified. It is surely absurd to suppose that all subhuman species are equally versatile at association detection and, as before, Macphail presumably means that qualitative differences are undemonstrated rather than nonexistent. I suspect that he should be challenged about them being undemonstrated, for some of the evidence looks pretty convincing.

Cognitive maps. Judson Herrick (1924) likened the cerebral cortex to the filing cabinets in government offices, and the stored knowledge, cognitive maps (Tolman 1932), and working models (Craik 1943) in an animal's brain must be crucially important for intellectual behaviour. This aspect of intelligence is not very well tested in most learning studies, since experimenters understandably want to keep relevant aspects of their subjects' experience under their direct control, and hence avoid testing knowledge that the animals bring with them to their tests. In contrast, anecdotal evidence claiming to demonstrate animal intelligence very often implies that they understand some aspect of the environment better than might have been suspected. Whether or not such claims are right, the adequacy of the cognitive map an animal builds from its experience cannot be ignored in judging its intelligence, and I do not think Macphail pays enough attention to this.

Language. With regard to the crucial importance of language, Macphail is more likely to be believed, but his conclusion should provoke some questioning here too. Would't you expect talking and listening to convey just *information?* How then does it engender mankind's preeminent intelligence? Language is a versatile representational scheme for the environment we live in, and perhaps the major benefit it confers lies in the filing system it makes our brains adopt, rather than the information placed in that system through its use. This filing system has been evolved quite recently by our local tribe of conspecifics to suit our current surroundings, and it has the further advantage of being standardised, at least locally. It should be an enormous improvement on any ontogenetically determined filing system, particularly under conditions when the environment is changing rapidly.

To summarise, Macphail's target article is a powerful irritant, and it is to be hoped that the reactions it provokes will lead in the end to more sensible conclusions. Among these might be the recognition that association formation is a measurable operation, that its versatility as well as its efficiency is important for intelligence, and that language aids the efficient and versatile formation of associations through the representational scheme it confers, not simply through the communication it makes possible.

The supremacy of syntax

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The initial reaction to Macphail's target article from anyone outside the comparative intelligence community (and doubtless some within it) is likely to be one of incredulity. Is he claiming that, say, a frog and a dog share the same general intelligence? If so, why don't people keep pet frogs? Why don't they train them to come when called, or to retrieve twigs from ponds? Then the thought occurs that it may be the whole concept of intelligence that's at fault.

Macphail thinks it unnecessary to define intelligence; the lay sense is good enough. Maybe an even better idea would be to banish the word altogether. For if all it involves is the power to form associations, as Macphail suggests, this surely doesn't add up to what lay persons mean by intelligence (what makes dogs more fun to play with than frogs). It seems to me there really is a *scala naturae*, based not on the power to form associations, but rather on the variety and plasticity of the behaviors over which this power ranges. The reason you can't train frogs to retrieve twigs (I assume – I haven't really tried!) is because frogs can't do much beyond catch flies, jump in and out of ponds, mate, and croak. Certainly they don't pick things up in their mouths and play with them as puppies do, thus (even if their associative powers are on a par with a dog's) they cannot be operant-conditioned into doing the kinds of things dogs do. But to call behavioral variety plus plasticity plus associative power plus maybe other capacities "intelligence" is no help either. The narrow definition seems trivial; the broad one would merely label a ragbag of heterogeneous qualities.

There can be little doubt, however, that Macphail is right (if perhaps inconsistent) when he attributes our own species' "general intelligence" to the possession of language. What a relief it is to find a nonlinguist who does not chant the mantra "Language is function, language is communication"! No one would have much to communicate about (or think about) if language didn't first provide a structured inventory of the world's contents and principles that allow complex propositions to be formed quite automatically. Indeed, language is not merely the source of our peculiar intelligence, as Macphail argues, it also largely determines the structure of human theories and beliefs, as well as of many other species-specific behaviors (Bickerton, in press).

Macphail could make out a stronger case for language than he does. What holds him back, as it does everyone who sets foot in the field of "animal language," is the famous "problem of interpretation." If creature A learns X (X a plausible candidate for the category "feature of language"), has A learned (a part of) language? A simple question cuts to the root of this muddle.

Is language an indivisible whole, a list of heterogeneous (and perhaps independent) attributes, or some third thing? Many linguists would give the first answer, many psychologists would seem to assume the second. In fact, evidence from a variety of fields ("animal language," first and second language acquisition, pidginization, etc.) indicates that the third answer is correct (Bickerton 1987; in press). Language appears to consist of two tightly knit components, what Chomsky (1980) has called the conceptual and computational components, which normally act together but can be decoupled, and may have emerged at different stages of hominid evolution. The first involves the ability to use signs referentially, the second the ability to form complex propositions according to a set of highly abstract and task-specific principles. Trained apes, pidgin speakers, and children under two (among others) use the first (and earlier) component but not the second. They can arrange signs in ad hoc linear strings, but that isn't syntax.

Macphail, incidentally, seems to think apes can't use signs referentially, but he doesn't cite Savage-Rambaugh (1985), who answers the earlier criticisms he *does* cite and shows, to my satisfaction at least, that chimpanzees Sherman and Austin have mastered at least some aspects of true reference. I would suggest that in fact the species barriers are roughly as follows:

(a) Anything that can press bars or peck buttons can match signs with objects in its perceptual field and produce short strings of such signs where appropriate, which entails neither component of language.

(b) Primates (and just possibly dolphins) may, under intensive training, use signs appropriately in the absence of their referents, which entails the conceptual, but not the computational, component of language.

(c) Our species alone can acquire syntax, the engine of higher "intelligence."

There remains the residual problem "What is syntax?" This has been hopelessly muddied by the common assumption that syntax consists merely in arranging words in a regular serial order, or in using the same words in different orders to mean different things ("Me tickle Roger" versus "Roger tickle me"). In fact, syntax can use the same words in different orders to mean the same thing (as in (1)) or the same words in the same order to mean different things (as in (2)).

(1a) John gave Bill a book
(b) Bill was given a book by John
(2a) The woman hit the man that kicked the dog
(b) The woman that hit the man kicked the dog

As a further diagnostic feature, both "ape language" and human language contain "empty categories" – missing subjects or objects of verbs that are felt to be implicitly present. These empty categories (indicated by e in the examples that follow) are interpreted variably according to context in "ape language," whereas in human language they are interpreted unambiguously by applying fixed principles of interpretation:

(3) e eat orange
(4) John is too stubborn e to talk to e

The identity of e in (3) would depend on who had the orange and similar situational variables. In (4), regardless of context, the first e is interpreted as "anyone except John" and the second as "John." These features, together with recursiveness and others, always occur in clusters. That is, there is no language (nor has any animal ever learned a "language") that shows the phenomena of (1)-(2) without those of (4), or vice versa, or shows recursive embedding without (1)-(2) and (4), and so on. This suggests that we are dealing with a single system (the computational component) and not a mere list of features some of which might be acquired independently of others.

These are simple facts, not dependent on any particular linguistic theory, and they should be more widely considered. The question "Has it acquired syntax?" will then be easily answered, whereas the question "Has it acquired a part of syntax?" will be revealed as meaningless, since syntax (but not language) is indivisible.

Evidence of divergence in vertebrate learning

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To "show in general" how he arrives at the conclusion that differences in the intelligence of nonhuman vertebrates have not been demonstrated, Macphail considers the successive negative contrast effect, long known in rats but "elusive in goldfish." He cites the original experiment by Lowes and me (1967) in which successive negative contrast failed to appear, then some work with rats which suggests to him that "such failures could very well be due to inappropriateness of one of the contextual variables critical to the appearance of the effect" as, for example, the type of reward used or the response measured. Finally, although he admits they "leave much to be desired," Macphail cites two patently deficient papers by Breuning and Wolach (1977; 1979) that do report the effect in goldfish.

Other experiments. The wide range of conditions under which successive negative contrast has failed to appear in competent experiments with goldfish (Bitterman 1984; Couvillon & Bitterman 1985; Gonzalez et al. 1974; Gonzalez et al. 1972; Mackintosh 1971) is hardly suggested by Macphail's "review." Several types of reward have, in fact, been used (Noyes fish pellets, live *Tubifex* worms, and liquid foods differing in quantity or in quality), and a variety of responses have been measured (starting, swimming, and goal-entry in the runway, striking a target separate from the feeding place, and consummatory responding at a liquid feeder). Congruent results obtained in experiments of other designs should be considered as well. Rats extinguish more rapidly after training with large as compared with small reward (Gonzalez & Bitterman 1969; Hulse 1958; Wagner 1961) – a special case of successive negative contrast – but resistance to extinction in goldfish increases with amount of reward (Gonzalez et al. 1972); it was an early indication of this difference between rats and goldfish that prompted the Lowes experiment. Successive negative contrast is also a factor in the spaced-trials partial reinforcement effect found in rats trained with large reward (Gonzalez & Bitterman 1969; Hulse 1958; Wagner 1961). Goldfish (Schutz & Bitterman 1969) and African mouthbreeders (Longo & Bitterman 1960) fail to show the partial reinforcement effect in spaced trials.

Other vertebrates. Nor should experiments with other vertebrates be ignored. Successive negative contrast has been found in monkeys (Tinklepaugh 1928), in chimpanzees (Cowles & Nissen 1937), and, more recently, in didelphid marsupials of two species (Papini et al., in press). There has not yet been a conventional successive contrast experiment with pigeons, but they do show the spaced-trials partial reinforcement effect (Roberts et al. 1963). Results like those for goldfish have been obtained in work with descendants of older vertebrate lines – with toads (Schmajuk et al. 1981) and with painted turtles, who also fail to show the spaced-trials partial reinforcement effect and are more resistant to extinction after training with large than with small reward (Pert & Bitterman 1970; Pert & Gonzalez 1974). There is a pattern here that is meaningful with respect to the evolutionary relationships among the animals compared and not, I think, to be lightly dismissed by selective appeal to the inappropriateness of contextual variables. An explanation that is at least equally plausible is that the mechanism of successive negative contrast (whatever it may be) evolved in some common reptilian ancestor of birds and mammals. Supporting ontogenetic evidence is provided by the work of Amsel and colleagues referred to by Macphail, who treat age as if it were just another contextual variable.

Two questions. Macphail tends to run together two questions that should be clearly distinguished. The first is whether successive negative contrast is a general phenomenon of vertebrate learning. The second is how an animal who never showed the effect (if ever we could be convinced that there was such an animal) might differ from animals who do. I have suggested several possible answers to the second question, rejecting one of them on the basis of some work on within-compound association in goldfish that Macphail chooses to describe in detail. The work has absolutely no bearing on the first question, although Macphail implies that it has when he claims that "the apparent failure of fish to form expectancies has not been explained away as the effect of some unspecified contextual variable." In fact, failures to demonstrate successive negative contrast in goldfish are "explained away" in exactly those terms, and only in those terms.

Two null hypotheses. The null hypothesis accepted by Macphail and urged upon his readers is that there are no differences in the learning of nonhuman vertebrates. His acceptance of the hypothesis rests on his rejection of a second null hypothesis, which is that the mechanism of successive negative contrast does not exist in goldfish, although both hypotheses might conceivably be accepted since it is possible that whatever may be lacking in goldfish is not a learning mechanism at all (Bitterman 1975). Of the two hypotheses, it is the second which, it seems to me, is better supported by available evidence and should guide our future research. The danger inherent in accepting the first is, of course, that the range of animals studied will remain narrow and that we will remain ignorant of any broad divergences in vertebrate learning which may actually have occurred (Bitterman 1960).

Within-species variations in *g*: The case of *Homo sapiens*

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An auxiliary argument developed by Macphail to support his main thesis – differences in intelligence do not distinguish nonhuman vertebrates – centers on the fact that within-species variability, attributable to innate individual differences, is expected to be minimal or nonexistent. Obvious individual differences in human intelligence that we observe day-in and day-out are assumed to be the product of a species-specific language-acquisition device rather than to general intelligence.

There are two problems with Macphail's arguments: (1) cognitive-intellectual structures, which presumably are biologically rooted but which unfold as a function of specific environments, seem to precede the emergence of language skills, and (2) early appearing signs of g (or innate general intelligence) are characterized by extreme individual differences and appear to have dramatic consequences for academic performance and job success (Jensen, in press).

The first of these points deals with the issue of causal directionality: Does intelligence precede, follow, or coexist with language devises? In point of fact "innate" intelligence may be a forerunner of the language-acquisition device that Macphail uses to account for the superior intellects of humans. If language itself can be shown to be dependent on cognitive structures, and if these structures show striking individual differences, then much of the observed variability in human intelligence – variability that distinguishes mentally retarded, average-ability, and gifted individuals – is, in fact, rooted in innate structural differences (Borkowski 1985). Kahn (1975; 1981) has shown that language acquisition in profoundly retarded children is dependent upon their development of sensorimotor skills. Furthermore, developmentally delayed children, trained to stage six in the sensorimotor period, showed sizable gains in language acquisition. These data suggest two facts relevant to Macphail's argument: Early-appearing individual differences characterize the acquisition of sensorimotor skills and also predict the subsequent emergence of language, especially when its development is set into "slow motion" by gross impairments in central nervous system functioning. The point to be made is that all later-appearing, higher-order intellectual skills (such as executive functioning or insight) might be proximally related to Macphail's language-acquisition device but, in fact, are remotely (and fundamentally) linked with innate differences in intellectual structures. The remainder of this commentary focuses on the nature of these structures and the importance of their varition in individuals.

Perhaps the most striking demonstration of individual differences in Spearman's g has been promulgated by Jensen (1981; in press). Jensen's theory rests on the repeatedly demonstrated relationship of g with speeded information processing. For example, the slope of the reaction times (RT) for simple and complex tasks is related to biological substrates (e.g., the averaged evoked potential); it is relatively stable across time and settings, and predictive of important real-life achievements such as academic success. It is likely that speed of processing information is a fundamental aspect of human intelligence, accounting for many of the differences we observe among individuals.

Bachelder and Denny (1977) have emphasized "span ability," a structural and innate aspect of intelligence, as the cornerstone of their theory. Span ability is whatever makes it possible to achieve a particular level of "span" – with span "defined as the highest level of task complexity that yields a consistently high level of accurate performance" (p. 135). What is important about the concept of span is that it forces the sensory-perceptual system to maximum efficiency if a high degree of task complexity is to be mastered (e.g., reporting a string of 9 digits).

Bachelder and Denny (1977) have presented several important arguments about the nature of span ability. (1) Production of a response string in a span test occurs because *each* stimulus element elicits *each* response element in the string. (2) Span does not measure associative memory; rather, it involves an assessment of the perceptual system. (3) It is insensitive to improvement through practice. (4) It follows a regular developmental sequence, reaching a plateau in early adulthood. (5) It is correlated with other measures of intelligence (e.g., WISC full scale) and (6) It is useful in the theoretical understanding of individual differences in tasks that reflect human intelligence, such as discrimination learning, language development, and reading.

If Bachelder and Denny's analysis is tenable, then span ability reflects a fundamental architectural feature of intelligence: the efficient registering and reporting of a string of information. There is obvious overlap between Bachelder and Denny's notion of span and Jensen's use of speeded efficiency in processing of information. Both procedures, span and RT, require the organism to function efficiently while perceiving and reporting information of both a simple and complex nature. How rapidly the organism responds in the face of challenge defines a major, early-appearing, innate aspect of human intelligence. Within the human species, both span and RT have been shown to vary directly as a function of age and IQ. I suspect similar individual differences in more biologically based components of intelligence might be found within other species as well.

It is important to note that architectual features – such as speed of processing and span of apperception – have long been the centerpieces of intelligence theories, from Aristotle to Binet to modern-day theorists (e.g., John Horn and Ann Brown). Higher-order mental processes, such as metacognition and insight (Borkowski 1985), arise as much from the architectural base as from Macphail's language-acquisition device. Furthermore, variability within species and mean differences between species are probably tied to fundamental differences in the architectural aspects of general intelligence.

Although many other examples could be marshaled concerning the importance of variability in human perceptual processing – such as Fagan's (in press) recent demonstration of the fundamental role of recognition memory in the first year of life for the appearance of more complex forms of intelligence at ages 3 and 4 – the more general issue has been sufficiently documented: Individual differences in fundamental aspects of information processing develop early in life, are rooted in biologically based structures, and seem causally related to the appearance of more complex intellectual skills. In fact, it is plausible to argue that variations in the language-acquisition device itself are linked closely to more fundamental cognitive skills (speed of processing, span of exception, and recognition memory) and cognitive structures (sensorimotor development). In this sense, individual differences in the language-acquisition device are a consequence of more basic "signs" of human intelligence.

Animal intelligence: A construct neither defined nor measured

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I shall comment first on some focal issues in Macphail's target article and then more briefly on some more peripheral issues. The most critical problem I see with the paper is the failure to come to grips with the problem of defining intelligence. Macphail provides two reasons: "We all – as speakers of English, rather than as psychologists – know what 'intelligence' means" and "there are disadvantages in attempting a formal definition." Macphail is right that "a conventional understanding of the term 'intelligence' *is* sufficient to delineate our general area of interest." Students of "aggression" have successfully done without a definition for years. The problem comes when one goes beyond this to reify the construct; this is what Macphail does. He invests the construct with a reality that is to be quantified and compared across species. Some species have more of this "stuff" than others. We read that "Intelligence is a capacity of adaptive significance, so if within-species endemic variation were available, there would exist a selective pressure in favor of those possessing higher intelligence." We are also told of "the major empirical question: What species differences in intelligence have been demonstrated by experimental investigations?" With such uses, Macphail goes well beyond the mere delineation of a general area of interest, investing the construct of intelligence with a reality that is to be quantified and compared across species. If this is to be attempted, the problem of definition cannot be bypassed as Macphail attempts to do.

Macphail addresses the "central question" of whether species differences in intelligence have been demonstrated. In order to compare, we must first measure. He is fully aware of at least some of the difficulties of making these comparisons, such as species differences in sensory, motor, and motivational systems. After surveying the literature, Macphail concludes that he cannot reject the null hypothesis of a lack of species differences in intelligence (Macphail 1985). Given the lack of a precise definition and a rather loose working definition as "general problem-solving," the failure to reject the null hypothesis should come as no surprise. What is an "arbitrary, nonnatural" problem? How can we possibly present problems that do not create a bias favoring some species, such as the use of visual stimuli, with which species such as birds and primates do so well? With olfactory stimuli the performance of rodents is much closer to that of primates than when they are presented with visual problems (e.g., Slotnick & Katz 1974). These and other complexities overlie the substance that Macphail believes exists and wants to measure; they make it nearly impossible to measure intelligence unmasked. We thus have a construct that is neither defined nor measurable. The case for the utility of the construct is not made effectively.

Macphail is right that when the early literature on "biological constraints" was first developing it was presented as an alternative to general process learning theory. However, various authors have shown that a reasonable rapprochement between the constraints of literature and process-oriented theory can be effected (e.g., Domjan & Galef 1983; Garcia & Holder 1985). It is quite possible that one or a small number of learning mechanisms serve a wide range of uses in different species. However, the ways in which these common mechanisms are used may differ greatly. Indigo buntings attend to patterns of star movement and can orient in relation to what they learn (Emlen 1972). Marsh tits are remarkably effective at finding their food hoards (Shettleworth & Krebs 1982). Socially foraging marmosets display remarkable one-trial learning (Menzel & Juno 1985). Such demonstrations need not be treated as a challenge to general-process learning theory but suggest predispositions in the application of learning processes to ecologically relevant situations in ways more complex than those suggested by Macphail. It is likely to be the ability to solve real problems that recur in nature that confers differential reproductive success, not the possession of more "intelligence." However, no fundamentally new mechanisms would be required. In such contexts, the meaning of "intelligence" remains obscure.

Several other issues concern me: (1) Macphail perpetuates the view that throughout the century there have been declines in ranges of both the species and problems studied in comparative psychology. A case can be made that the analysis on which this conclusion is based is flawed (Dewsbury 1984, pp. 18–26). (2) Macphail would restrict comparative psychology to work in which there is a clear attempt to compare and contrast species. I disagree (Dewsbury 1984, pp. 2–8). (3) Macphail seems to favor a return to "what was, after all, originally the main goal of comparative psychologists: establishing the course of evolution of intelligence." I agree that this was close to the original goal; it remains a goal. However, it became clear that such questions could not be readily addressed without a firm understanding of the species under study and of its naturally occurring behavior and ecology. The goals of comparative psychology have changed and broadened as new knowledge has been gained. Neither chemistry, nor genetics, nor comparative psychology was bound to the goals of its founders. (4) I balk at the logic that permits Macphail to go from the demonstration that goldfish form within-compound associations to the conclusion that they form "expectancies." (5) I agree with Macphail that meaningful comparative research can be conducted on distantly related species. However, I would emphasize that the processes of evolutionary differentiation are most likely to be elaborated with comparisons at the "species" level (King 1970). The logic of this conclusion does not depend on the acceptance of the notion of anagenesis.

Macphail has tackled some very difficult problems – problems that all comparative psychologists would like to see solved. Although one must admire his fortitude in addressing these issues head-on, I fear that not much headway has been made.

Comparative cognition: Inadequate approach, precipitate conclusions

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There is certainly general agreement with Macphail that "establishing the course of evolution of intelligence" is a main goal of comparative psychology. That goal, establishing the course of evolution, is shared with other fields such as comparative anatomy, physiology, and ethology. In those decades when comparative psychology was focused on rats and preoccupied with the assumption of uniform vertebrate intelligence, knowledge was accruing in other disciplines concerning the mechanisms of evolution and how it should be studied. We would be wise to consider those achievements when resuming comparative studies of intelligence. Macphail ignores them and thus repeats old fallacies.

A core result of evolutionary investigations is that equality of a performance in itself says *nothing* about its evolution. Identical outcomes can be the result of common origin (homology), but also of convergence from different origins (convergent homoplasy) or of common evolutionary pressures in species of the same taxon (parallel homoplasy). The case is only slightly better with different performances. Differences show the variety that can appear and need explanation – and that is an important reason for collecting data from different animals and ecologies – but any particular difference may follow from early divergence or from apomorphisms.

Neglecting this problem, Macphail equates rules of performance with the underlying mechanism and thus identifies similar outcomes with homology – "The widespread distribution of similar learning phenomena is positive evidence of the equally widespread distribution of identical underlying mechanisms" – which is incorrect. As a consequence, all discussions based on this assumption, such as anagenesis or general process theory, are obsolete. As long as we remain only at the level of comparing performances, we will not solve these problems and will be no better off than comparing legs by their performance (e.g., detecting that the dolphin's fin is most similar to that of fish).

Ignoring homoplasy is more serious. Macphail points to a very powerful potential source of convergent and parallel evolution, namely, the causality of the world. This causality sees to it that under particular circumstances a specific behavior is consistently rewarded or punished, or that after one event another event consistently follows or is absent. A species that can adapt to such relations by forming operant associations, classical associations, or by habituating, may have a better chance to survive than one that cannot. Due to the uniform and pervasive nature of causality, the general rules of such relations are independent of the correlated events. This supports the evolution of common rules for the formation of the corresponding associations throughout the animal kingdom, vertebrates *and* invertebrates. The existence of such common rules for the outcomes, however, by no means implies that the underlying mechanisms are identical. There are many examples of equal abilities that have evolved independently several times and are based on different mechanisms. The same argument applies to other forms of intelligence.

A general procedure used to test for homoplasy is to examine additional characters which are connected with the one under investigation but not subject to the same evolutionary pressures. Consider the neural basis of intelligence, for example: If an apparently similar learning process in two species occurs by changes in mutually nonhomologous neurons, then the learning is not homologous, no matter how similar the outcome. Such approaches could contribute considerably to questions about general or specific capacities. [See also Ewert: "Neuroethology of Releasing Mechanisms" *BBS* 10 (3) 1987.]

A second criticism concerns the supposed pattern of intelligence. Evolution selects for successful solutions without bothering about whether a problem has been solved by a new specialized capacity or by the expansion of a preexistent capacity to a more general one. Hence we might find a variety of specialized and more general intellectual capacities, and these could even cooperate in some tasks. As Macphail states: "It is an empirical matter . . . whether there do exist mechanisms involved in problem-solving that are common to different species." As a consequence, as long as we cannot decide between alternatives, our approaches and concepts must be equally open to all of them. This openness is lacking in Macphail's target article. The arguments run in terms of a uniform *scala intelligentiae* rather than a phylogenetic tree of intelligence, and intellectual differences are only considered in more-or-less terms: "quantitative difference," "qualitative difference" (which means in this paper that one species has capacities *in addition* to all of the other species), "wider range of problems," "superior intelligence," "level" and "grade of intelligence," and so on. These differences refer not simply to specific tasks, but to the intelligence of whole species. Consequently, Macphail sees only "two ways quantitative differences in intellect might manifest themselves" – namely, that one species is inferior to another at all or at only some tasks – and he disregards the possibility that both species may excel independently at different tasks.

It is evident that the *scala intelligentiae* model has considerable methodological implications (e.g., regarding which differences are acknowledged as "relevant" and, accordingly, how to test for these differences). Unfortunately, the criterion for the relevance of a difference remains vague. Another implication concerns what should be investigated. Macphail's reference point is human intelligence – the top of the scale – with its "very general . . . range of application." In an evolutionary context, however, to be a generalist is but one type of specialization among many. Surely it is interesting to see how this particular specialization has evolved, but to study the course of evolution in intelligence we have to consider all forms of intellectual development.

Finally, the "conclusion" about the evolution of intelligence is not justified. First, Macphail emphasizes that no intellectual differences between animals have been demonstrated because testing has been insufficient. This, however, implies that his hypothesis has not been tested sufficiently either. Second, he describes "problem-solving as an important aspect of intelligent behavior", but "very little attention was paid to the literature on that topic . . . because that literature is not comparative." Not only is the criterion of neglect not tenable (what would remain if it were applied to the literature on human intelligence?), but this statement means that the hypothesis has not been tested at all with regard to this important aspect. Third, the sample of species tested for intelligence is insufficient and biased with regard to learning. Less than 1% of vertebrate species have been tested rigorously, their phyletic distribution is extremely uneven, and the majority of taxa have never been tested. Moreover, one of the criteria for testing a species is its readiness to demonstrate learning in situations designed by humans, or in other words its similarity to learning in humans. No one has tried so far to find out why amphibians or other species are so refractory to conditioning based on human experimental designs. Thus, instead of being able to adopt a null hypothesis, we have only an untested hypothesis. To propose adopting the null hypothesis is to purport sufficient knowledge in an area where the data are insufficient to support any assumption about the evolution of intelligence.

It is of merit that Macphail forces a confrontation with the issue of the comparative investigation of intelligence. Nevertheless, the approach he offers does not meet the complexities of evolutionary processes. It is premature to draw conclusions about the course of evolution in intelligence. The comparative study of vertebrate intelligence has just restarted after decades of silence, and there is not even a methodological agreement among the investigators yet. This new growth should not be stunted by narrow views or precipitate conclusions.

The several meanings of intelligence

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Psychologists have always been at daggers drawn in their discussions of intelligence, not so much because their views differed, but because they were talking about entirely different concepts. There are at least three different meanings of the term "intelligence," and what is true of one may not be true of another. The first meaning of the term refers to *biological* intelligence, that is, the structure of the nervous system which enables us to behave intelligently – learn, memorize, solve problems, and so forth. It is this sense of intelligence that distinguishes us from stones, trees, and black holes.

Second, we have *psychometric* intelligence – intelligence as measured by IQ tests. These usually aim to measure biological intelligence, but fail to do so because performance is, to some extent at least, influenced by social factors such as education, culture, and parental upbringing. The fact that IQ tests show a strong genetic determination, amounting to something like 70%, indicates that biological intelligence does play a prominent part in IQ measurement, but it also indicates that environmental factors, too, are important. Hence psychometric intelligence is not to be identified with biological intelligence (Eysenck 1979).

Third, we have what may be called *social* or *practical* intelligence, that is, the application of IQ in practical situations of everyday life. Practical intelligence is often equated with successful adaptation, and no doubt successful adaptation is to a large extent determined by IQ, but there are also a large number of other factors which come into this, from health and drinking habits to personality and the socioeconomic status of one's parents. The concept is too broad to be of any scientific use, but many of the writers cited by Macphail in the animal field do seem to adopt such a conception.

It is difficult to define a concept like intelligence without specifying the phenomena which justify us in postulating it. In the case of humans the evidence is essentially that (a) all cognitive tests intercorrelate positively (a positive manifold) [See Jensen: "The Nature of the Black-White Difference on Various Psychometric Tests" *BBS* 8(2) 1985.] and (b) the matrices of correlations so produced are usually of a low rank and may under specifiable circumstances reduce to unit rank. It has proved difficult to account for these facts other than by postulating a concept of general intelligence (*g*), and the psychometric evidence collected justifies us in doing so (Eysenck 1979).

A scientific approach to the question of intelligence in animals would require us to proceed along similar lines. There are many proposed tests of intelligence for say, rats, such as the mazes test, the Lashley jumping stand, and so forth; a proper investigation of the concept of intelligence in rats would require us to use a fair number of these on a group of rats, to calculate the correlations between them, to show the existence of a "positive manifold," and to demonstrate also the existence of a low rank in the resulting matrix of intercorrelations.

This has never been done, and such correlations as have been observed are relatively low, and may be nonexistent, suggesting that these are not tests of a general factor of intelligence. There are of course many great difficulties in carrying out work of this kind. Strong fear reactions may cause a rat to freeze, or to react in unpredictable ways, thus creating difficulties in measuring his potential for solving the problems involved. There are many other difficulties, but the main one seems to have been an absence of training in psychometric principles on the part of animal psychologists and a general disdain for such apparently nonexperimental procedures and considerations. Nevertheless, it remains true that until and unless such studies are done, we cannot rationally talk about "intelligence" in subhuman species, we cannot affirm the existence and relevance of such a concept for animals, and we certainly cannot compare one group of animals with another along scientific lines, even though from a common sense point of view a monkey is clearly more intelligent than an earthworm which may only mean that certain innate reaction patterns are different, and both may be equally adaptive.

Are there differences in intelligence between one earthworm and another, or between one monkey and another? Was Sultan really superior to his colleagues in intelligence, or was he merely less emotional? These questions cannot at the moment be answered, because of lack of evidence. What is needed is a combination of experimental and psychometric skill to be brought to bear on this particular problem. Until this is done, we simply do not have the basic facts to make any judgment on the problems raised by Macphail.

Chimps and dolphins: Intellectual bedfellows of the goldfish?

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I am in sympathy with most of Macphail's thoughtful review. However, I believe that his final secondary conclusion – that human and nonhuman intelligence is differentiated "by the existence of a species-specific language-acquisition device" – is unwarranted at this time. In his final paragraph Macphail warns of the "natural tendency to regard a monkey as being more intelligent than a frog, and so to accept as genuine tests of intelligence tasks in which the monkey outperforms the frog." A similar natural tendency applies if for "monkey" we substitute "human" and for "frog" "nonhuman." Assume, for example, that several attempts to train pigeons to emit random sequences failed but that humans were shown to acquire this ability. We might be quick to regard this as an example of superior problem-solving in the human and to leave it at that. But suppose instead that the opposite occurred; humans could not be trained to emit random sequences but pigeons could. As of 1985 the results supported the latter conclusion. I don't think anyone would take this as evidence of superior problem-solving in the pigeon. Instead, more careful experiments would be done to show that, with appropriate training humans too could behave randomly (see Neuringer, 1986, for the relevant confirming work with humans and a review of the earlier work).

There is, however, a more serious and *unavoidable* bias inherent in any comparisons of human and nonhuman problem-solving: All the problems are designed by humans. Given this fact, together with what we know – and Macphail amply demonstrates – about the vast influence of contextual variables (involving perception, motor skill, motivation, and other basic attributes of problem-solving) on problem-solving performance, how can we ever presume to have a reasonably constant basis of comparison, for example, a "species-fair" set of tasks?

There are other reasons for being unenthusiastic, not about comparative psychology, but about the comparative psychology of intelligence. These reasons may be inferred from the target article. In the first place, we don't know how to define intelligence. Macphail wisely avoids defining intelligence, giving two reasons. The first, that "we all . . . know what 'intelligence' means," I found baffling. In any event, my own disagreement disproves the statement. The second reason given simply underscores the difficulty of agreeing on a reasonable definition. Even if we assume we know what intelligence means, however, we also know that its measurement is fraught with difficulty even in comparisons within a species. A variable such as delay of reinforcement may have a profound influence on some types of problem-solving (e.g., those involving self-control or foraging) but very little influence on others (e.g., those involving taste aversions) (Fantino & Abarca 1985; Fantino & Logan 1979).

Given the enormous difference subtle contextual variables may make, how is one to ever conclude with confidence that the null hypothesis with respect to species intelligence differences may be rejected? The answer in the target article is appropriate with respect to nonhuman vertebrates: One cannot reject *this* null hypothesis. I would go a bit further in two respects: (1) I don't see what data might have permitted us to reject the null hypothesis with reasonable confidence – this null hypothesis is one which is almost inviolate *in principle;* (2) instead of adopting the null hypothesis of the target article – that nonhumans cannot acquire grammar – and the additional assumption that this difference underlies a putative superiority in human intelligence one might more conservatively adopt the null hypothesis that there are no differences in intellect among vertebrates. Most of the arguments in Macphail's engaging article are more consistent with this stance, as are the difficulties in defining intelligence and in conducting species-fair tests of intelligence.

In conclusion, I find it implausible to assume that only humans can acquire language in the face of suggestive work to the contrary with chimps and especially the ongoing unpublished dolphin work of Herman and his colleagues (Savage-Rumbaugh et al. 1983). The possiblity of *a continuum of linguistic skills* remains strong. The effects of Macphail's implausible assumption are compounded when a major intellectual dichotomy – that between humans and nonhumans – is based entirely on this assumption. In fact, these two conclusions lead the author to lump the chimp and dolphin together with the goldfish while leaving humans occupying a conveniently exalted and isolated position. This implication should be enough to suggest that something is seriously amiss.

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Artifactual intelligence

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Macphail favors a comparative psychology of intelligence based upon the core assumption – the "null hypothesis" – that there are no species differences in nonhuman vertebrate intelligence. Tests of this hypothesis with distantly related species are to be carried out in "arbitrary" situations, a strategy that, it is claimed, will reveal whether learning mechanisms are specialized adaptations to niche-specific challenges or common solutions to problems posed by global characteristics of a world in which all species have evolved. At present, Macphail finds no evidence to refute the null hypothesis. We share the optimism for finding common mechanisms, but we don't believe that this translates into a common metric for intelligence.

"Intelligence," like any construct, is an artifact; it is useful to the extent that the manner in which it is defined resonates with the regularities in our world. How is it defined? Macphail is not of much help here. Wittgenstein tells us to look for the word's use in its natural language game. This doesn't help much either, for the usage in the vernacular is too varied to permit extrapolating all the way to nonhuman animals. We favor a version of Sternberg's (1986) definition – intelligence is the successful selection of, shaping of, or adaptation to the environment relevant to one's life – an evolutionary biologist might paraphrase this as goodness-of-fit to one's niche. If this is accepted, we see that intelligence is niche-specific; another human's "intelligence" is always estimated relative to what *we* would do in that situation, not to what our canary would do. Intelligence may be compared only when animals compete for the same niche; behavior that is intelligent for a teamster may be dumb for a teacher.

But there are some general selection pressures, for example, gravity (except for tiny creatures) and georhythmicity (except for benthic creatures). Events move forward in time; temporally and spatially contiguous events are more probably causally linked than noncontiguous ones. There are also general adaptation strategies, such as building a model of the relevant parts of one's niche so that one can anticipate important regularities (as evidenced by circadian rhythmicity). As Macphail suggests, one can accomplish this through causal modeling that may have some general properties, despite its superficial differences, and despite the tendency for successful models to become hard-wired reflexes. We expect that when viewed as a process of causal inference (e.g., Killeen 1978; Revusky 1985) the mechanisms of learning might be very general indeed.

Similar issues have been raised recently by Shepard in connection with human cognition. In a recent series of papers (e.g., Shepard 1984; 1986) he has outlined a view of perception and mental representation that is in many ways an extension of James Gibson's ecological approach (e.g., Gibson 1979). Chief among the relevant points are the following: (1) that the perceptual and/or representational system has evolved over evolutionary epochs in such a way as to allow the pickup of invariants corresponding to objects and events in the world, (2) that the invariant features of the world have become genetically internalized and serve to guide perceiving, imagining, thinking, and dreaming, and (3) that the important invariants are features common to all niches. These points are summarized by Shepard (1986):

> Considerations of the evolutionary basis of behavioral predispositions usually focuses on those predispositions that are characteristic of a particular species. The uniqueness of such behavior attracts our attention and motivates us to look for a special property of that species' ecological niche that might have favored genes for that particular behavior. However, some properties of the world are so pervasive and enduring as to be relevant for the success of a broad spectrum of species. I argue that in the evolutionary long run, these general properties would tend to become genetically internalized. Each individual animal would then not have to learn about each such property "de novo" by trial and possibly fatal error (p. 1)

Macphail treats the detection of causal links as a necessary prerequisite to prediction in all environments. Spatial (e.g., Bowe 1984) and temporal (e.g., Mackintosh 1974) constraints on conditioning may thus reflect fundamental causal constraints shared by all terrestrial environments. Many of the basic "facts" of learning (e.g., US [unconditional stimulus] habituation, latent inhibition, US intensity effects) follow from this view, perhaps reflecting internalized invariants of causal inference (see Revusky, 1985, for a convincing demonstration of this point).

The notion that general properties of the world have been internalized requires a theoretical and experimental program that proceeds along two fronts (Shepard 1981). First, we need to identify the relevant invariants. Some may be relevant to all environments, others to particular classes of environments; there may in fact be a hierarchy of relevant properties. Second, we must seek to relate patterns of behavior to these invariants. The methods advocated by Shepard and others (e.g., Revusky 1985) are radically nonecological, involving laboratory experimentation in "arbitrary" situations, methods that have been criticized by scores of ecologically minded behavioral scientists (e.g., Johnston 1981; Schwartz 1974). Arbitrary situations may serve to illuminate the influence of internalized invariants in ways that naturalistic situations cannot, however. In the case of visual perception, results obtained under restricted or impoverished viewing conditions (e.g., the Ames room) have served to elucidate the rules of perceptual inference that are otherwise transparent (Shepard 1984). For the study of learning, misbehaviors may provide the same sort of evidence for a general learning process.

The points we have raised should be qualified in several respects. First, although rules of causal inference may be similar for all environments, the mechanism of adaptation may be different for different species. This seems unlikely, but as Lehrman (1970, p. 28) put it, "nature selects for outcomes, not processes of development." Second, there are alternatives to the either-or positions implied by ecological and general-process views. One has been suggested by Rozin (1976a), who states that intelligence should be considered as increasing accessibility to adaptive specializations that originated as solutions to specific problems. The specializations can be viewed as modules that, when linked together, confer very general problem-solving abilities, an approach that brings to mind the modern faculty psychology of Fodor (e.g., Fodor 1985).

We believe that the study of these issues will be very fruitful, but they should not be the tail of a kite raised by the bluster of "intelligence." Different environments will demand different amounts of problem-solving. Are we to call *Limulus* dumb because it fails to master shift-reversals, despite mastery of its niche for tens of millions of years? Consider the validation of the Wechsler by placing subjects in "arbitrary" environments – Arctic tundra, Brazilian rain forest, Australian outback, midtown Manhattan . . .

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Cognitive science and comparative intelligence

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The good news, with which I concur, is that comparative psychology is as valuable scientifically as, say, comparative anatomy or physiology, and that a focus on the construct of "intelligence" makes sense even if it does not lead directly to an understanding of how it evolved. The bad news is that, given the emphasis over the years on the ability to solve certain kinds of "complex" problems, there is no convincing evidence for differences in the "mechanism" of intelligence used to solve such problems across nonhuman vertebrates.

The equation of intelligence with the ability to solve problems of a certain sort or in a certain way neglects other important aspects of the range of behaviors thought to be intelligent. In contemporary cognitive psychology, which is presumably the area of human psychology most concerned with "intelligent" behavior, problem-solving has certainly become of increasing interest; few texts, however, devote more than several chapters to problem-solving as such, usually toward the end (along with language, I might note). Other major themes include: the representation of information, and the coordination of "analog" and "semantic" forms of knowledge; perceptual and motor skill; attention and the ability to flexibly "allocate resources" among concurrent tasks; and remembering as a form of skill (cf. Anderson 1985; Glass & Holyoak 1986).

Among those with a more comparative orientation, Bindra (1976), for example, includes only one chapter on problem-solving. His view of intelligent behavior includes: flexibility of goal-directed behavior, rather than goal-directedness as such; the range and level of transfer of learning, rather than rate of acquisition; the degree and remoteness of foresight, or the extent to which current behavior is controlled by probable future events; the uncertainty in predicting details of an organism's actions in the performance of a certain task; and the subjective experience of "consciousness," which a cognitive scientist might equate with the ability to build and maintain a representational model of the environment (pp. 3–14). In her coverage of primate intelligence, Jolly (1985) includes chapters on tool use, which we might broaden to "perceptual-motor skills," a Piagetian analysis of conceptual skill, which includes the traditional laboratory tasks such as delayed match-to-sample, language, of course, and, interestingly, chapters on social learning and on play.

The implication is that intelligence comprises a wide variety of skills and abilities, including abstract representational skills, an extensive repertoire of knowledge and strategies, and learned aspects of perception and movement which are sometimes excluded in the comparative laboratory as just the kinds of things that "contextual variables" affect. A more catholic view of what constitutes intelligent behavior might derive "information-processing components" or mechanisms other than association formation that differentiate among contemporary species in a way more consistent with our everyday experience, and with our knowledge of neurophysiological differences among species.

Since many of the tasks used in the comparative laboratory were derived from an associationist framework in the psychology of learning, it is not surprising that we arrive at association formation as the suggested universal "mechanism of intelligence." This may be misleading. It seems analogous to demonstrating that, at a genetic level, the "process" of transcription and the genetic "code" are universal across vertebrates, and concluding that there is therefore no difference in the genetics of these species, or showing that there is a universal mechanism of synaptic transmission and thence concluding that all brains are equally competent and there are no differences in neural "mechanisms."

An analogy to attempts to develop intelligence in artificial systems may be useful. The "basic mechanisms" of "unintelligent" and "intelligent" artificial systems are universal, much as those of association formation might be argued to be. But the question remains whether, in order to build or to understand such a system, more complex structures and operations need to be included as primitives in programs for them to behave in an intelligent fashion and for us to be able to describe them in a scientifically satisfying way.

Artificial intelligence may be offering a case study of the evolution of intelligent systems at this more molar level of analysis. There is a great deal to learn from the specific instances where, in making a system more intelligent, an AI programmer develops processes or structures, independently of psychological research, that converge with mechanisms also described by that research.

This notion of convergence among artificially and naturally intelligent systems also suggests a strategy for the comparative study of intelligence; namely, to look not for evidence for "anagenesis" of intelligence, with the same stages observed across diverse species, but for a convergence from diverse origins toward similar intellectual abilities. This, more than anything else, would suggest the evolutionary and environmental constraints on intelligence and its "natural structure." In comparative anatomy, we have the analogy of convergent evolution of lens structures of the eye, for example, among certain vertebrate and nonvertebrate species. In comparative linguistics, recent work on "creole languages" provides another analogy for descriptions of convergent evolution, here of grammatical structures. [See Bickerton: "The Language Biogram Hypothesis" *BBS* 7(2) 1984.]

All this suggests an important place for a comparative psychology of intelligence in the more rigorous view of intelligent systems that we hope is emerging in cognitive science. For my own part, Macphail correctly predicts that while I haven't given up my biases about intelligence among animals, I'm at least more ready to consider the null hypothesis as one to be tested. As an undergraduate, I spent a series of weekends trying to get goldfish to avoid a shock in a shuttle maze. As I listened to the crowd cheering in the football stadium, and watched trial after trial as the goldfish serenely ignored the imperative light stimulus, I concluded that goldfish, after all, were not very bright. But now I realize that in contrast to his experimenter, the goldfish could at least escape the noxious situation.

Wither comparative psychology?

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Even more remarkable than the great diversity of living forms is Macphail's denial of diversity in the intellectual processes of vertebrates, barring only humans, who are granted special status owing to their possession of language. If Macphail is right that there are no differences in "intelligence" among nonhuman vertebrates, then surely there is little point in pursuing research in comparative psychology. We find Macphail's "null hypothesis" to be ill-founded, implausible from the standpoint of neurobiology and evolutionary biology, and at odds with a diverse body of knowledge from cognitive and developmental psychology. Indeed, we feel that the null hypothesis merely restates the historical bias in learning theory against phyletic differences, a bias which has been destructive to the enterprise of comparative psychology.

A central problem with Macphail's argument is that he virtually equates intelligence with associative processes, that is, those processes that involve repeated pairings of stimulus events and responses. The only other processes allowed in Macphail's psychology of learning are habituation (nonassociative learning), latent learning ("at least, not overtly" associative) and language learning (the only phyletic specialization allowed). More complex cognitive tasks such as concept formation and learning-set formation can, in his view, be reduced to associative processes. Although we do not deny that associative mechanisms are common to all vertebrates, including humans or that they account for various and important learned responses in their behavioral repertoires, we do not share Macphail's conviction that cognition can be entirely reduced to associations. One kind of intelligent behavior that cannot be easily reduced to associative processes is behavior based on short-term or working memory. In working memory, unlike associative learning, the relationship between stimuli, responses, and reinforcements changes from trial to trial in an unpredictable manner and, by definition, responses must be executed on the basis of remembered, trial-specific information. Examples of experimental paradigms based on short-term memory mechanisms include the spatial delayed-response test (Goldman & Rosvold 1970; Jacobsen 1936) and the delayed matching-to-sample and nonmatching-to-sample tasks (Mishkin 1978; Zola-Morgan & Squire 1984; 1985). These tasks are used in studies of learning and memory with both humans (Friedman & Oscar-Berman 1986) and macaque monkeys (see preceding references).

According to Macphail an associative learning mechanism is a "device whose function was to detect contingencies between environmental events." It should be underscored that such a mechanism is actually antithetical to performance on working memory tasks because any tendency to repeat a previously reinforced response or to adopt a strategy like "win-shift" will undermine performance on these tasks. In working memory tasks, the animal must "erase" the information that has guided its just-completed action. It can be argued that the evolution of a working memory mechanism allows the regulation of behavior by mnemonic representations of stimuli rather than by the stimuli themselves (for review, see Goldman-Rakic 1987).

The point we wish to make is that it is only by restricting his definition of intelligence to associative learning processes that Macphail could reach the nihilistic conclusions that there exist *no* species differences and *no* individual differences within species, including humans. Indeed, the logic of his argument seems to entail that the *development* of intelligence in an individual is nothing more than the accumulation of associations. There is no room in Macphail's psychology for the maturational changes in cognitive structure that have been demonstrated by Piaget and many other developmental psychologists. This is a particularly important point, because if different cognitive organizations can exist at different points within the life of an individual, then it is plausible to suppose that different cognitive structures – diverse intelligences, if you will – could have evolved in different animal phyla.

In evaluating Macphail's "null hypothesis," it is important also to consider the evidence of comparative neuroanatomy. Lashley's view that mammalian species vary only in the amount of cortex that they possess, and not in its intrinsic connectional organization, has been a powerful influence for forty years and is compatible with general-process, associationistic psychology. The last decade's revolution in cortical neuroscience clearly demonstrates that Lashley was wrong: The brains of the various mammalian phyla, though sharing a fundamental "plan," nonetheless vary in the number of areas and the connections between areas (Allman 1982; Kaas 1980; 1987). There is now good evidence that the number of cortical sensory representations ("maps") has increased in several lineages during the evolutionary diversification of mammals. For example, primates and carnivores have independently evolved a dozen or more "maps" of the visual field beyond the lower-order visual areas (such as V-I) which are the common heritage of all mammals. In his book Macphail (1982) dismisses multiple sensory representations as irrelevant to intelligence; in his view, they are germane only to perception. Thus, he regards perception as something very distinct from intelligence. We suspect that many psychologists would object to a rigid separation between intelligence and perception, as there are clearly important interactions between perception, knowledge, and expectation. From a neurological perspective, furthermore, the finding of multiple working memory areas in the prefrontal cortex of macaques, which are organized in series with higher-order "perceptual" centers in posterior cortex (Goldman-Rakic 1987), challenges the simplistic notion that perceptual capacity evolved while intellectual capacity remained static. The prefrontal areas critical for working memory may have evolved *pari passu* with the "perceptual" areas to which they are conncected.

Finally, as a guiding principle for comparative psychology, we find the "null hypothesis" to be genuinely destructive. The history of learning theory has been dominated by general-process theorists such as Thorndike, Hull, and Skinner, and there has long been a powerful bias against phyletic differences in learning and intelligence. There is hence nothing really new about Macphail's null hypothesis. Workers have for many years accepted the null hypothesis, the burden of proof falling more heavily on those arguing in favor of differences than on those favoring similarity. The result has been the creation of almost insurmountable methodological barriers to the demonstration of phyletic differences and the uncritical acceptance of arguments in favor of similarity. Suppose that on a given task in a given apparatus, Species A performs better than Species B. It is usually argued that the testing situation is not appropriate for Species B and the task is modified until a version is developed on which Species B performs well. The conclusion is reached that there is no difference in the capacity tested, when in fact changes in the testing conditions may allow Species B to compensate for the absence of capacities possessed by Species A. The latter possibility is typically not considered and rarely evaluated, since similarity is the favored outcome under the null hypothesis. Furthermore, if it proves difficult to devise a task in which Species B performs like Species A, it is then argued that the matter hasn't been examined thoroughly enough – that the most salient stimulus has not been tried, that the most tempting reinforcer hasn't been used, and so on. The null hypothesis, pursued with vigor, promotes the mere gainsaying of phyletic differences. And when gainsaying fails, one may simply ignore the evidence of phyletic differences. Consider Macphail's treatment of successive negative contrast effects. In challenging Bitterman's theoretical interpretation of *why* goldfish and rats behave differently on these tasks, the importance of the fact that rats and fish actually *do perform differently* seems to be lost on Macphail, although he acknowledges the fact himself!

We believe that the historical bias in learning theory against phyletic differences has been a great burden to comparative psychology, resulting in its virtual extinction as a discipline. Macphail's "null hypothesis" is merely the epitaph on the headstone of comparative psychology. The rejuvenation of an evolutionary psychology of learning and cognition requires that similarity and difference be treated *symmetrically* from a methodological standpoint. That is, arguments supporting similarity must be examined as rigorously as arguments in favor of difference. For similarity and difference are both facets of evolution. Evolution does not accord priority to one over the other, and comparative psychology should not either.

Comparative psychology, cognition, and levels

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It is by now a maxim that Darwin put an end to our special place in the universe and put the human species back into nature. Macphail, however, would resurrect the old anthropocentric view and divide the animal world into two parts, "man" and "all other nonhuman vertebrates," at least with respect to "intelligence." The special emphasis Macphail places on the concept of intelligence reflects both the influence of the contemporary "cognitive revolution" and Macphail's outmoded approach to comparative psychology. Thus, Macphail would return comparative psychology to its original goal of comparing mental processes (i.e., intelligence) among animals. This dated approach is also reflected in Macphail's revival of the various criticisms of comparative psychology popular a decade and a half ago (Hodos & Campbell 1969; Lockard 1971). Many agree, however, that those criticisms have been addressed successfully (e.g., Gottlieb 1984). It is now recognized that comparative psychology had a theoretical/philosophical orientation almost from its inception, that of evolution by natural selection; comparative psychology is accordingly widely defined as the study of the evolution and development of behavior.

This is particularly clear from the approach to the discipline taken by its foremost theoretician, T. C. Schneirla (Aronson et al. 1972; Maier & Schneirla 1935/1964). Schneirla developed a parsimonious and nonvitalistic, nonreductionistic account of behavioral origins. He recognized that comparative psychology should be concerned with behavioral similarities *and differences* between species. Indeed, the significance of this was acknowledged by Hinde's (1970) comment that "Animals at different phyletic levels differ markedly in their behavioral capacities, but the task of defining the differences is one of considerable difficulty" (p. 675).

Whereas Macphail's approach disregards behavioral differences, Schneirla developed a means of systematically accounting for them (Greenberg, in press; Tobach & Schneirla 1968). In this proposal animals are ordered not in the morphological manner typical of much current taxonomy, but rather in terms of behavioral plasticity. As one proceeds to evolutionarily more advanced organisms, behavior becomes more malleable. In an important sense, this malleability may be likened to the species' intelligence, although for some reason Macphail prefers not to define what he means by that concept. The important attention paid to behavioral differences led Schneirla and Tobach (1968) to identify five behavioral "levels." At the three lowest levels (Taxis, Biotaxis, Biosocial) organisms are closely tied to the physical presence of stimuli; at the two highest levels (Psychotaxis, Psychosocial), mediation and ideation become possible, permitting organisms to interact with stimuli in their physical absence. In addition to conforming to the concept of levels of organization (Feibleman 1954; Novikoff 1945), Schneirla's approach allows us to make some sense of what might otherwise be confusing; order seems to be necessary to achieve understanding.

I cannot help but believe that Macphail's concessions to cognitive influences underlie his belief that there are some dimensions on which animals do not differ. The current effort in cognitive psychology permits the rejection of "a hierarchical study of species' cognitive processes, and instead concerns itself with the identification of basic cognitive processes which exist across species. A crucial assumption is that no basic cognitive processes are unique to any species (Rilling & Neiworth 1986, p. 30)." The only exception is human beings and their language capacities, according to Macphail; we've got it and no other nonhuman vertebrate does.

Without getting into the controversies that surround this belief, I have pointed out elsewhere (Greenberg, in press) that Schneirla's levels approach permits an interpretation of the controversial "ape language" phenomena. Thus, although primates (including ourselves) function behaviorally at Schneirla's highest level, the Psychosocial, it may be that this is really two levels: Psychosocial I, typified by primates without language, and Psychosocial II, to which true language-using primates would belong. The levels scheme, although useful, is still premature and subject to revision. Its utility in this context, however, seems apparent.

Phylogenetically widespread "facts-of-life"

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Macphail argues that the intelligence of vertebrate animals exhibits no fundamental qualitative differences in kind, although human language is held to render our species a unique exception. He is less convincing in his denial of quantitative differences, for the difficulties in measuring intellectual capacities, which he discusses in detail, render it quite premature to rule out the large differences in degree of versatility and complexity. One important contribution of this target article is to reiterate that biological evolution has been a multiply branching arborization rather than a linear phyletic scale. I am mildly disappointed that the discussion is limited to vertebrate animals, because quite similar arguments can reasonably be advanced concerning some of the cephalopods or social insects. But our phylum is a big enough bite for one essay.

One of the most important ideas advanced in this provocative paper is the recognition that "causality is a constraint common to all ecological niches." This point is often overlooked in discussions of comparative intelligence. There are obvious differences in the details of types of food to be sought or avoided, particular forms of shelter to be selected, or specific predators or other dangers to be avoided or evaded. But coping successfully with basically similar problems requires much the same types of choice among alternative patterns of behavior. Social relationships also fall into broad and almost universal categories such as dominance, submission, affection, dislike, and aggression, and these are common to virtually all animals. When stated in basic intellectual terms, the cognitive requirements for dealing with these challenges tend to converge, regardless of the sensory or motor mechanisms at the animal's disposal. In other words, successful coping with the pressing problems of animal life under natural conditions may require an understanding of basic relationships that vary far less among various nonhuman taxa than is ordinarily assumed. If so, similar cognition must be achieved by the central nervous systems of animals that succeed in solving comparable problems.

We may have relied far too long on a nineteenth century assumption that cognitive processes are closely correlated with the gross morphology of central nervous systems. Rational behavior, adapted to unpredictable circumstances through the recognition of simple cause-and-effect relationships, does not require any particular packaging of interacting neurons and synapses. Creatures whose central nervous system is widely dispersed through the body, as in paired ventral ganglia, have traditionally been assumed to be genetically programmed robots incapable of adjusting their behavior according to experience. But recent investigations of honeybee behavior, for example, strongly indicate that pattern recognition, cognitive mapping of the environment, and basic types of learning do not differ in any fundamental way from the comparable phenomena in vertebrate animals (Gould 1985; 1986; 1987). Only quite simple and basic relationships are probably important to most animals, but these may nevertheless provide a fabric for understanding which Macphail calls the "common constraint of causality." This implies that basically similar internal cognitive or mental processes go on within a wide variety of central nervous systems.

Animal general intelligence: An idea ahead of its time

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Macphail is in very good company when he sidesteps a formal definition of intelligence. Contemporary textbooks of comparative psychology or animal behavior generally have no chapters on intelligence and the word rarely appears in the index. A notable exception is a recent textbook of animal behavior by McFarland (1985), which devotes a chapter to a discussion of animal intelligence. The term "intelligence" sometimes appears, in passing, in symposium volumes on animal cognition, in which a writer may imply that a particular behavioral paradigm is related to intelligence, but rarely is the assertion made outright.

Since specialists in animal behavior are reluctant to deal with intelligence, perhaps the ideas of experts on human behavior will be of use in characterizing the phenomenon. A recent reference work *Handbook of Intelligence* (Wolman 1985), devotes more than one-third of its nearly one thousand pages to a discussion of the definition of human intelligence. This discussion reveals that intelligence theorists still have not agreed on the resolution of a fundamental conflict, which dates back to the origins of intelligence testing; namely, is intelligence a single entity (i.e., general intelligence) that can account for an individual's performance in a wide variety of situations or is it a multidimensional phenomenon in which each independent dimension represents a unique intellectual ability?

As observers of both human and animal behavior, many of us feel intuitively that intelligence must be a unitary entity. For example, our linguistic use of the term forces us in that direction; we do not use the word "intelligences" in our everyday speech. But in spite of this intuition, we must consider that there is no way to measure general intelligence directly; its existence is inferred statistically from the pattern of intercorrelations between a large number of tests of specific abilities. In other words, there is no single behavioral test for general intelligence; it can only be determined by searching for what is common in the results of a number of individual tests of diverse abilities. To complicate matters further, human intelligence theorists, such as Sternberg (1985), have argued that there may be three or more types of general intelligence. [See also Sternberg: "Toward a Triarchic Theory of Human Intelligence" *BBS* 7(2) 1984]

Although Macphail refuses to provide us with a formal statement of what he means by animal intelligence, he does describe some properties of human intelligence that he feels are applicable to animals. His statement that "human intellectual capacity appears to be very general in its range of application" and his subsequent remarks suggest to me that he has general intelligence in mind when he uses the term "intelligence" in the animal context. But demonstrating general intelligence in animals and drawing conclusions about its magnitude in different classes would require collecting data from behavioral experiments that represented many specific abilities, sorting the data by classes, and producing tables of intercorrelations that could yield a general intelligence factor for each class. Such a task would be quite enormous and, in any case, it would be impossible to perform at the present time. The bulk of data existing today that might relate to intelligence is from mammals (especially rats and monkeys) and birds (mostly pigeons). Although some data exist for fishes and reptiles, studies on the cognitive capacity of amphibians are in very short supply. Any conclusions we could come to from the present data base would be hopelessly biased by our results from this handful of species.

From a practical perspective, our understanding of animal intelligence will proceed more rapidly if we abandon the search for general intelligence and concentrate our efforts on the study of specific intellectual abilities such as speed of learning, retrieval of information from long-term memory, decision making, problem solving, communication in symbolic form, counting, spatial-relations ability, concept formation, rule learning, and tool use. The performance on these tasks by animals from various taxonomic groups can be studied profitably now and might some day lead to measures of animal general intelligence. But at the present time, we should not become bogged down with a general intelligence concept for animals because its measurement is well beyond our grasp.

Psychometric considerations in the evaluation of intraspecies differences in intelligence

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My knowledge of the literature of comparative psychology and ethology and my research experience with vertebrates other than man are severely limited; I shall accordingly avoid comment on the substantive content of the research reviewed by Macphail. I do have a background of training and experience with respect to the measurement of human intelligence that is relevant to his discussion and leads me to a principal criticism. A much more explicit definition of intelligence is needed than a resort to an unspecified consensus. The attribution of the source of the consensus to our common language indicates that it may have no more biological validity than an origin myth.

Human intelligence tests sample common cultural acquisitions that human societies value; and because they value them, societies place pressure on their members to learn them. Advanced societies with well developed educational systems and school attendance laws require more common acquisitions than the less developed. The problems in comparing intelligence in literate and preliterate societies parallel the problems in comparing vertebrate species.

Of course not all cultural acquisitions are cognitive or intellectual. I have relied on consensus to define the domain of intellectual tasks (Humphreys 1971; 1985), but I have defined intelligence as the body of cultural acquisitions. This definition removes the construct from the domain of humanistic speculation and, because its object is measurable, allows it to enter scientific discourse. A standard test, such as a Wechsler or a Binet, samples the repertoire of acquired skills and knowledge considered cognitive or intellectual at a particular point in time. Responses to the most novel problems or situations require a learned repertoire, but this does not rule out the possibility that biological differences within the human species make a nontrivial contribution to variance in the acquisition and utilization of that repertoire.

Depending on the aspect of the data that one emphasizes, intelligence so defined can be considered highly specific or highly general. A typical correlation between two binary items in an intelligence test is in the twenties (i.e., 0.2–0.3). For two tasks scored on a continuum, when those tasks are limited in scope (*not* the final grade in a calculus course), the typical correlation is somewhat higher. There are many sources of variance for any given item or unitary task. The attribute that we are trying to measure typically makes a minor contribution so that success or failure on the item or task is primarily the result of other factors. From this point of view intelligence is highly specific.

If we focus on the total score obtained by a linear combination of item or task scores from a well-constructed test, however, there is abundant evidence for generality. No matter how heterogeneous the items or tasks may appear to be, as long as a consensus exists that they are cognitive, intercorrelations in large samples of the general population are, with few exceptions, positive. The items or tasks do measure a common attribute, but other sources of variance are localized in small subsets of items or are unique to a given time. Thus, when a linear composite is obtained over a large number of seemingly heterogeneous items, the variance of the shared attribute increases in the total score as the number of items increases. Simultaneously, the total contribution of the many sources of variance not held in common shrinks relative to the common variance. It is an apt analogy to characterize the systematic introduction of heterogeneity as a method of increasing the signal to noise ratio.

It is not easy to sample the skills and knowledge already acquired by vertebrates other than man, so that comparative psychologists have turned to laboratory learning tasks. It is informative, therefore, to consider the characteristics of an intelligence test for humans based on measures of learning. The test would require a wide range of materials to be learned, different sensory modes, different learning paradigms, and different response modes. In a wide range of talent, intercorrelations would be positive and small, smaller even than those for the items in a standard test of intelligence. It would require a large number of heterogeneous learning tasks to develop a total score in which the variance of the attribute shared by the tasks would equal in size the common attribute in a standard test of intelligence. When that is achieved, however, I predict that the correlation between the standard test and the learning test would closely approach the reliability of the standard test. The total scores of the two tests would be measuring the same construct.

The application of this reasoning to comparative psychology, ethology, and behavioral genetics requires a major research effort, but anything less is not convincing. The first question requiring an answer is the degree of generality in an unselected population of some convenient species. A wide variety of tasks must be used on a large sample from the population. Each task requires preliminary research parallel to the item analyses used in developing psychological tests. If population correlations are as small in the nonhuman vertebrate species selected for study as they are in the human, 100 subjects would hardly be sufficient. With $N = 103$, the standard error of the z-transform of r is .10. If the population correlation is .20, 95% of random samples would be found between correlations of .007 and .399. The usual direction of inference, however, places the confidence interval about the sample values. For establishing the degree of generality a sprinkling of correlations close to zero in a sample of 100 is not very informative. Such a finding would not be an adequate basis for the rejection of a wide degree of generality.

If an appreciable number of tasks are measuring something in common with each other, albeit at a relatively low level, scores on an appropriately weighted composite would furnish the preferred basis for the selection of low and high groups for a selective breeding experiment. Whether the composite can be considered a measure of general learning ability or something more restricted is an empirical matter psychometrically. If generality is an acceptable conclusion, whether the composite is a measure of the species' intelligence is not an empirical matter. This is a question of definition. Even if psychometric generality were supported empirically, one might still choose to place a floor on task correlations in defining generality. Wahlsten (1978) does this implicitly. Something more explicit than a folk definition is required.

Searles' (1949) research is deficient in two respects as a basis for rejecting individual differences in intelligence in his strains of rats. Genetic selection was based on a single task that measured several attributes, including the hypothetical general intelligence. He also had only 10 rats in each of his extreme groups. Inability to reject the null hypothesis for some measure of performance on a different learning task is a highly ambiguous conclusion on statistical grounds. Rejection of the null hypothesis when the difference is in the wrong direction is an ambiguous finding as a result of the selection of the continuum that served as the selective breeding criterion.

Logical and ecological inadequacies in Macphail's account of intelligence and learning

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Just what is intelligence? Macphail never provides us with a definition of this term, which makes it hard to determine whether the various conclusions that he draws about the characteristics of intelligence in nonhuman vertebrates are actually warranted. Section 4 of his target article, entitled "Definition of Intelligence" begins by explaining why there is no need to define the term, although he goes on to offer a few hints about what he takes intelligence to be. Macphail bases his comparative analysis on a brief assessment of human intelligence, which he says is: (1) a very general capability; (2) involved in solving problems; and (3) heavily dependent on learning and memory for its exercise. Much of the rest of the paper is devoted to arguing that intelligence, thus characterized, shows neither quantitative nor qualitative differences among nonhuman vertebrates, and that the only evolutionary specialization relevant to intellectual performance in any species is the human language ability.

Given the starting point that he provides, Macphail's conclusion about the phylogenetic generality of intelligence is hardly surprising. If the intellect is "very general in its range of application" then of course there will be no ecological specializations of intellect. They would be ruled out as examples of intelligence by the definition just given. This point is made explicitly when Macphail considers the case of song-learning, an ability found in only a relatively few vertebrate species. Suppose, he asks, we were to test a songbird and a nonsongbird in a variety of laboratory learning tasks and we found no difference between their performances. Would the ability of only one of the species to learn song contradict the claim that there is no difference between the species' intellectual capacities? Macphail answers: "Not according to the case made out here. The pattern of results outlined would suggest that song-learning was not relevant to the species' general capacity, which must in turn appear to be genuinely general." This circular argument gets us precisely nowhere, except back to Macphail's starting point, namely, that a species' intellect is whatever general (i.e., not species-specific) capacity for learning the species possesses.

Having defined intelligence as a general ability, Macphail naturally finds evidence that it is indeed general, because he can exclude from consideration anything that might suggest the existence of specialized learning abilities (as in the song-learning example above). At the end of his paper, he discusses the issue of heritable (a better term than "innate," which Macphail uses) differences in intelligence, drawing on Tryon's (1940) classic work on artificial selection for maze-learning in rats. Macphail points out that subsequent testing of Tryon's maze-bright and maze-dull strains by Searle (1949) revealed that they differed only in maze-learning tasks and not in any of a variety of other learning tasks. This seems to me to be the strongest kind of evidence that learning ability is appropriately viewed as a collection of specialized abilities. The data show that if it is selectively advantageous for an animal to be able to learn a particular task (such as solving mazes) then that ability will evolve in the population (given the availability of suitable heritable variance in the trait); there will be no tendency for other learning abilities to evolve as well. If learning ability were a general ability, surely we would expect a population like Tryon's maze-bright rats that got better at one learning task to get better simultaneously at lots of others. Macphail quotes Wahlsten (1978) to the effect that such results undermine belief in a general intellectual ability (as they clearly do), but then he remarks that "that is not the position adopted here." Why not? It seems to be a position that is strongly supported by the data presented.

Naturally enough, Macphail is eager to find evidence that different species (especially if they are not closely related) show similar performance on learning tasks. Thus he cites with approval the finding by Roberts and van Veldhuizen (1985) that pigeons' spatial memory in a radial-arm maze is equivalent to that of rats. Earlier workers (Bond et al. 1981) had suggested that pigeons do not learn in the radial-arm maze, but Roberts and van Velhuizen "made relatively minor changes in training technique and in the maze itself" (writes Macphail) and found that pigeons could learn in the maze just as well as rats. The "relatively minor changes" involved specially graduated and extended training (involving up to 200 trials) as well as the introduction of colored cards to provide intramaze cues, neither of which is required to obtain comparable maze performance in rats. These findings suggest that, at the very least, rats are quantitatively superior to pigeons in spatial memory abilities. A recent study by Spetch and Edwards (1986) sheds some interesting light on the difference in performance between rats and pigeons and also supports the view that a species' learning abilities should be understood as adaptations to the requirements of its natural environment (Johnston 1981; 1985). Spetch and Edwards tested pigeons in an "open-field maze," where food was made available on widely dispersed perches to which the pigeons could fly, rather than in the alley maze used by Roberts and van Veldhuizen (1985). Under these conditions, the pigeons' performance was comparable to that of rats in the radial-arm maze, but without the special training that Roberts and van Veldhuizen found necessary. Spetch and Edwards's conclusion was that pigeons' spatial memory is adapted to the circumstances provided by their normal feeding behavior (which involves flying from place to place, not walking along the arms of a maze), and is best assessed under experimental conditions that approximate those of the normal feeding context.

The different uses that can be made of the results from these experiments by proponents of "general intellectual ability" such as Macphail, and proponents of "ecological specializations of learning" like myself, are interesting. Macphail concentrates on the final performance of the animals in the task, dismissing as "relatively minor" whatever experimental contortions are needed in order to get the subjects to perform as required by his theoretical position. From the ecological perspective, however, the fact that one of the successful experiments (Roberts & van Veldhuizen 1985) involved extensive training in an apparatus that bears no resemblance to the pigeons' natural environment, whereas the other (Spetch & Edwards 1986) involved much more limited training in a close approximation to the pigeons' normal feeding situation is of prime theoretical importance. If learning abilities are ecological specializations, then it is expected that they will function most readily in environments that resemble the ones to which they are adaptations. The fact that a sufficiently persistent experimenter can produce similar behavioral outcomes in other environments is, in itself, neither theoretically interesting (Johnston 1981, p. 166) nor even especially surprising. The vertebrate nervous system (especially in birds and mammals) is a remarkably adaptable device and, if it is bludgeoned with sufficient ingenuity and vigor, can be persuaded to adopt a wide variety of strange and unusual states, a fact that professional animal trainers have known for a long time. The variety is not infinite, but it is wide enough that different species can probably be forced to produce overlapping performances, such as remembering the location of several sources of food.

From an ecological perspective, the relationship between the animal and its environment is critical to the theoretical analysis of learning. Learning is not definable in terms of the animal alone, but only in terms of an animal in an environment (Johnston 1985; Johnston & Turvey 1980). The question "Do pigeons have spatial memory?" is meaningless from an ecological perspective, because it fails to specify the environment with respect to which the question is to be answered. Because pigeons have evolved in an environment with particular properties of relevance to the analysis of their spatial memory, it is this natural environment that must serve as the second term in the relational definition of learning. Just as the locomotor skills of cheetahs, orangutans, or dolphins must be analyzed in relation to the particular ecological circumstances to which they are adapted, so the intellectual skills of pigeons and rats must be analyzed in relation to the environments in which those species normally learn. The disagreement on these issues between general-process and ecological learning theorists is not going to be resolved by an examination of data. The two positions derive from different sets of assumptions about the nature of learning (whether it is a property of animals or a kind of relation between animals and environments, for example), and so dictate that different kinds of experiments be accepted as relevant to the analysis of learning.

Boiling down intelligence

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This is a strange excursion into the psychology of a psychologist. Suppose I discover that my calculator and the university mainframe can both do simple arithmetic. They are equally accurate, and their rate of processing is trivially different, dominated by the cumbersome peripheral problem of my typing rate. Do I conclude they have similar capacity and uses, because most or all of the mainframe's activity is interpretable as a form of arithmetic?

One of Euan Macphail's conclusions – that association learning is a widespread adaptation to deal with cause and effect and thus that it reflects the structure of the universe – is profound and possibly true. But why ever posit his null hypothesis that association learning is all there is to differences between species?

The only way is by defining all observed differences as irrelevant. The songbird's capacity for song-learning and the human propensity for language acquisition Macphail sets aside as specialized devices, not elusive general intelligence. The titi monkey's deliberate deciphering of shortcuts, which is clearly related to its stealthy, cryptic life style in fear of predators, and the saddle-backed tamarin's readiness to remember the clues to concealed food, which probably relates to its small, dispersed food sources in the wild, Macphail would likewise dismiss as peripheral motivational factors (Fragaszy 1981; Menzel 1982; Terborgh 1983). The chimpanzee's political subtlety (de Waal 1982; Goodall 1986; Byrne & Whiten, in press; Whiten & Bryne, in press) would merely be an aspect of its giddy social whirl. Social trickery is not considered commensurable with, and hence not relevant to, the kind of association learning displayed by a sophisticated goldfish. The only serious conclusion to draw is that the goals of comparative psychology, and the "commonsense definition" of intelligence as understood by comparative psychologists, just don't jibe with the observations of people who find the differences in animals' performances more *interesting* than their similarities.

The political implications for humans may be where this target article started. It is very tempting to argue that there are no innate differences in intelligence between individual humans, and that theoretically there should be none. However, the recipients of this kindly argument might not be flattered to learn that this is because their intelligence equals that of a goldfish. Some of us prefer instead to enjoy individually eccentric qualities of mind – and will retain a conviction, which would have to be expunged according to Macphail's view, that we have met some people brighter than ourselves.

Species differences in intelligence: Which null hypothesis?

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Once upon a time, a group of comparative psychologists from the planet Zypton landed on Earth hoping to compare the intelligence of various Earth species. Unfortunately, they landed just after a virus had killed off the entire animal kingdom. Undaunted, the Zyptonian comparative psychologists set out to compare the Earthlings' mechanical calculating devices.

They compared an abacus, a slide rule, a battery-powered calculator, and several computers. On simple tasks such as counting and arithmetic, the various devices showed no differences in intelligence. (Their differences in speed and precision were considered motor rather than intellectual differences.) On more complex tasks, differences seemed to emerge. The abacus failed on trigonometric and logarithmic functions. The slide rule proved inadequate for determining all the prime numbers between 1 and 10^{100}. The computers could quickly solve certain complex questions which the calculators could not solve within the Zyptonians' patience limits.

Most of the Zyptonians believed they had demonstrated a hierarchy of intelligence levels among calculating devices. But then one comparative psychologist objected: Maybe the abacus and the slide rule would have been capable of all the same things as the computers if they had been tested under the right conditions. In certain ways, the underlying mechanisms of calculation were the same for all the devices. The only real difference in intelligence was that one of the computers was hooked up to a speech synthesizer.

In a dispute such as the one the Zyptonians faced, or in the challenge Macphail has presented to us, where does the burden of proof lie? Does it lie on those who claim the calculating devices or animal species differ in intelligence? Or on those who claim all species are the same?

Ordinarily, the burden of proof is on those who wish to reject the null hypothesis. To argue against ESP, (extrasensory perception), for example, it is sufficient to point out that the defenders of ESP have failed to demonstrate a replicable phenomenon, despite ample opportunity and effort [see Alcock: "Parapsychology" *BBS* 11 (1) 1988, this issue]. It would seem, therefore, that the burden of proof is on those who believe animal species differ in intelligence. If, after a century of experimentation, we have still failed to demonstrate such a difference to everyone's satisfaction, we should at least be embarrassed.

In this case, however, we are faced with mutually contradictory null hypotheses. Macphail's null hypothesis is that all species are the same in intelligence, until it is proved otherwise. Another null hypothesis is that frogs, lizards, and the like are incapable of delayed matching to sample and other complex skills, until it is proved otherwise. Apparently the only way Macphail would agree to reject *his* null hypothesis is if someone proves the validity of the *other* hypothesis – demonstrating that although one species can perform a certain task, certain other vertebrate species cannot perform it under any circumstances. (Curiously, with regard to language, Macphail switches null hypotheses: Nonhumans are presumed to *differ* from humans until it is proved otherwise.)

Macphail has, moreover, phrased the question in a way that makes a demonstration of species differences in intelligence particularly difficult. To demonstrate that two species differ in intelligence, according to Macphail, an experimenter must demonstrate not only that their performances differ, but also that the difference is independent of differences in sensation, motor control, motivation, and attention. If our definition of intelligence excludes the effects of sensation, attention, and so forth, it may well turn out that all species are the same. But after those exclusions, the interspecies equivalence may not be particularly interesting. By analogy, one could argue that a computer does more than an abacus only because the computer can accept a greater variety of inputs and produce more rapid and more precise outputs. If we exclude such "sensory" and "motor" differences, both computer and abacus are reduced to devices that perform fundamentally equivalent binary calculations.

Although I think Macphail may have excessively narrowed the definition of intelligence, and although I think he has unfairly tried to defend one null hypothesis by asking its opponents to prove a different one, I nevertheless believe his proposal is what comparative psychology has needed for decades. In the early part of this century, Yerkes (1905), Hunter (1913), and others set out to compare the intelligence of various species. That enterprise fell into obscurity, partly because it turned out to be surprisingly difficult, and partly because everyone seemed to agree on what the final results would be anyway (Kalat 1983).

That is, it hardly seemed worth a great deal of effort to demonstrate that a monkey is smarter than a frog, unless someone doubted it to begin with. Finally, in Macphail, we have found someone who doubts it. Perhaps his skepticism will reinvigorate this area of research and enable us to find out what, if anything, we mean when we say that monkeys are more intelligent than frogs.

Associative learning and the cognitive map: Differences in intelligence as expressions of a common learning mechanism

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In both artificial intelligence and cognitive psychology causality and associatve learning are treated as separate, unrelated topics – if they are considered at all. Macphail has shown that they are not only important but intimately related. In addition to arguing for the pervasiveness of a basic associative learning process, he shows its power as a means of coding causality (or, more broadly, of predictive relations in general).

In defense of these important and neglected themes, Macphail unfortunately calls upon a further hypothesis which is not only unnecessary to the basic argument, but very likely false as well. The assumption that intelligence (as most people use the term) does not vary across species is unlikely on the face of it, and not even likely within the framework that Macphail creates. The critical issues here involve the two factors that Macphail acknowledges do vary across species: "special mechanisms" and quantitative differences. I shall attempt to demonstrate that these factors can lead to differences in intelligence even if the basic associative learning mechanism were common across species, as I, too, believe to be the case.

Since the basic learning mechanism depends on numerous repetitions of continguously occurring events, it tends to be rather slow and insensitive. Here the "special mechanisms" are likely to play a particularly important role by enhancing and speeding up this process. Since the circumstances under which such mechanisms are called into play are likely to vary from species to species, the type of information learned is also likely to vary.

To see how this might be the case, let us assume for the moment that something like Hebb's (1949; 1980) consolidation hypothesis (or Miller's [1963] rather similar "go mechanism") determines those circumstances during which the associative learning process is to be enhanced. Consider then the contrast between an organism in which this mechanism is activated primarily on the basis of reward as opposed to an organism in which the mechanism is activated when a successful match has been made between an external event and an internal pattern. The latter organism is likely to build internal models of the experienced environment: the former is more likely to restrict storage to those aspects of the environment directly related to reward.

This "special mechanism" difference thus leads to storing different sorts of information about the environment. In both cases, the information will be causal or predictive; nonetheless, there will be important content differences. It is thus likely that these two sorts of organisms would be differentially able to solve certain classes of problems.

The second class of species differences Macphail acknowledges are quantitative differences. It may well be, however, that at a certain point quantity translates into a qualitative difference. Again, let us consider individuals of two different species, one having a relatively small number of neurons capable of forming associative bonds whereas the other has a much larger number. If it takes a certain number of elements to manage sensory information and to control responses in both species, then the less well endowed species may be limited in the number of "extra units" not directly involved in input and output.

Such extra units are likely to serve two vital functions. First, they permit abstraction. Since these extra units are not tied to input and output, they make it possible to generate internal structures which are more general or schematic. Second, they may permit the organism to indulge in "off line" neural activity. Extra units make possible patterns of activity that can function in an "as if" mode without restricting the organism to the immediately present environment and without necessarily leading to motor output. [See also Ballard: "Cortical Connections and Parallel Processing" *BBS* 9(1) 1986 and Smolensky: "On the Proper Treatment of Connectionism" *BBS* 10(4) 1987.]

Thus an organism with a sufficient number of extra units has the possibility of considerable intellectual power:

1. It can build abstract representations of objects in its environment.
2. Given an associative learning capability and a causally structured environment, it can build associative links between these object representations, thus generating an internal model (Gregory 1969) or cognitive map (Kaplan & Kaplan 1982).
3. With the capability of off-line neural activity, it can run its internal model (or explore its cognitive map), enabling it to utilize its predictive structure in a "lookahead" mode (Samuel 1963).

Such a cognitive capability offers a substantial adaptive advantage. As the British psychologist K. J. W. Craik (1943, p. 61) so elequently put it:

> If the organism carries a "small-scale model" of external reality and of its own possible actions within its head, it is able to try out various alternatives, conclude which is the best of them, react to future situations before they arise, utilize the knowledge of past events in dealing with the present and future, and in every way react in a much fuller, easier, and more competent manner to the emergencies which face it.

Thus, higher organisms may well incorporate information into their learned structures that is broader and less specifically pay-off oriented; they may be able to code such information in more abstract (and hence more generalizable) form, and they may be able to use such information in an off-line mode that permits more appropriate decisions. These are all aspects of what would ordinarily be considered intelligence. There is thus reason to suspect that there are meaningful species differences despite an underlying communality in the associative basis of learning.

Animals possessing these intellectual assets might be expected to show a number of distinctive characteristics. Their off-line capability would increase their capacity to delay. Their capacity to look at a situation from an "as if" perspective makes possible, perhaps unfortunately, the practice of deception. Their more general and more extensive predictive capacity will more often provide opportunities for expectation, and hence for disappointment. Unfortunately, it may be difficult to observe some of these potential indicators of greater intelligence in lower animals. As Hebb and Thompson (1968) point out, higher animals have a greater susceptibility to emotional reaction. Thus, a temper tantrum – a useful index of disappointment – may simply be absent from the typical amphibian's repertoire. The constraint of studying comparable behaviors may indeed rule out some of the most powerful indicators of intelligence. Higher animals may in fact not be superior in the context of conditioning tasks, and they may have no need to be. Their intellectual and adaptive power, according to this analysis, although based on conditioning, far transcends it.

But these various concerns should not detract from the important perspective that Macphail offers; there may well be a single basic associative process that is sensitive to the causal structure of the environment. Such a process may in fact underlie the diverse behavior of vertebrate species. Indeed, the above comments can be construed as an effort to make the world a bit safer for this functioning hypothesis.

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Bony argument

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Macphail's target article will no doubt evoke a spate of commentaries extolling the capacities of this or that vertebrate species. But why has Macphail excluded any consideration of invertebrates? He argues that similarities of intelligence may be related to the universal need of organisms to form associations and to detect causal relations. Invertebrates also find it useful to detect causality, and lord knows they have had the time to evolve appropriate mechanisms. Indeed, recent studies suggest that for both invertebrates and vertebrates, individual neurons may have the capacity to detect contingent events, and that for both groups of animals, this capacity may be related to the influx of calcium, which acts as a universal intracellular signal (Abrams 1985; Alkon 1984; Byrne 1987; Dudai & Zvi 1984; Hawkins et al. 1986; Livingstone et al. 1984; Lynch et al. 1983; Ocorr 1985; Walters & Bryne 1983). Furthermore, behavioral studies in invertebrates such as the gastropod molluscs continue to indicate that in many respects their sensory, motivational, and learning capacities are comparable to those of their bony relatives (e.g., Cook & Carew 1986; Hawkins et al. 1983; in press; Kupfermann 1974; Sahley et al. 1981; Susswein & Schwarz 1983). So if we cannot prove the null hypothesis anyway, why not include the invertebrates in the company of all the other equally intelligent forms?

Is a Darwinian taxonomy of animal learning possible?

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Did Beach, Hodos and Campbell, Lockard, Lorenz and Tinbergen attack and discredit the comparative psychology of learning and intelligence, as Macphail claims? Maybe so, in the same sense that Darwin and Huxley attacked and discredited the "real biology" of their era. All of them are, however, comparative psychologists themselves, in the sense that the main progenitor of that discipline would have used the term. In addition, the past three or four decades represent the all-time high in the amount of information and insight that has been obtained on animal learning and intelligence. It is true that I include here studies which are concerned with identifying and analyzing the sorts of problems animals face in the world at large, and how they solve these problems – studies Macphail apparently views as irrelevant. But that just goes to show that it is not the case that "a conventional understanding of the term 'intelligence' *is* sufficient to delineate our general area of interest" (target article, sect. 4, para. 2; cf. Menzel 1986; Neisser 1979).

If Macphail's views were indeed either conventional or Darwinian (at least I understand these terms) he would hardly have come up with his proposed taxonomy of animal intelligence. His "prototypically intelligent animal" (cf. Neisser 1979) is human and, almost by definition, superior to all, and few folk-taxonomies would say otherwise. But monkeys and frogs, pigeons and chimpanzees all (I infer) have equal rank and show equal degrees of similarity to the prototype. To me, this makes sense only insofar as one shifts the discussion from comparisons between actual living beings to some "essence of intellect" that is somehow quite independent of the bodies in which "it" is found. Can such a metaphysic be reconciled with Darwinian metaphysics (Jerison 1982; Lewontin 1983)? Here, I shall simply try to spell out the problem. It is indeed a most important one.

As the majority of comparative psychologists and ethologists would see it today, their general goals are the same: to account for actual variations in actual living beings, in a fashion that is consistent with the principle of natural selection and the known laws of physical science. Does natural selection imply that all animals are fundamentally similar or that each individual is unique? Does it argue for mental continuity or for specializations in adaptation? Does it emphasize genetic or environmental constraints on behavior? As I understand natural selection, the answer in each case is "both," for the alternatives are not mutually exclusive.

Who, then, would not agree with Macphail that there are general environmental constraints that affect all animals in all niches? But at the same time, it seems awfully vague to simply say that "causality" is a case in point. Specialized constraints surely come in again as soon as one gets any more concrete. Consider one example of Newtonian causality – gravity. It is certainly a general constraint. Its laws are rigorous. No animal literally flouts it as opposed to exploiting it. Gravity also affects the nature and distribution of all resources on which any animal depends and the entire structure of its habitat. Nevertheless, there are still countless ways in which animals have become specialized as a result of gravitational constraints, and many of these specializations are irreversible. Should physicists ever wish to formulate a general theory of motion that includes animals, they would still have either to look at a variety of different animals in a variety of environments, or to consult zoologists, for they are not "general gravity theorists" but specialists in inanimate objects. If, moreover, they wished to know how fish happen to be fish and birds to be birds or how and why these animals move and "behave" in such different ways, Malthus and Darwin would be more instructive than Newton and Einstein, even though physical principles are obviously still relevant.

Lumping all animals into only two or three classes, as Macphail advises us to do, is by itself not necessarily non-Darwinian. However, to maintain that there are no further differences, either qualitative or quantitative, is not very helpful, taxonomically speaking. It is analogous to proposing a university library card catalog that would use a total of two or three different identification numbers for all its books. Obviously, a viable alternative to Macphail's null hypothesis is used here. Each and every book (even a "clone") is treated as unique, and is given a different identification label; and a binomial system is used, so that both similarities and differences can be recognized at many, hierarchically nested, levels of classification. The differences between Darwinian and library (or "psychological") classification rest heavily on the issue of "arbitrariness," and here too the target article appears to miss the point of the authors it criticizes, both with respect to one's choice of subjects and apparatus, and with respect to the choice of criteria by which "fundamental similarity" is to be judged. Similarity is judged by criteria that are so loosely analogical that, for example, simple robots (Walter 1953) as well as pigeons (Epstein et al. 1981) could be said to be "doing the same thing" that chimpanzees do when they confront a mirror (Gallup 1970; Menzel et al. 1985).

If investigators prefer to study how animals solve laboratory tasks of their own devising, or to look for similarities in what all animals do, more power to them. The question is how well they can account for the diversity and variation that occurs in the rest of the world. To know that requires that one recognize and document such diversity and variation rather than deny it, ignore it, or treat it as irrelevant. Failure to find any significant differences in the intellects of nonhuman vertebrates might well be expected if one could actually control for all possible differences in structural and functional anatomy, physiology, sensory, motivational, and social organizations, and past experience. But what is left? Macphail might call it pure associative ability but another strong possibility is that it's a dead animal or a figure of human speech.

In conclusion, here is how I would interpret and expand upon the passage from Darwin that Macphail cites in section 4: Everybody knows, for example, that cuckoos migrate and lay their eggs in other birds' nests. I am interested in these and other natural phenomena as such, and in how they originated. This defines what I mean by a study of instinct or intelligence. Indeed, I could have used precisely these same phenomena to define both instinct and intelligence, for as paradoxical as it might sound to common sense, instinct is intelligence, and vice versa. All mental concepts must, in other words, be reformulated in the light of how bodies evolved, for minds are functions of bodies. Plato said that one can define instinct or intelligence without specifying *whom* one has in mind, and Descartes said there can be thought without body, but I cannot understand how either of them could be right.

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Proto-, pre-, and pro-intelligence: Little evidence but a necessary assumption

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We are told that comparative psychology has failed to demonstrate any differences in intellect among nonhuman vertebrates. Let us accept this conclusion for the moment and consider the consequences. There are two possibilities: (1) All nonhuman vertebrates have the same intellect, and (2) all nonhuman vertebrates have *no* intellect. Macphail prefers the initial possibility, although at some places in his target article he changes his stance and argues in favor of the second possibility. Both arguments, however, are in radical conflict with Darwin's theory of evolution since it is inadvertently suggested that the human kind of intelligence developed without phylogenetic ancestry or, alternatively, developed in an abrupt process about two million years ago when the first vocally communicating hominids appeared. All other characteristics of the human body developed gradually by the process of evolutionary change over a period of hundreds of millions of years. Is it possible that intelligence is the only exception? If one assumes Darwin's theory of evolution to be correct, and one applies it not only to bones and teeth but also to nervous tissues and their "products" (e.g., behavior, mental processes, intellect), then it would be logical to assume that human intelligence has not developed from a sudden imaginary starting point but stepwise from our evolutionary phylogenetic relatives.

This conflict arises from the manner in which Macphail uses the term "intelligence." He points out that as a speaker of English, rather than a psychologist, one understands the meaning of the word intelligence and that this in itself renders a carefully considered definition unnecessary. However, there is unfortunately no clear "common" understanding of the term, either in lay or academic fields. If we restrict the meaning of intelligence to the human kind of problem-solving, information gathering, and language-based social information sharing, then it is clear that nonhumans are nonintelligent by definition (see second possibility above). This is an unsatisfactory solution to the problem. One should ask what are the characteristics of "general intelligence" and the "intelligence that man shares with nonhumans." Rules of associative learning are of little use (as pointed out by Macphail), since the basic constraints for extracting a causal relationship between environmental events from contingencies are tight and more or less identical for all animals. The analysis of learning strategies has also been of little use, as is illustrated in Macphail's article. What we need are more and better behavioral experiments that search for the internal handling of mental representations in the absence of actual motor expressions during the process of handling. I see a continuum between manipulatory problem-solving strategies (motor expressions of trial and error) and the highly advanced mental problem-solving strategies (internal manipulation of representations). The advantages of the latter are obvious: They are faster, more energy-efficient, more flexible, more general. But where in the animal kingdom does one find protoforms of the internal handling of past experience and how can we analyze and compare these strategies in the context of evolutionary succession?

Mental representations can still only be inferred from behavioral analyses, since it is impossible at the present time to achieve direct access to the significance of high-order neural activity in complex neural networks. For example, does an animal generalize higher-order relationships without ever experiencing them? Does an animal communicate wrong information for its own advantage? How do animals respond to information (preferentially provided by a conspecific) which is contradictory to previous experience? How do groups of animals come to a consensus for group action if they receive controversial information? Let us consider the last question and use an invertebrate as an example. A honeybee swarm comes to a social consensus about where to build a hive from information gathered by scout bees who, after visiting potential hive sites, transfer this information to the rest of the colony in the form of ritualized movement. Lindauer (1955) found that this process of social decision-making was both intra- and inter-individual, and it is the latter which is of particular interest to the question at hand. For example, a bee that reports on a suitable hive site in the form of a moderately active dance changes its role to that of an observer in the presence of a more vigorous dance. Using the information contained within this dance it flies to the new site and, if it decides that this is in fact more suitable than the original site it found, returns to the hive and also dances in a more vigorous fashion. In other words, the bee compares the complex features of the two nest sites (Seeley 1982), transposes its decision into a symbolic movement, and then judges the reaction of the other colony members to its dance. One can certainly consider the neural processes that enable an individual bee to make a decision on such a complex comparison as an endless line of stimulus–response connections. However, if one were to observe a similar situation involving higher-order vertebrates and vocal language, would one not be prepared to assume internal handling of mental representations that included important features of "general intelligence"? I used bees as an example in order to demonstrate that even insect behavior raises the question of prototypical intellect, although insects are traditionally considered to be genetically programmed robots that communicate in a rudimentary fashion by means of symbolic "language." The assumption of the internal handling of mental representations can always be considered as being superfluous, but it would be exciting and rewarding to uncover the prototypical elements of intelligence that underlie such behavior. This may only be possible if we accept that intelligence is not only a function resulting from the capacity for vocal language.

In short, I agree with Macphail that there is no evidence for a human kind of intelligence in nonhuman vertebrates, but this does not exclude proto-, pre- or pro-forms of general intelligence in all animals and a phylogenetic succession with a gradual increase in complexity. The central issue of comparative behavioral studies should accordingly be problem-solving, with a specific emphasis on the question of mental representations and their internal manipulations.

The epistemology of intelligence: Contextual variables, tautologies, and external referents

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In his questioning of the nature of intelligence and how we measure it across species, Macphail's thoughtful, thought-provoking target article reminds us of some very basic and persistent philosophical dilemmas in psychology. One key element of Macphail's null hypotheses of no qualitative or quantitative cross-species differences in intelligence is the idea that valid cross-species comparisons can only be made when one has eliminated the effect of "contextual variables," such as cross-species differences in the motivational value of rewards, differing physical and perceptual capabilities, and so on, as potential causes of cross-species differences in task performance. The need to consider contextual variables has been discussed in, for example, the diagnoses of developmental disorders at the individual level in humans (Gollin 1984). In this commentary I will use the practices and findings of cross-cultural psychology to delineate the kinds of dilemmas relevant to all psychological research that arise when one realizes the importance of such contextual variables.

It is obvious that you cannot take a vocabulary test developed for a white, middle-class American sample, administer it in a non-English-speaking society, and then validly conclude that there is a qualitative difference in verbal *abilities* between members of the two cultures. Even if one took into account the language difference, one would still have to be concerned about cross-cultural differences in such variables as relative importance of verbal ability for social functioning, level of technological sophistication, relative frequency of use of vocabulary items, familiarity with test taking, and so forth – in other words, contextual variables.

In cross-cultural psychology, in order to assess some *qualitative* difference between cultures on some behavioral construct such as intelligence one must first establish the *functional* equivalence of one's measures in the cultures of interest. Functional equivalence implies that one is in fact measuring the same construct in all cultures. As with establishing contruct validity, establishing functional validity involves the demonstration within each culture that one's measure is predictably correlated and uncorrelated with other variables in the culture. For example, if intelligence is defined as being an adaptive behavior, then in all cultures one's measure of intelligence should be positively correlated with measures of social success (as defined *within that culture*). Macphail argues that if Tryon's (1940) maze-bright and maze-dull rats were genetically selected for "general" intelligence, then the two lines should also have differed on other measures of association formation. Similar reasoning would be used to establish the functional equivalence of measures of intelligence across species. Macphail makes a good case for the assertion that once a researcher develops a functionally equivalent measure of intelligence (as defined in terms of association formation) across species, then no qualitative cross-species differences in intelligence have ever been found.

In cross-cultural psychology, in order to assess some *quantitative* difference between cultures on some behavioral construct one must establish the *metric* equivalence of one's measures across all cultures. Metric equivalence is extremely difficult to demonstrate, since it requires both functional equivalence and the demonstration that there is a meaningful one-to-one correspondence between scores assigned in one culture and scores assigned in another. Macphail's null hypothesis of no quantitative cross-species differences in intelligence remains unchallenged simply because no one has come up with testing procedures that even a majority of researchers would agree have metric equivalence across species.

It might now appear that once everyone understands the concepts of functional and metric equivalence and perhaps even uses the techniques developed in cross-cultural research for establishing these equivalences, we would have a means of verifying or refuting Macphail's hypotheses. Unfortunately, the findings from research on cross-cultural differences in intelligence would suggest otherwise.

In analyzing the often contradictory findings from cross-cultural psychology it is useful to understand where a researcher stands on the continuum from the pure *etic* to the pure *emic* tradition. The etic tradition, derived from mainstream psychology, gives low priority to contextual variables in favor of imposing the same theoretical and metric framework across all cultures. The emic tradition, derived from cultural anthropology, gives the highest priority to developing theoretical and metric frameworks within cultures. As might be expected, as one moves from findings of adherents of the etic tradition to findings of adherents of the emic tradition, one finds that qualitative cross-cultural differences in intelligence tend to disappear; and then even the quantitative differences disappear (e.g., Cole & Schribner 1974; Nyiti 1902).

The inherent tautology is that one cannot validly infer cross-cultural differences in, for example, intelligence without first establishing the functional and metric equivalence of one's measures, but the most obvious evidence of having achieved such equivalences is success in eliminating cross-cultural differences. If one substitutes "cross-species" for cross-cultural in the above discussion, it becomes apparent that Macphail's null hypotheses of no qualitative or quantitative cross-species differences in intelligence are unassailable within a narrowly defined theoretical framework in comparative psychology. Then, of course, there are also the inevitable tautologies that arise from one's particular definition of intelligence.

To get out of a tautology, one must analyze it from a set of reference points external to the components of the tautology. Establishing the validity of these external referents may, in fact, be tautological, but that does not diminish their usefulness in resolving the tautology of interest.

The construct "intelligence" cannot be directly observed and validated; it can only be inferred from the correlations of a set of observable, agreed-upon behaviors – the construct itself does not come with an automatic set of external referents. On the other hand, components of evolutionary theory provide a number of different sets of external referents for testing Macphail's null hypotheses. Macphail, in fact, provides a lucid discussion of what the proponents of optimal foraging theory would have to do to use this theoretical framework adequately as a test of his hypotheses. He also makes a good case for getting at possible evolutionary developments in intelligence by studying the behaviors of closely related species. Another set of external referents is provided by evolutionary changes in brain size and organization which may be systematically related to cross-species differences in intelligence, although Macphail himself (1982) dismisses this evidence in its present state.

It should be apparent that understanding any behavior, animal or human, is a dynamic, interactive process. It is refreshing when someone like Macphail can shake us out of our old frames of reference.

The quest for divergent mechanisms in vertebrate learning

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Macphail reaches several conclusions in his target article, as well as in previous papers (e.g., Macphail 1982; 1985a; 1985b), but I would like to discuss only one of them, namely, that "there are neither qualitative nor quantitative intellectual differences among nonhuman vertebrates." Although I concede that there is no general agreement about this issue, acceptance of Macphail's null hypothesis poses at least two problems for comparative research.

First, the empirical basis for the acceptance of the null hypothesis should be compelling and exhaustive. But examination of Macphail's (1982) extensive review reveals that the amount of systematic research carried out on this topic is scanty: Besides the rat and the pigeon, no other species has been submitted to the kind of systematic inquiry that a quest for divergent learning mechanisms calls for. Moreover, the nature of the null hypothesis is such that, once accepted, it cannot be rejected simply because appropriate comparative experiments would lack theoretical support.

Second, the null hypothesis does not always seem in agreement with Morgan's canon [that we should assume no more intelligence than necessary]. If we accept that all vertebrates share the same mechanisms of learning, then we must accept that, for instance, fish possess some problem-solving capacities for which there is no empirical evidence (i.e., see Macphail 1982, pp. 77–79, on choice strategies). The null hypothesis cannot be said to be unique in its encouragement of research in this vein, because even if we admit the existence of a divergence, we still need to determine the generality of those mechanisms supposedly common to all vertebrates. In addition, in order to sustain the null hypothesis, Macphail forces us to accept theoretical accounts of some learning phenomena which are still disputable. For example, Macphail (1982, p. 98) cites the demonstration of overshadowing and blocking in goldfish (*Carassius auratus*) and carp (*Cyprinus carpio*) (Tennant & Bitterman 1975) as support for his argument about the presence of attentional mechanisms in fish. But overshadowing and blocking have sometimes been explained in nonattentional terms (e.g., Rescorla & Wagner 1972). It can even be argued that the recently reported failure to obtain latent inhibition in goldfish (Shishimi 1985), coupled with the positive finding on overshadowing and blocking in the same species, suggest that these phenomena may be based on different mechanisms. Perhaps support for the hypothesis that, whereas latent inhibition is an attentional phenomenon, overshadowing and blocking are associative phenomena will finally be provided by comparative research.

The comparative analysis of learning mechanisms has greatly benefitted from Bitterman's (1960) concept of control by systematic variation. Although it is true that this procedure does not completely eliminate the role of contextual variables and that it does not tell us "how many systematic replications are sufficient" (Hollis & Overmier 1978, p. 178), it is still the best methodological tool for dealing with interspecies comparisons in learning experiments. However, systematic variation may be complemented by two additional methodological features. First, the comparative data base of learning phenomena needs to be broadened to encompass selected species from new taxons. To the extent that negative and positive results fall within a meaningful phylogenetic pattern, it would be difficult to explain them in terms of contextual variables. Second, systematic variation should also be complemented by comparisons based on phenomena supposedly caused by the same mechanism. Again, it would be difficult to account for a consistent pattern of results in terms of contextual variables. By contrast to the null hypothesis, this theoretical background encourages comparative research, thus ensuring that the quest for divergence will eventually achieve a firm conclusion.

Perhaps the clearest line of research open to a systematic assessment is the hypothesis advanced by Bitterman (e.g., 1975) about the role of stimulus–stimulus (S–S) associations or expectancies in instrumental learning. The hypothesis is based on a pattern of data from goldfish–rat comparisons involving the successive negative contrast effect (SNCE), the partial reinforcement extinction effect, the magnitude of reinforcement extinction effect, and related phenomena. All of these are related not only to S–S associations and expectancies, but also to primary and anticipatory frustration (e.g., Amsel & Stanton 1980). It seems clear that although it cannot be presently argued that there is a strong case for the existence of a divergence, this is mainly because the analysis of these phenomena has not been carried far enough.

For example, consider the problem of whether goldfish are capable of forming S–S associations. In the target article, Macphail describes an experiment by Bitterman (1984b) on within-compound associations that is supposed to show the presence of such associations in the goldfish. But a closer look at the data shows that such a conclusion seems premature. First, Bitterman's experiment is poorly described. Although it is true that, as the within-compound association hypothesis predicts, discrimination is faster in Group Nonreversal than in Group Reversal (see Bitterman 1984b, Figure 7), it is similarly true that this hypothesis would also predict a higher performance level with the S+ in Group Nonreversal, and a higher performance level with the S− in Group Reversal. Neither of these predictions can be properly evaluated since statistical analyses are not reported. Second, although it is tempting to attribute a rapid development of the discrimination to Group Nonreversal, it seems that differential responding was already developed in the first session. Perhaps nonassociative factors could account for this group's perfect performance from the outset. Third, Macphail goes directly from S–S associations to expectancies: "Goldfish form within-compound associations and are hence capable of forming S–S associations: they should, like rats, be capable of forming expectancies." But even assuming that this result is correct, we should also know whether these "expectancies" show properties similar to those used to explain the instrumental behavior of dogs, rats, and pigeons (e.g., Overmier & Lawry 1979; Peterson 1984; Trapold & Overmier 1972). For example, would such "expectancies" play some role in response selection during choice in the goldfish? Clearly, more research is needed before the presence of S–S associations and expectancies in goldfish can be firmly accepted or rejected. A similar statement applies to frustration.

Macphail cites some of the results obtained by Amsel and his colleagues (see Amsel & Stanton 1980: Stanton et al. 1984) in infant rats as support for an interpretation of negative results in SNCE in goldfish in terms of contextual variables. However, he fails to point out that a coherent pattern of data is emerging out of these developmental studies, showing that various learning phenomena supposedly related by common mechanisms appear simultaneously during the ontogeny of the infant rat. As Amsel and Stanton (1980) pointed out, there is a striking parallel between developmental and comparative studies that becomes evident through the analysis of phenomena related at the process level.

There is an additional point I would like to touch upon in this commentary. There is substantial agreement that the concept of anagenesis is useful in understanding the research strategy developed by comparative psychologists in their search for similarities and differences in learning mechanisms. However, even if learning mechanisms diverged in a given group of living species, and even if the divergence can be usefully described in terms of levels of complexity (i.e., the noncognitive and cognitive levels suggested by Amsel and Stanton [1980]), the evolution of each level must still be explained. Ideally, explanations should use the same concepts that account for the evolution of biological traits, such as inclusive fitness; thus, the classical approach to comparative learning based on anagenesis is not necessarily opposed to the theory of evolution by natural selection. If there are in fact different levels of organization, the anagenetic approach provides an important, even more relevant, piece of information – it describes some of the actual variants that have evolved during phylogeny. (Of course, we will never know about those variations uniquely present in extinct lineages because, as Macphail states, there is no "fossil evidence of the evolution of intelligence.")

Metacomparative psychology

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When speaking to the public or to members of the media, I am frequently asked about the intelligence of one species relative to another. I might be asked, for example, "Are pigs smarter than horses?" My stock response usually runs something like this: "That is a very difficult question to answer. Each animal is likely to appear very intelligent in the environment for which it evolved and may appear very stupid when faced with other kinds of demands. Comparing animals' intelligence is like comparing their ability to move. Do fish move better than horses?"

According to Macphail, I have been giving the wrong answer. I should say: "No, there is no evidence that pigs are smarter than horses. In fact, there is no evidence of any differences in intelligence among any nonhuman species." It seems to me that this conclusion is unjustified. I see a number of weaknesses in Macphail's methods that seriously undermine his otherwise valuable attempts to summarize animal intelligence.

One of the first difficulties with Macphail's position in his equation of intelligence with performance on arbitrary tasks. Although this equation would receive substantial endorsement, it is still quite controversial. The question of whether there is such a thing as general intelligence has plagued the intelligence-testing movement for many years. Working from a different perspective there is also a great deal of current controversy regarding the modularity versus generality of human intelligence (e.g., Fodor 1983). Aside from the conceptual difficulties with focusing on generality, there is also the practical problem of determining those tasks that are genuinely general and tapping this general intelligence. Apparently, the only basis available for selecting tasks is the intuition of the experimenter. Intuitions are a very poor substitute for theory. A task may be general and arbitrary for one species, but bizarre for another. Two other problems derived from Macphail's definition of intelligence still remain.

First, even if the arbitrariness problem can be solved, there still remains a difficulty with interpreting performance on this arbitrary task. The task that is most general will also presumably be the one that taps the lowest common intellectual factor among species (I will call this the LCIF hypothesis). Finding that animals do not differ on such fundamental processes does not tell us very much about their intelligence, because the tasks on which they are tested are chosen to be maximally general and so minimally sensitive. The argument that arbitrary tasks tap the lowest common intellectual factor is different from the surplus abilities argument. The surplus abilities argument suggests that performance on arbitrary tasks is an epiphenomenon resulting from otherwise unique adaptations. The LCIF argument, in contrast, is that performance on arbitrary tasks taps capacities that are common among species because they are either fundamental cognitive processes or because they reflect common evolutionary developments. For example, the nature of causation is such that all animals capable of learning about causation, presumably through classical conditioning, would be expected to show similar patterns of learning abilities, precisely because these abilities evolved (once or many times) in order to take advantage of the causal relations in the environment. By this argument, there is no surplus in the surplus ability.

Second, Macphail's definition seems to take the biology out of comparative psychology. Animals did not evolve in order to solve arbitrary general problems. They evolved in a particular niche in response to the demands of that niche. Animals occupying certain kinds of niches may be very intelligent when dealing with problems from that particular niche and not very different when dealing with problems from outside that niche (see Roitblat 1987). Defining species differences out of existence, as insisting on a general definition of intelligence does, seems to preordain the results of the investigation and ignore precisely those factors that would result in species differences. Furthermore, if one takes the LCIF position rather than the surplus abilities position, then the question is not whether animals possess nothing more than task-specific adaptations, but whether they possess nothing more than arbitrary abilities. The strategy derived from this alternative position is then to seek species-specific adaptations that show intelligence, where intelligence is defined, for example, as the ability to make rapid, functionally appropriate modifications to ongoing action (Gallistel 1980).

As Macphail does recognize, however, the relationship between evolutionary niche and intelligence is a subtle problem. For example, a number of investigators have argued that the rat's excellent ability to perform in the radial-arm maze is a product of a strategy and a well-developed memory for information about spatial locations. Some of these investigators have gone on to argue that these two factors are niche-dependent species characteristics. Animals are expected to have this combination of strategy and memory if they forage on rapidly depleting food sources. Other animals that feed on more homogeneous resources would be expected to lack similar abilities unless they also exploit some other spatially distributed depleting resource (see Roitblat 1982). This particular hypothesis has not been born out. Animals, such as pigeons, that presumably lack the critical ecological factor, still show apparently good abilities on tasks that require memory for spatially distributed food. It is not clear, however, what one is to make of the apparent failure of this particular hypothesis. First, although rats excel at performing memory tasks involving a "win-shift" rule, they are also capable of performing tasks that require the animal to return to sites in which it received food (e.g., Hermann et al. 1982; Roitblat & Harley, in press). Therefore, the use of a win-shift rule is not necessary for a rat to perform a spatial memory task and it may not be surprising if other animals, even those specialized for employing a win-stay rule, are able to perform a task requiring a win-shift rule. Second, many factors are involved in solving a problem like the radial maze (in addition to unspecified contextual variables), factors that can account for differences and similarities in animals' performance on tasks like these. Third, even if the niche-specificity hypothesis proves convincingly to be false, it may mean nothing more than that it was incorrect. Some ecological variable other than the distribution of the animal's canonical food source may be the critical determinant for spatial memory abilities. Therefore, although the studies showing unexpected memory abilities are interesting, relevant, and suggestive, they are also not yet conclusive.

The discussion in the previous paragraph highlights another difficulty with Macphail's approach. It is not clear how to treat data from multiple studies, some of which are inevitably criticized. The mere fact that data are criticized does not imply that they are either false or worthless. One must weigh the power of the criticism. For example, Macphail is willing to dismiss all of the work on language-like phenomena in dolphins because Premack (1985) criticizes the work. Premack's criticisms are merely his opinions; they are not data. In the absence of careful analysis regarding their strength and validity, these criticisms hardly seem adequate to dismiss a line of important research. Whether or not Premack is right in his criticisms, this problem is only one example of an endemic difficulty. Comparative psychology has grown so vast and complicated that no single researcher can expect to critically appraise every finding and every criticism. The point is that simply noting that a potential species difference has been criticized is a poor methodological basis for inferring important characteristics about a species or about all nonhuman species. The best it can do is to highlight those areas that require additional research.

Another difficulty with Macphail's metamethodology is its insensitivity. Granting that the appropriate task is to find differences in animals' abilities to perform arbitrary tasks, one then needs a methodology that will detect differences in this ability. The only measure Macphail seems willing to use is an all-or-none criterion regarding whether or not an animal can learn a task. All other differences are attributed to contextual variables. My intuitions (and I assert they are as good as anyone else's) tell me that a "can do" criterion is inadequate because the same task can be accomplished in multiple ways, and because intelligence is a quantitative as well as qualitative variable. Simply looking at whether an animal is right or wrong, or whether it has acquired a task or not, is not a particularly sensitive measure of that animal's cognitive functioning. For example, one could look at the set of tasks the animal performs well and those it performs poorly and on that basis attempt to infer the cognitive mechanisms that the animal has versus those that it is missing (one of the goals of comparative psychology). Even if the animal performs correctly, however, there are many mechanisms that could produce that correct performance in a single, admittedly arbitrary task. For anything more than a cursory analysis, one needs to look at more features of performance than whether it is successful or not. Animals may not differ in the set of arbitrary tasks they can and cannot perform (this may be all we mean by arbitrary), but they may differ in their facility. A month's training may be necessary to train one species in a task, but only an hour for another. Is the animal requiring less training more intelligent? Perhaps, but this is not a simple question to answer. As Macphail points out, there are many variables other than intelligence that can modulate ease of acquisition.

All of these criticisms do not preclude comparing animals' intelligence. They simply point out that an adequate comparative psychology, like any other area of science, must rely on the presence of an underlying theory. To do the kind of comparative psychology that Macphail advocates we need a theory of each task, a theory of the nature of intelligence, and a theory for the evolution of intelligence. Although we do not yet have adequate examples of such theories. Macphail has made inroads toward developing them.

Natural selection and intelligence

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I presume that Euan Macphail's intention is to be provocative, and something of value may be gained by this stance if it forces the advocates of the unitary and the adaptive specialization views of learning and memory to show their cards. But there is a danger too in supposing that the case for a single and widespread set of mechanisms is best stated in the extreme form that Macphail favors. Empirical support for the occurrence of the same basic processes of learning and memory over a great range of animal species is perfectly secure, and does not require that equally clear evidence for the occurrence of variation in these processes be swept under the carpet. To do so only makes the assertion that general processes exist seem dubious. It is rather like arguing that *Archaeopteryx* is really a reptile and not a bird (or vice versa). Such disputations can only arise because *Archaeopteryx* is obviously some of both.

The broad question that Macphail's target article deals with is what the proper concern of students of animal learning and memory should be. Although the comparative psychology of intelligence is nominally the focus of the paper, it is a set of familiar phenomena – habituation, classical and instrumental conditioning, and "complex" learning – that are considered relevant by Macphail. Students of animal learning and memory should be concerned, he argues, with general capacities that rely on experience, and with how closely these capacities approach those of people. This stance is provocative because many researchers consider restricted learning and memory capacities equally interesting, and find that the degree of similarity to processes in people is not of much help in trying to understand learning and memory in animals.

The restricted or specialized learning and memory capacities that are found in animals are by now as familiar as the general processes: song-learning (Konishi 1985; Slater 1983), imprinting (Horn 1985), and orientation (Hasler & Scholz 1983; Emlen 1970; Wiltschko & Wiltschko 1976). Poison avoidance, the phenomenon of central theoretical importance in the development of the idea of adaptive specializations (Rozin & Kalat 1971), is nowadays sometimes included in the list and sometimes left out (Roper 1983; Domjan 1983). All of these capacities have unusual rules of operation, coexist with other learning and memory processes within the individual, and are not found in such a wide range of species as the general processes are. The function of these capacities is also fairly clear, and is in each case to solve a specific behavioral problem. Macphail regards these specialized abilities as not relevant to questions about the evolution of intelligence because, according to his definition, intelligence must be of a general nature. The reason many other researchers nonetheless regard them as relevant is that the existence of these specialized abilities suggests that intelligence may not be a single capacity but a collection of capacities. Support for this view can be found not only in animals with specialized abilities that function to solve specific ecological problems, but also in the species that Macphail takes as the benchmark for his definition of intelligence – ourselves. At least two categories of human memory can be identified on the basis of neuropsychological and cognitive data. One, often called episodic or declarative memory, deals with specific situations or episodes and permits one-trial learning, whereas the other, often called semantic or procedural memory, deals with the acquisition of habits and skills and is gradual or incremental in its operation (Squire, 1982; Tulving 1983 and multiple book review *BBS* 7(2) 1984). Performance on tasks requiring one capacity can be uncorrelated with performance on tasks requiring the other; amnesiacs with neurological damage may be impaired in one kind of memory but not the other (Milner et al. 1968; Schacter 1983) and some drugs can dissociate performance on tasks that require these two kinds of memory for their solution (Nissen et al., in press). Both capacities are general, depend on experience, and so qualify as "intelligence" in Macphail's usage, but they clearly do not constitute a unitary process. If our own "intelligence" is made up of multiple processes, is there any sense in excluding from consideration multiple processes in animals?

Macphail closes with an argument concerning heritable variation in learning and memory. There can be no heritable variation in these capacities, he argues, if the processes themselves do not vary within vertebrates. The results of experiments showing that there is enough heritable variation to select for problem-solving ability are not relevant, according to Macphail, because the abilities selected are not general, but restricted to the task used as the basis for selection. But these results should raise a warning flag to anyone supposing that learning and memory are not a collection of processes. If we accept that learning and memory arose through natural selection, and artificial selection can do no more than bring forth specialized problem-solving abilities, is it not likely that natural selection can also result in specialized adaptations in learning and memory?

The comparative method, if it can teach us anything, ought to teach respect for the diversity of organization in animals. A natural comparative question to ask is, how much diversity occurs in learning and memory? To show, as Macphail does, that all occurrences of a general learning and memory ability are, by definition, occurrences of a general learning and memory ability, and to conclude that there therefore exists no diversity in these processes, leaves no room for the variety of questions that a comparative approach can profitably address. What kind of selection produced the state of affairs that we currently observe in animal learning and memory, namely, a number of widely shared processes and the sporadic occurrence of unusual capacities? Are certain processes widespread because of common descent or because of convergence? If the latter is the case then we would expect the operation of learning and memory systems to be the same in functional outcome but to differ in their details of operation, much as the wings of birds, bats, and pterosaurs serve a common function but by different means. Are specialized learning mechanisms adaptive modifications of more general processes (Rozin & Kalat 1971), or are these purpose-built learning mechanisms instances of the kinds of capacities from which more general abilities evolved (Rozin 1976; Tierney 1986)? And finally, if general processes function to detect causality, as Macphail quite plausibly suggests they do, what kind of natural selection can have led to their evolution?

Intelligence: More than a matter of associations

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It is easy to demonstrate that species do not differ in intelligence if one has first defined "intelligence" so that it could not possibly differ across species. This is what Macphail has done. He first, unexceptionably, defines "intelligence" as general problem-solving ability. This is then equated with associative learning, which is defined as the ability to change behavior in response to experiencing certain kinds of formally defined event relationships. Since there is now abundant evidence that slugs, bees, rats, pigeons, and many other animals are capable of associative learning, Q.E.D.

Yet there is something missing here. Why *would* one consider a rat, say, more intelligent than a slug, and is this mere prejudice or is it based on potential kinds of evidence that Macphail dismisses too easily?

I briefly mention three considerations calling for a different conclusion from Macphail's. First, even if one accepts associative learning as the only constituent of "general problem-solving ability" worth considering, one must also take into account the range of problems to which the associative learning mechanism is accessible. An animal that can only learn about a few aspects of the world is surely less "intelligent" than one that can perceive and learn about a wide range of subtle aspects of its environment. Macphail appears to claim, however, that how wide a range of events an animal can learn about is a feature of perception, of no concern to a comparative psychology of intelligence. Animals that can learn about more aspects of the world simply have more sophisticated perceptual systems. This view of the matter leaves out an important contribution to the generality or lack of it available to any problem-solving mechanism.

Moreover, what events can enter into associations is not merely a matter of what events can be perceived. There is now good evidence in a number of cases (see Domjan 1983) that some pairs of events are better associated than others. This dependence on the nature of the events to be associated is becoming accepted as itself a general feature of associative learning. In the extreme, however, it means that associative learning is not truly general but constrained to certain combinations of events. One might suppose that these constraints are more rigid in some (less "intelligent"?) species than in others.

A second objection to confining the comparison of general problem-solving ability to associative learning is that animals clearly have available other means of solving the problems that confront them in nature. For example, both bees and pigeons can learn to trial and error how to obtain food in novel ways. But pigeons also have a second way to solve the same problem: observational learning (Palameta & Levebvre 1985). "General problem-solving ability" must include the whole range of learning mechanisms available to a species. This view is supported by the numerous recent discussions of multiple learning and memory systems, or modularity of intelligence, in all species, man included (Sherry & Schacter 1987).

Finally, all the comparative approaches to "intelligence" discussed by Macphail are essentially anthropocentric. His is just more blatantly so than some of the others. There are many ways in which animals use experience to solve the problems with which life presents them, just as there are many social systems and reproductive strategies. Surely it is time to develop a more comprehensive approach to comparative psychology, one which encompasses the full range of mechanisms animals use to solve naturally occurring problems, such as finding food, mates, and homes. This view is developed further in Shettleworth (1984a; 1984b). In one sense (*not* Macphail's), all existing species *must* be equally intelligent, if all are performing more or less successfully in their respective niches. However, we are likely to develop a theoretically richer and more accurate account of their various intelligences if we do not confine our investigations to the study of performance in a narrow set of learning paradigms. The possibility that what and how animals learn is to some extent niche-specific does not preclude comparisons. Rather, it suggests a whole range of comparative questions not admitted by the view that "intelligence" consists of associative learning ability.

Difficulties in comparing intelligence across species

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In the field of intelligence, as in many other fields, scientists often leave a research paradigm in droves when they lose interest in the questions that paradigm can address, or when they realize that the paradigm is not as fruitful for answering the questions it addresses as they had supposed. For example, the factor-analytic paradigm for studying intelligence has declined during the last two decades both because psychologists' interests have moved from questions of static structure to dynamic process and because the debates over the factorial structure of intelligence seemed to be generating more smoke than fire:

Factor analysis just didn't seem adequate for distinguishing among alternative models of the mind. A large number of different models of intelligence could be supported through alternative rotations of factorial axes, and mathematically there was no determinate way of distinguishing which of these rotations was correct.

Macphail notes in the very second paragraph of his target article that the last three or four decades have seen a sharp decline in the standing of comparative psychology. From Macphail's point of view, this decline is unfortunate. I would have agreed with him – until I read his article. The article makes it clear why the paradigms of the comparative psychology of intelligence, at least, have declined: However interesting the question of the comparative intelligence of different species may be, Macphail convinces me that the current paradigms of comparative psychology are inadequate to addressing the question.

We know from hard experience how difficult it is to compare intelligence between different racial and ethnic groups of the same species (namely, humans), or even to compare levels of intelligence across different age levels within the same racial or ethnic group. In each case, it is difficult to construct tasks that equally well represent the intelligence of the various groups. Different ethnic groups, for example, have often grown up in different cultural milieux and what is intelligent in one milieu may actually be unintelligent in another (see Sternberg 1980; Sternberg & Suben 1986). The same applies to people of varying ages: If one thing has become clear in the last decade, it is that children are often quite a bit smarter than they appear, but their intelligence does not always show through on tests that were designed by adults and scored in ways that represent the thinking of adults (see Gelman & Baillargeon 1983). The result is that comparisons across racial, ethnic, and even age groups are fraught with difficulties, and can be drawn only roughly and conservatively.

Macphail's target article makes it clear that interspecies comparisons are several orders of magnitude more difficult than even the exceedingly difficult comparisons within species. It is not surprising that there is so much disagreement among comparative psychologists as to the intellectual capabilities of the various species. Macphail's review of the literature suggests that the results of the extent literature can be interpreted pretty much the way the investigator wishes to interpret them, without fear of strong disconfirmation. If investigators obtain no difference between species, it is always quite plausible that the methods used were insufficiently sensitive to detect the differences. (After all, one cannot prove the null hypothesis.) If differences between species are allegedly ascertained, it is at least as likely that the differences reflect differences in the context of testing, or what it means to be intelligent for the various species, as that they reflect anything else. When all is said and done, despite his noble tries, Macphail's arguments rest more on exhortation than upon reasoned examination of data. It is not that Macphail fails to draw on his data, but rather that the data seem to support alternative positions as well as they support his own.

To a reader interested in the field of intelligence, the current article is a depressing one. Macphail concludes that there are no differences in intelligence among vertebrates, but the evidence would argue equally persuasively for the existence of differences. Macphail believes that humans are more intelligent than other vertebrates, but his first substantive statement in the section on human intelligence tells it all. He states that it is clear that humans can solve a much wider range of problems than any nonhuman: Human intelligence is therefore either qualitatively or quantitatively superior to nonhuman intelligence. Ultimately, this argument, just like the one that other vertebrates do not differ, is made on faith. After all is said and done, we finish this article not knowing in any definitive way how different species compare in their intelligence. It is no wonder that comparative psychology in general, and the comparative psychology of intelligence in particular, has declined as a field. Interesting as the questions may be, and noble as the attempts may be to answer them, the results are simply inconclusive: Macphail has made a valiant but not wholly successful effort.

Overcoming contextual variables, negative results, and Macphail's null hypothesis

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Macphail discounted my approach to assessing comparative intelligence as well as Barlow's (1983) and Bullock's (1986), noting that such schemes "cannot be accepted until experimenters consistently report failures by certain species to master specific tasks." This is an unfair condition owing to the well-known difficulty in publishing "failures" or negative results. Typically, the difficulty is due to the confounding effects of contextual variables (e.g., sensory, motor, and motivational ones) on the assessment of intelligence. Discounting my approach overlooks its strength in avoiding such contextual confounding. After summarizing my approach, which offers a way to reject Macphail's "null hypothesis," I will consider perhaps the most widely used "complex" task with vertebrates as an example involving the issue of publishing negative results in the context of efforts to reject his hypothesis.

My scheme (Thomas 1980) posits an eight-level *hierarchy* of types of learning; capacity to learn was equated with intelligence. *All* learning (laboratory and natural habitat) may be reducible to components of the hierarchy. The eight levels are (1) habituation and sensitization; (2) classical conditioning; (3) operant conditioning; (4) chaining; (5) concurrent discrimination learning; (6) responding to absolute and relative class concepts; (7) responding to conjunctive, disjunctive, and conditional concepts, and (8) responding to biconditional concepts. (See Thomas [1980] for rationale, definitions, and caveats.)

The learning-hierarchy approach avoids confounding contextual variables, because the sensory, motor, motivational, and other aspects of exemplary tasks at each level are adapted to each species. The same kinds of discriminanda, response demands. and incentives used at one level can be used at other levels. Then, for example, if an animal succeeds at one level but fails at another, the reason would be the intellectual demands of the task rather than contextual variables. An exception might be the onset of fatigue, but that could be determined by returning to a lower level task.

Meaningful sublevels are possible beginning with level 4. This will be illustrated with the oddity problem, a level 6 task, because it is relevant to comments below. The order of the alpha-numeric "names" shown below reflects an order of task difficulty (Noble & Thomas 1985; Thomas & Frost 1983). Typically, the oddity problem involves one odd and two identical, nonodd stimuli. With color, shape, and size varying, the odd stimulus might share no attributes with the nonodd stimuli which, when identical, share all three (the O0N3 task), or the odd stimulus might share one or two attributes with the nonodd stimuli (O1N3, O2N3). In "dimension-abstracted oddity," the nonodd stimuli are not identical but have more attributes in common than with the odd stimulus (e.g., O0N2, O1N2, O0N1).

The oddity problem has probably been used with more different species of vertebrates than any other "complex" problem. Except for studies using nonhuman primates and one study using pigeons, claims for the use of the oddity concept by other nonhuman animals do not withstand close scrutiny (Thomas & Frost 1983). The issue is whether it was possible that the animal learned associations between the *specific* odd stimuli and reward or rather responded to oddity conceptually. The best control for specific versus conceptual responding is to analyze only the first-trial performance on new oddity problems. Despite the aforementioned criticism and control having been noted several times at least since 1948, a number of recent studies using pigeons unjustifiably claim that the oddity concept has been used. Some investigators were surely aware of the criticism and control before they published. My guess is that lurking in some of their files are data showing failures by pigeons to respond reliably to the odd stimuli on the first trials.

The exception among the pigeon studies was Lombardi et al.'s (1984) which used oddity test problems with reinforcement always withheld; this was mixed in with other oddity problems (presented repeatedly) in which reinforcement was administered, and the pigeons chose the odd stimulus at better than chance frequencies on the test problems. However, pigeons are unlikely to succeed on the higher-level oddity problems described above, and the authors of such studies are unlikely to publish their negative results.

Similarly, the few studies assessing the rat's use of the oddity concept are inconclusive, including those which claimed positive results. My recent effort to publish a "negative" result was rejected for nonmethodological reasons ("Visual and olfactory oddity learning in rats: What evidence is necessary to show conceptual behavior?") One reviewer and the editor mentioned the "negative" results. The rats received a total of 300, five-trial oddity problems. The rats learned to respond better than chance on the second trials of new problems early in training but remained at chance on the first trials throughout. This showed that sensory, motor, and motivational variables did not account for the failures on trial one and suggested that success on trial two was due to learning quickly what specific stimulus and reward contingencies were in effect on each five-trial problem. In other words, they showed evidence for learning set formation but none for knowledge of the concept of oddity. I will persist in publishing this study, but how many might not?

None of this commentary diminishes Macphail's main point that, so far, the data do not refute his null hypothesis. My approach to the comparative assessment of intelligence offers a way to reject it – provided the "failures" necessary to reject it become part of the published record.

Editorial commentary

In a spirit aptly captured by the Maine joke about the out-of-stater's request for directions – to which the reply after some weighty reflection is: "You can't get there from here" – one can ponder an intuitively puzzling phenomenon in comparative cognition: Why can't *everything* (the decline of the Roman Empire, quantum electrodynamics, the indeterminancy of radical translation) be successfully explained to *everyone* who is able to speak the language? After all, there exists a string of sentences (possibly long, possibly several alternative ones) that will get *some* people "there" from "here." Why not everyone, everywhere? The first prima facie answer is that not everyone is sufficiently interested or attentive. Let's set these people aside. Then there is the problem that not everyone is starting from the same place: Fine, let's use more sentences to get them all to the same starting point. (Of course, this runs up against an antecedent version of exactly the same problem: It's not clear that you can get everyone to the same starting point.) But even presuming equal motivation, attention, and prior knowledge, it seems evident that people vary considerably in where you can get them from there (and how, and how quickly, and how permanently). Why? And what is varying here? Command of the language?

An exact parallel to this problem emerges with attempts to teach animals language: Why can some animals be taught to reliably label objects, whereas others cannot? And why is it that those that can, and can even string together the labels into what seem to be simple "sentences," cannot go on to acquire and use a full-blown language, intertranslatable with English?

One can go even lower: The technique of shaping an operant response by successive approximations and reward seems to be universally applicable to any perceiving/responding organism. Why is it that, within the limits of its sensory and motor apparatus, *every* organism cannot be taught *every* operant response? The same can be asked of the learnability of associations. (The scope and limits of associationism as a general *mechanism* of cognition are currently under investigation and debate in connection with the "new connectionism" – see Smolensky: "On the Proper Treatment of Connectionism" *BBS* 11(1) 1988 – but that is a different problem.)

Puzzling questions. Perhaps the fault lies in the assumptions: Maybe the ways in which people and animals vary in motivation, attention, memory, sensorimotor capacities, and response dispositions account for all the variance. Evolutionary contingencies, genetic heritage, and individual experience may have shaped all of these "noncognitive" variables; and, apart from them, all species and individuals are cognitively equivalent. The alternative is that the abstraction of cognitive function from its noncognitive context is not realistic; perhaps they are inextricably intertwined. It may make sense to compare performance capacities under given conditions, but it may be impossible to make commensurable inferences about an independent underlying cognitive capacity or "module" called "intelligence."

Author's Response

Comparing intelligences: Not easy, but not impossible

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Faced with the daunting task of considering 30 commentaries, I have been obliged to respond to what I see as the major points made by each commentator and to ignore what I see as minor points. I hope that my perception of major and minor is not too far different from that of the commentators.

Problems of definition

A number of commentators take issue with my remarks on the definition of intelligence. Two recurrent themes center on what is meant by the term "general," and on whether intelligence can or should be "reduced to" association formation. Before responding to those points, I should gratefully acknowledge **Hodos**'s contribution in pointing out that much time may be spent on attempting to define intelligence without there being any chance of achieving a consensus. Few of my critics have ventured to suggest what would be a satisfactory definition, and I do not find the few positive suggestions helpful: **E. W. Menzel**, for example, suggests that instinct is intelligence and vice versa, and **Fetterman & Killeen** offer a definition of intelligence which is as appropriate for a plant as for an animal.

General intelligence. It is argued by **Johnston** that in defining the intellect as being general, I have ruled out ecological specializations of intellect, since he takes me to mean by "general" that which is not species-specific. But that is not my intention: By "general" I mean only general in range of application, and a species could very well possess a device of general application which was peculiar to that species (language in humans, for example).

Anderson, Hodos, Roitblat, and **Sherry** caution against the notion that intelligence might be regarded as unitary, and in fact I do not regard general intelligence as unitary. I do not assume that all "arbitrary" tasks are solved using the same mechanism, and the conclusion that all vertebrate species perform such tasks in the same way would imply only that if several mechanisms are involved, then all the species possess the same set. Of course, the suggestion that association formation lies at the core of nonhuman problem-solving does imply that (at least) one mechanism is involved in all general problems, and so provides a parallel with the human "g." Even that speculative proposal, however, would not imply that general intelligence is unitary. [See also Jensen: "The Nature of the Black-White Difference on Various Psychometric Tests: Spearman's Hypothesis" *BBS* 8(2) 1985.] **Anderson** and **Hodos** propose that comparative psychologists should concentrate upon the component cognitive processes of intelligent behavior; I can only agree, and point to the fact that in my 1982 survey I did consider work on short- versus long-term memory in animals, a topic inspired by concepts drawn from human cognitive theory (Macphail 1986). Explicit interest in problem-solving does not rule out consideration of memory (or other cognitive processes), since it is clear that the properties of memory processes will be critical to any organism that uses previous experience adaptively.

Dewsbury, while agreeing that my loose definition of intelligence is sufficient to indicate the general area of interest, argues that I (incorrectly) go on to reify the concept, and to attempt to quantify and compare its magnitude across species. He cites two examples, the first being the section – which follows the main discussion – in which I discuss potential endemic variation in intelligence and inquire into the consequences of the conclusion that the set of available intellectual capacities is the same in all vertebrates. In one sense, this could be seen as reification; but it seems to me that the reification consists only in the acknowledgment that intellectual activity is the reflection of the operation of specific processes that each have a physical embodiment in the nervous system. Dewsbury's second example of reification concerns my asking what species differences in intelligence have been demonstrated. In this case also I cannot see that unjustified reification has occurred. In the section concerned I am referring to the set of intellectual capacities possessed by animals, and in suggesting that both qualitative and quantitative differences should be sought, it is clear that I have made no presupposition that some indivisible whole exists.

Association formation and intelligence. It is claimed by **Goldman-Rakic & Preuss** and by **Shettleworth** that I have restricted my definition of intelligence to associative processes, but this is not the case: What I have suggested is that associative principles may be sufficient to explain a wide variety of behavioral tasks. That is a matter, not of definition, but of the interpretation of experimental results. Shettleworth further argues that by equating intelligence and associative learning, I have predetermined that intelligence could not possibly differ across species. The notion that associative learning should not be expected to differ between species is also supported by **Fetterman & Killeen,** who regard intelligence as niche-specific but agree that many environments have features in common – features which would allow the evolution of similar devices in different species. They illustrate their argument very nicely by citing work on perceptual devices. We cannot assume, however, that associative learning will proceed in the same way in all species. Shishimi (1985), for example, claims that latent inhibition – one of the basic facts of learning according to Fetterman & Killeen – does not occur in goldfish. Although I am not yet convinced that latent inhibition will not be found in goldfish, I would certainly not attempt to rule it out on the grounds that goldfish, like other vertebrates, live in a causally structured environment. Similarly, I find it very odd that anyone should regard **Bitterman**'s recent report that goldfish can form S–S (stimulus–stimulus) associations as merely a demonstration of what was inevitable and already known to all investigators of animal behavior.

Bickerton suggests that if all that intelligence involves is the power to form associations, we should dispense with the word. Intelligence, however, is concerned with problem-solving; if problem-solving in nonhumans is found to be mediated by association formation, it would mean that the capacity to form associations is more powerful than previously believed. If laymen accepted this, there would perhaps be no difficulty in using the word despite the theoretical analysis.

Jolly objects to my suggestion that association formation might form a central role in intelligence by citing a number of examples of complex behavior seen in the wild – behavior she assumes cannot be "reduced" to association formation. The problem is that we do not understand what processes underlie those complex behaviors and whether the processes involved are available for other tasks. It seems to me unlikely that animals have, for every task they face, an entirely independent set of learning mechanisms which are used for that task and that task alone. But until we have analyses of complex behavior which are adequate to identify the component processes and their range of application, we simply cannot say what relevance the behavior has to general intelligence.

Kaplan points to the important fact that even if associative processes are common to all species, differences in the context of associations could lead to important qualitative differences in intelligence. He contrasts, for example, an organism in which the associative mechanism is activated primarily by reward and one in which it is activated by a match between an external event and an internal pattern. The difficulty is that there is no evidence yet for a necessary role of reward in association formation in any species: One of the important implications of Bitterman's (1984) demonstration of within-compound conditioning in goldfish is that they learn to associate two neutral stimuli if one stimulus is contingent upon another.

Fischler suggests that even if associative processes are universal, there may nevertheless be other more complex processes, not to be reduced to association formation, which may differentiate between species. Fischler also suggests that artificial intelligence may provide useful insights into the ways in which comparable performance might be generated by very different mechanisms. Both points are in harmony with my own view. In the target article, I expressed the hope that workers seeking to disprove the null hypothesis will attempt to devise novel tasks for comparative work – tasks which associative devices could not solve. Notions derived from artificial intelligence may be helpful in conceiving such tasks.

Goldman-Rakic & **Preuss** suggest that short-term memory tasks provide examples of learning which cannot be reduced to associative principles and emphasize that a wind-shift strategy will impair performance on many such tasks. But they ignore Restle's (1958) analysis of those tasks; until they show why they believe that this analysis is inadequate, I can see no reason to accept the argument. It is also pertinent to observe that Wagner's (e.g., 1981) formulation of SOP (standard operating procedures) theory, which is an account primarily of associative learning, appeals quite specifically to the notion of a distinction between short-term and long-term memory: There is no conflict between an account of learning in terms of association formation and an acknowledgment that different memory stores exist.

Papini and **Dewsbury** argue that I should not equate S-S associations with expectancies, and I have no objections to this. Bitterman introduced the proposal that fish were pure S-R (stimulus-response) animals partly on the basis that expectancies were involved in the SNCE (successive negative contrast effect), and I only wish to make the point that it is now clear that fish are not pure S-R animals. Whether their performance would be comparable to that of rats in all tasks for which expectancies have been invoked as an explanatory notion is something we shall not know until the relevant comparative work has been carried out.

Ecology and learning

The general point is made by **Shettleworth** that problem-solving ability must include the whole range of mechanisms available. If by that is meant the whole range which find application in general problems, I agree; more specifically, I agree that "biological constraints" and observational learning are relevant. It is at present far from clear, however, that the constraints literature does require significant modification of a general-process account, and there are almost no comparative data on observational learning; not enough, certainly, to be able to say that some vertebrate species is intellectually incapable of it.

E. W. Menzel argues that the general goal of comparative psychologists and ethologists is to account for variations in living things; I agree, and see no conflict between my conclusions and that goal. My suggestion is that variations in learning task performance are to be explained in terms of differences in such processes as perception, motivation, and motor capacities. E. W. Menzel points out that a common constraint, such as gravity, does not necessarily lead to the same "solution" in all species. Naturally not, but then I have not argued that because of the existence of causality all species will develop identical association-formation devices. I have suggested that the evidence currently available is best interpreted in terms of a universal capacity for association formation, which is best understood in a causal framework. The ways in which animals solve problems cannot be worked out from first principles, but from evidence. All vertebrates can solve problems in situations far removed from their "natural niches." I am interested to know how this is achieved, and I believe that the question can only be answered by analyzing the performance of different species in "unnatural" tasks.

Greenberg argues that my approach systematically disregards behavioral differences. This seems an odd objection, given that my view in fact encourages the search for differences, and assigns considerably more importance to differences than to similarities. Greenberg also recommends Schneirla's (Tobach & Schneirla 1968) concept of "levels" as a tool for explaining differences. Unfortunately, he does not make clear precisely which behavioral data encourage him to believe that some vertebrates occupy different levels than others. It is in any case those data, rather than any conceptual framework for their explanation, which are critical.

Roitblat argues that the tasks used by comparative psychologists are chosen to be maximally general, and so will test the lowest common intellectual factor (LCIF). I find this a strange argument when applied, for example, to learning-set formation or to language acquisition. In addition, the LCIF notion implies that everyone already knows the results of comparative studies on, say, latent inhibition or the SNCE, without any need for them to be done: I made a similar point, it will be recalled, in the preceding section (of this Response). I prefer to keep an open mind on both the question of whether "simple" tasks might discriminate between species and the question of whether species *must* have developed different learning mechanisms because they inhibit different niches.

Johnston criticizes my interpretation of the Roberts and van Velduizen (1985) experiment on radial maze performance in pigeons, and implies that the changes in technique made in that study were hardly minor; he suggests, moreover, that the subsequent demonstration of efficient spatial memory by Spetch and Edwards (1986) supports the specialization view because the task used was a "close approximation to the pigeons' normal feeding situation." These arguments seem to me to illustrate the grave difficulties that exist in trying to bring evidence to bear on the specialization school. What predictions can be made? Suppose Spetch and Edwards's experiment had failed to show good spatial memory – could it not equally well have been argued that the situation was *not* a close approximation? Do pigeons in their natural environment find food in metal boxes on the walls of small enclosed rooms?

Pico and Davis (1984) found that mice showed no evidence of spatial memory in one version of an enclosed maze. In another "sensory enhancement" version, overhead lights were turned off, alley doors and arm covers were removed, and extra cues at the ends of arms were removed; under these conditions, mice showed excellent spatial memory. Pico and Davis described those changes as minor, and I agree. The fact is that pigeons and mice, like rats, are capable of highly efficient performance in laboratory tests of spatial memory, and minor changes in procedure may influence performance dramatically. The effects of procedural changes are readily understood in terms of such factors as reliance on visual cues, fearfulness in enclosed spaces, and so on. Johnston argues that the difference "between general-process and ecological learning theorists is not going to be resolved by an examination of data." I believe that it can and should be, and that at present there is very little support for the "surplus" account of general learning capacities.

Sherry suggests that I regard "specialized" capacities as irrelevant to "general" intelligence. But in fact I specifically suggest that the possession of a given specialized capacity such as, say, song-learning, might influence performance on other (nonspecific) tasks (the notion of "surplusage"). **Johnston** cites my discussion of a comparison between a songbird and a nonsongbird, and criticizes as circular the argument that if no differences between the species could be found in other learning tasks, then there would be no difference between the species' intellectual capacities. Although it is true that this conclusion derives from my definition of intelligence as implying general application, its whole force rests on the empirical failure to demonstrate differences outside of song-learning. The ecological specialization view supposes that the capacity to behave adaptively outside an animal's niche is a by-product of (unspecified) specialized capacities. If this view is correct, then those specialized capacities that *do* contribute to performance outside an animal's niche constitute, in my view, mechanisms of general intelligence. If song-learning capacities do not contribute to adaptive behavior in any other context, then they are not relevant to intelligence. To take an example which is not hypothetical, the discovery of efficient spatial memory in the wild has stimulated research into the question of whether this ability is available in "arbitrary" memory tasks (e.g., Shettleworth 1985). The answer to that question will have an important bearing on whether or not spatial memory should be seen as contributing to general intelligence.

Johnston and **Sherry** suggest that the results of Searle's (1949) work on maze-bright and maze-dull rats support the "specialized capacities" view by showing that attempts to select for general intelligence result in the development only of a specialized capacity. But, as **Humphreys** observes, the maze task would measure several attributes, not intelligence alone. If we suppose no within-species variation in intelligence, individual differences in maze performance may be explained as consequences of differences in reactions to some contextual variable – in, for example, reliance on visual as opposed to kinaesthetic cues. Selection would therefore result not in differences across learning tasks in general, but in differences in performance which would reflect the contextual variables common to the tasks used.

Interpretation of experimental data

Evidence of qualitative differences. It is argued by **Papini** that there are data currently available which contradict the null hypothesis. He cites Shishimi's (1985) work on latent inhibition, and Bitterman's (1984) report on within-compound associations. Shishimi's work does provide an important challenge to the null hypothesis, but I still have reservations about concluding that fish do not show latent inhibition. The fact is that when a to-be-conditioned stimulus is preexposed to fish, subsequent acquisition *is* retarded (Braud 1971; Shishimi 1985). But Shishimi found that preexposure to one stimulus retarded subsequent acquisition with other, quite different stimuli. Such a finding can be interpreted as showing either that fish show broad generalization of latent inhibition or that stimulus preexposure in fish has some nonassociative retarding effect on acquisition. I do not believe that we have sufficient evidence yet to allow a decision between these alternatives.

Papini suggests that Bitterman's (1984) study may not have demonstrated S-S learning in fish, but his criticisms of the work are not convincing. He resorts to an appeal to unspecified nonassociative factors to explain a difference in performance between groups whose previous experience, when pooled over the counterbalanced conditions, was identical. The only difference between the groups was the relationship between the stimuli discriminated in Stage 3 and those experienced in Stages 1 and 2; it is difficult to conceive of a nonassociative explanation of the consequence of that procedural difference.

Bitterman emphasizes the number of failures to obtain the SNCE in goldfish, in contrast to the ease with which the effect can be demonstrated in mammals. He also distinguishes between the two questions of whether goldfish show the SNCE and why an animal might not show the effect. He regards these questions as wholly independent. This is a position which warrants some examination. My argument will be that the decision about whether goldfish could ever show the SNCE is inevitably linked with the question of whether a coherent theoretical account of its absence is available. Rats do not show an SNCE in a runway when a sucrose reward is shifted from a high to a low concentration (e.g., Flaherty et al. 1973). Theories based on the idea that the SNCE reflects disappointed expectancies have never satisfactorily explained that finding. A different account of the SNCE is provided by Mackintosh (1974); this account supposes that the SNCE is an instance of stimulus generalization decrement occasioned by a sudden reduction in magnitude of the aftereffect of the preceding reward. Independent support for such an account is provided by the finding that rats do not show response patterning when high and low concentrations of sucrose are alternated; they do not, that is, run faster on trials in which high concentration solution is available than on trials in which a low concentration is available (as they do when different numbers of food pellets are alternated; see Mackintosh, 1974, for a review).

The view now espoused by **Bitterman** is that, unlike rats, goldfish do not "associatively reinstate" the memory of the preceding reward when placed in the start-box at the beginning of a trial. The memory in this case acts in a way equivalent to an aftereffect, so that a change in the memory occasions generalization decrement. If this is so, then why is there no SNCE in goldfish when a short interstimulus interval (ITI) is used (e.g., Gonzalez et al.

1974, who used a 15 sec ITI)? Bitterman (e.g., 1975) assumes, after all, that the aftereffects of reward do persist at short ITIs without any need for associative reinstatement. A more economical account would seem to be that fish find the aftereffects of the food rewards used to date less discriminable than those typically used with rats, with the result that their performance resembles that of rats tested with differing concentrations of sucrose. There is independent evidence (Mackintosh 1971) that goldfish are relatively insensitive to reward aftereffects, and there is as yet no evidence that goldfish may acquire patterned responding to the alternation of different sizes of reward. It is true that a number of variations in the types of food reward used have been tried without obtaining an SNCE in fish, and this does pose a problem for the plausibility and economy of the account in terms of poorly discriminable aftereffects. However, on the assumption that associative reinstatement is not involved at short ITIs, it must surely be even less plausible to argue that the failure to obtain the SNCE at *any* ITI in fish is due to a failure of associative reinstatement.

I resist **Thomas**'s claim that I discounted his approach, particularly given that I described it as "valuable." Nor can I be held responsible for the fact (which I regretfully accept) that it is difficult to publish "negative" results. I can only hope that the case made out here for the central importance to comparative psychology of *failures* to learn may serve to counteract current editorial prejudices. I should add two remarks about Thomas's (1980) scheme. Thomas suggests that his proposal overcomes the contextual variable problem because the same contextual variables are experienced throughout testing: a success at one level and a failure at another could not be interpreted in terms of such variables. But this argument ignores the fact that contextual variables may interact with tasks so that learning one task is affected by a contextual variable, whereas learning another is not. Gonzalez et al. (1966), for example, ran two groups of pigeons in acquisition and a series of reversals of a red-green discrimination. Group Key chose between two illuminated keys, and Group Mag, between illuminated food magazines. Group Mag made marginally more errors in acquisition, but substantially (and significantly) fewer errors across the series of reversals.

On the topic of oddity learning, it is worth noting that multitrial oddity tasks may be solved in several ways (although only learning about oddity will allow correct choice on Trial 1). It appears that in **Thomas**'s experiment rats did perform reasonably well on Trials 2–5. Such a result can be accommodated on the assumption that specific S-R contingencies were more salient to rats than the oddity cue in this procedure; in other words, that they overshadowed oddity. A similar problem is encountered when considering data showing that pigeons are less likely than corvids to acquire an oddity concept (Wilson et al. 1985). Differences in the relative salience of cues each of which allows reasonably efficient performance need not reflect differences in intelligence. It might be more valuable than looking at Trial 1 data to run experiments in which only one trial with each set of stimuli was presented, a task which can only be solved in terms of oddity. If rats fail on that task, then the case against the possibility of oddity learning in them would be significantly strengthened.

Evidence of quantitative differences. There is indeed, as **Nagoshi** and **Barlow** rightly point out, no universally acceptable metric of intelligence in nonhumans; **Griffin** too finds my conclusion regarding the absence of quantitative differences less than convincing. I cannot claim strong support for the conclusion that there are no quantitative differences in intelligence, but specific proposals for quantitative differences have been made – for example, with reference to learning-set formation – and I have argued that none of these proposals survives objections (in terms, usually, of contextual variables shown to influence performance). Now, although none of the tasks used so far may on its own provide an accurate measure of intelligence, it may not seem unreasonable to expect that, if quantitative differences do exist, they should manifest themselves in at least some of the tasks used. Barlow's own suggestion for measuring the efficiency of association formation is an interesting one, although it is not yet clear to me precisely how it could be implemented experimentally. If and when it is, it may, of course, provide valuable quantitative data.

Finally, I should respond to **Elepfandt**'s contention that since so few comparative data on problem-solving are available and since so few species have been tested at all, there is simply insufficient evidence on which to base any conclusion. I imagine we all agree that we need far more information, but Elepfandt perhaps underrates the achievements of workers in comparative psychology. Elepfandt is not impressed by similarity in vertebrate performance across a wide range of learning tasks, but I suspect that he would have been impressed by a precisely similar quantity of work had that work succeeded in showing differences.

Perception and intelligence

Not all animals are equally versatile in the detection of associations, **Barlow** argues, and I would agree. But as *Shettleworth* notes, such differences could largely reflect perceptual processes which are or may be independent of intellectual processes. **Goldman-Rakic & Preuss** suggest that there is no rigid distinction between perception and intelligence and they object to my assumption (Macphail 1982) that an increase in cortical processing of sensory input is irrelevant to intelligence. Similarly, **Kaplan** argues that an increase in numbers of neurons may allow substantial extra processing, resulting, perhaps, in the formation of an internal model or cognitive map. The difficulty here lies in specifying what the relationship between perception and intelligence might be. Clearly, knowledge influences perception – consider "hidden figures" and "unusual views," for example – but the contribution of perception to intelligence is much less clear. Consider an animal with stereopsis and one without. The former will require extra neurons to process the critical disparity data. It will be able to see "better," will possess more neurons, and it may indeed build up a better representation of the world, but is such an animal more intelligent? I would argue that just as we do not suppose that deaf or blind humans are in general less intelligent than hearing and sighted humans, an animal without stereopsis is not thereby any less intelligent than one with stereopsis.

Status of the null hypothesis

The null hupothesis is not economical, **Papini** argues, because it leads to the assumption of capacities in species which have never shown such capacities. **Kalat** illustrates a similar argument with an entertaining fantasy. Perhaps I could respond by assuming a fantasy world in which contextual variables are irrelevant and in which tasks reflect cognitive processes directly. Suppose a novel task is introduced and species A is the first to be tested; the null hypothesis to be tested statistically is that species A cannot perform the task. Suppose that hypothesis is rejected and we now test species B in the task. The null hypothesis here is, clearly, that B cannot learn the task. Should we then assume that while species A can perform the task, species B cannot? No. Imagine instead that we test both species on the task in a comparative experiment; the null hypotheses tested will be, first, that neither species can learn the task and, second, that there is no species difference.

Fantino suggests that the null hypothesis is virtually inviolable in principle, but should nevertheless be extended to the proposal that there are no differences among vertebrates, *including* humans. Although it is logically possible to appeal to some (unknown) contextual variable to explain away any observed difference this is not what has actually happened. What has generally happened (Macphail 1982) is that some difference posited by an early report has been shown to disappear in some later report. It is for this reason that I reject Fantino's extension of the hypothesis to humans: It is thoroughly implausible to claim that there are no differences between the human and the nonhuman intellect. Whether or not one accepts the notion of a continuum of linguistic skills, as Fantino urges, the fact is that human mastery of langauge and human culture is far beyond the grasp of any nonhuman, and that difference cannot *reasonably* be attributed to contextual variables (cf. the EDITORIAL COMMENTARY). It is not even possible to conceive a useful experiment. *Which* contextual variables should be varied in order to teach a dolphin to do differential calculus? Thus, although Kalat argues that I adopt a different null hypothesis with regard to humans, I cannot agree. It is because humans master syntax and nonhumans do not that I infer a species difference. Moreover I regard this species difference as support for the view that the null hypothesis is not inviolable.

Goldman-Rakic & Preuss argue that workers have accepted the null hypothesis for many years. I rather doubt it, and in any case Goldman-Rakic & Preuss may take comfort from the fact that, to judge from the commentaries reproduced here, the pendulum has now swung the other way.

Evolutionary principles

If by intelligence we mean the human kind of problem-solving, **R. Menzel** argues, then no nonhuman is intelligent. He further suggests that this conclusion is in conflict with evolutionary theory, since the intellect should have developed "stepwise." I am not certain that I follow the first argument, but if his suggestion is that language is essential to all human problem-solving (which it may or may not be), then we are talking essentially about language, and I do not accept that Chomsky's (e.g., 1972) proposal for a species-specific language-acquisition device in humans is in conflict with Darwinian theory. One cannot reconstruct the evolution of either intelligence or language by appealing to Darwinian principles; one must look for evidence.

Elepfandt accuses me of ignoring the possibility that similar behavioral phenomena may reflect the operation of different underlying mechanisms, and that such mechanisms may have evolved quite independently in several different phylogenetic lines of descent. He also argues that if similar learning processes are carried out in two species by nonhomologous neurons, then the learning concerned is not homologous in the two species. Fascinating questions are raised by the demonstration of similar processes in nonhomologous neurons (are *any* of the neurons of a mollusk homologous with any of those in a mammal?), but I do not see that they are germane to the central issues here. If it were accepted that the processes of intelligence are common to all vertebrates, I imagine that – however those processes were represented neuronally in the various groups of vertebrates – there would be a general acceptance that the processes concerned evolved with or before the first fish, and that they have not changed since.

Language

Partly on the grounds that it is difficult to specify what would constitute evidence of human language ability, **Anderson** is skeptical of the value of the animal language work. This should not rule out the effort, however: If, after all, it did become possible to converse with an ape just as easily as with a human, there would surely be no issue of interpretation. It is because we cannot do so, because the ape achievement falls so short of the human, that difficult arguments ensue on whether what is achieved should be counted as language at all (cf. the EDITORIAL COMMENTARY).

Roitblat suggests that I am dismissing the work on language in dolphins because of Premack's (1985) criticisms, but this is not so. It seemed to me unnecessary (and in fact impossible in the space available) to review and to criticize all the language-related programs in nonhumans, and to show why, in each case, I found myself unconvinced that syntax may be mastered by nonhumans. My case is that the language programs are of central interest and importance, but that there is as yet no universally accepted evidence of language acquisition in nonhumans. I cite Premack (1985) (as I do Herman [1984]) as evidence for the proposition that universal acceptance has yet to be attained, even in the restricted community of those involved in the language programs.

Although **Bickerton** gives me some welcome support on the "animal language" issue, I would question his implied conclusion that only primates (and possibly dolphins) can use signs in the absence of their referents:

Where is the evidence that pigeons, say, cannot achieve what Savage-Rumbaugh's (1985) chimpanzees achieve?

Finally, I should register my agreement with **Barlow**'s suggestion that language has a function over and above the simple conveying of information. I believe that language does indeed have a dramatic and far-reaching effect on our general intellectual capacity, although precisely how it achieves that effect remains for me obscure.

Perspectives from human intelligence

Attention is drawn by **Eysenck, Humphreys,** and **Hodos** to the fact that there are virtually no data on the question of whether performance in one cognitive task correlates with performance in another, and Eysenck and Humphreys argue that, in the absence of such evidence, very little can be said about intelligence in animals. This is an odd conclusion, however, since it would mean that if there were no individual differences in intelligence, intelligence could not be studied scientifically. In fact, as Hodos implies, we can probe the processes that underlie intellectual performance quite well without exploring individual differences. Arguments, for example, about the distinction between short- and long-term memory in humans proceed with very little reference to psychometric data. Similarly, we can reason from phenomena such as overshadowing and blocking to underlying processes, and we can test the validity of those hypothetical processes using other experimental designs. It is the failure to discover phenomena demonstrable in one species which are not demonstrable in another that leads to the inference of similar processes in different species. If different species use the same processes, then those species possess, qualitatively at least, comparable intelligence.

Sternberg takes a distinctly gloomy view of comparative psychology, suggesting that the data available could be taken to support virtually any position. This is surely going too far, since there are many cases in comparative psychology of proposals which have been generally rejected (Macphail 1982). One such example is cited in my target article: **Bitterman**'s (1975) proposal that fish are "pure S-R" animals may now be rejected. The problems are, as Sternberg notes, extremely difficult, but they are not systematically insoluble. The frustration that Sternberg feels arises largely, I believe, from the fact that no convincing demonstrations of differences have emerged; if they *had*, then neither methodology nor theorizing would, I suspect, have attracted such an attack. Comparative psychologists have shown many impressive parallels in vertebrate species across a wide range of phenomena. It is odd that instead of welcoming this positive evidence of important cross-species similarities in learning mechanisms, critics prefer to reject the enterprise because it fails to confirm their predisposition to believe that species differences exist.

Borkowski assumes that I ascribe all variations in human intellectual capacity to variations in the efficiency of a language-acquisition device. Much of his commentary challenges the plausibility of such a view by presenting evidence favoring the notion that language acquisition itself is dependent upon other cognitive skills and structures. I shall not address myself to Borkowski's specific points, which I am not competent to assess, but I should make clear that I take my interpretation of the nonhuman work as support for the view that measured variations in human intelligence may be due to the operation of environmental factors and to innate variations in noncognitive factors such as motivation (e.g., Macphail 1985b; see also EDITORIAL COMMENTARY).

Nagoshi draws attention to the parallel between the problems facing the comparative psychologist and those facing the cross-cultural psychologist. Although **Eysenck, Humphreys,** and **Sternberg** have implied that the comparative psychology of intelligence is in a sorry state compared to the situation in human intelligence, Nagoshi's commentary suggests that comparative psychologists are not alone in their difficulties: It is apparently not yet clear how to decide whether there exist quantitative differences in intelligence between humans of different cultures, and for reasons similar to those which apply in comparative psychology.

Invertebrate intelligence

Regret is expressed by both **Griffin** and **Kupfermann** that I restrict my discussion to vertebrates, a regret which I share and which was caused at least in part by limitations of space. I have made clear elsewhere (Macphail 1985c), I am much impressed by the parallels between the phenomena of learning obtained in invertebrates and those known in vertebrates, and see them as evidence for a marked degree of commonality in learning mechanisms between vertebrates and invertebrates. On the other hand, it is surely still the case that we do not yet have enough data to extend the null hypothesis with any confidence to invertebrates. I would argue, however, that the null hypothesis is in a sense the standard against which comparative studies on intelligence in invertebrates should be measured. The null hypothesis for such research, then, must surely be that invertebrate intelligence is no different from vertebrate intelligence. There are at present no data of which I am aware which compel us to reject that hypothesis – but the fact is that we know very little about invertebrates.

Finally, it is reassuring to see **Griffin** making the point that the assumption that cognitive processes are closely correlated to gross morphology is an outdated one; it provides a nice contrast to **Elepfandt**'s claim that it is old-fashioned to see demonstrations of similar phenomena as evidence for the existence of comparable processes.

Labeling, association, and commensurability

The EDITORIAL COMMENTARY raises two empirical issues. The first of these points to a problem for those who believe that language is not an exclusively human achievement. I am in general sympathy with the point, although I would contest the claim that between-species differences exist in the ability to label objects, and I do not accept that the sign-strings generated (or responded to) in the language-learning programs to date *have* demonstrated sentence formation (or comprehension). I do believe, however, that if nonhumans were capable of sentence formation then they would inevitably become capable of communicating very much more interesting "thoughts" than the rather mundane utterances reported to date. The language programs have certainly failed to give us new insights into how nonhumans view their world. If nonhumans could learn to use language, some such insights should have been gained.

The general form of my response to the second issue raised in the EDITORIAL COMMENTARY is, like my response to the first, predictable from the tenor of my target article. Although species do differ in their readiness to associate certain classes of stimuli, these differences may be explicable in terms of general principles which apply equally to all groups. I would propose a similar analysis of the species differences in readiness to form response-stimulus associations. The readiness of a response to enter into an association depends on many factors that may vary between species; two such factors that spring readily to mind are the "spontaneous" frequency of occurrence of a response and the quantity and quality of feedback from the response. But I currently see no reason to suppose that there are species differences in the cognitive capacity to acquire new responses.

It will be appropriate to conclude by returning to the disturbing question of whether the comparative psychology of intelligence is possible. The central goal of comparative cognition is not to show whether one animal is more intelligent than another but to discover how animals learn, solve problems, and retain information. Progress in understanding how, say, a rat solves a problem would have an interesting consequence, however: It would allow us to use similar procedures with other species and to decide whether those species solved the problem in the same way. In other words, if we can work out how one species solves a problem, we should be able to work out how other species solve the same problem. If it turns out that two species do not solve a problem in the same way, we should have powerful evidence for a difference in cognitive function. However difficult it may be to conpare the processes available to different species, the conclusion that no such comparisons are possible would be pessimistic indeed: It would in effect mean that no understanding of the cognitive function of *any* species could be achieved. For my part, I remain an optimist, and prefer to see the failure to demonstrate differences as evidence not that our scientific procedures are weak but that the animal mind is not what we expected it to be. And after all, did we *really* expect that it would be?

EDITORIAL NOTE

The following commentaries were received too late for a response from the author. His reply will appear in a Continuing Commentary section of a later issue.

Clever pigeons and another hypothesis

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In general terms, Macphail's effort to reestablish the field of comparative psychology of intelligence is most praiseworthy. His book *Brain and Intelligence in Vertebrates* (Macphail 1982) is no doubt a landmark in this previously derelict area. In recent years it has been our own objective, partly inspired by his book, to demonstrate that pigeons are more intelligent than generally thought. We believe that we have made some progress. Lombardi, Fachinelli, and Delius (1984; see also Friesel, in preparation; Lombardi et al. 1986) showed that, given propitious circumstances, pigeons can learn to apply an identity/oddity concept to visual shapes and are able to transfer the principle to classify novel visual stimuli. This supports Macphail's (1982) conclusion, based on less satisfactory earlier evidence, that on this basis birds do not differ from primates. Von Fersen (in preparation; see Delius 1987 for a preliminary account) has demonstrated that pigeons can infer transitive relationships between stimuli. Given experience with pairs of stimuli bearing the relations A ← B and B ← C, in later tests pigeons behave according to the inference A ← C. They are in this respect equivalent to primates (Gillian 1981; McGonigle 1977).

Hollard and Delius (1982: see also Delius & Hollard 1987; Emmerton 1986; Lombardi, in press) found that pigeons are quite capable of solving problems of orientation-invariant pattern recognition. Problems of this kind are frequent nonverbal items in IQ tests for humans. Our results could also be superficially interpreted as generally supporting Macphail's position – assuming that the advantage he concedes to humans is limited to problems in which they can bring to bear linguistic processing. However, the experiments have revealed that pigeons are actually superior to humans in a particular class of orientation-invariance tasks (those that demand mental rotation; Shepard & Cooper 1984). This seems to contravene the spirit of Macphail's proposal. At present we see no alternative than to assume that the pigeons' superior performance on an IQ test item represents an adaptation to a peculiarity in the way of life of birds (Lohmann et al., in press).

Nevertheless, I find nothing wrong with the null hypothesis that there are no differences in intellect among subhuman vertebrates as long as it is only a working hypothesis. I cannot, however, go along with the conclusion that because it has not been so far strongly disproved (and that is already arguable!) "there are neither qualitative nor quantitative intellectual differences among nonhuman vertebrates." That style of argument was many years ago colloquially dubbed the "tobacco company trap" ("cigarettes have not been proven to affect health" therefore "cigarettes do not affect health"), once propagated by some, possibly too well-paid, statisticians. Less well-paid statisticians had much to say at the time on the issue (type II errors and all that). The present-day consensus seems to be that the latter's doubts were quite justified.

I find it instructive to consider briefly a counter-hypothesis. Have comparative psychologists suceeded in proving beyond reasonable doubt that all nonhuman vertebrates are equally intelligent? I would be disappointed if Macphail claimed they had. Thus, despite our own findings I go on assuming, based on good old common sense and much circumstantial evidence, that overall, pigeons are not as intelligent as chimpanzees, but more intelligent than goldfish, at least quantitatively.

There are many more points about which I would like to quarrel. For example, Macphail begins with a broad definition of intelligence, but as the target article proceeds an increasingly meaner definition is surreptitiously introduced but not explicitly stated. One cannot escape the feeling toward the end that as Humpty Dumpty said "when I use a word . . . it just means what I choose it to mean" (Carroll 1871). It is implied, for example, that the fact that humans can learn a language and monkeys cannot reflects a major difference in intelligence. When parrots can learn a fair number of words and pigeons are unable to learn a single one, however, then that apparently signifies no difference at all.

Macphail seems to be naive about the evidence on genetic variability of individual intelligence. Much has happened in the field of intelligence genetics since the days (and failings) of Burt (1966) and Kamin (1974), Tryon (1940) and Searle (1949), as consulting a recent genetics textbook readily reveals (Vogel and Motulsky 1986). In case there is after all genetic variability, Macphail seems to have a ready backup argument: since the laws of causality are the same for all nonhuman vertebrates (indeed for all organisms), convergent selection pressure has seen to it that all are equally good at detecting them. Can this be true when vertebrate nervous systems vary in computing power over a factor of at least 10,000 in terms of processing units, and when causality tangles vary in complexity between those involved in, say, a fall from a rotten branch and a fall from power in the course of a lengthy intrigue among peers?

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Brain differences determine different limits of intelligence

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Macphail's hypothesis that nonhuman vertebrates do not differ in their intellectual capacities and that the superiority of human intelligence depends on Man's species-specific language-acquisition device is open to two main points of criticism. The first is that vast interspecies differences in brain organization among nonhuman vertebrates are completely ignored, and the second is that no account is taken of studies on nonverbal intellectual functions in man.

Let's start with the first point. A statement which we will all obviously be willing to accept is that problem-solving depends largely on the neuronal system of an animal. One implication of this assumption is that we can study intelligence with two different approaches. The first is to study the "software" of a brain using behavioral techniques with which we can directly observe the performance of an animal during problem-solving. The second is to study the "hardware," that is, the anatomy and physiology of the brain. The software approach inevitably leads in comparative studies to endless debates on the comparability of different techniques or motivational states. To defend the null hypothesis in this tight jungle of arguments is relatively easy, since in the end nobody is able to rule out the possibility that even the most silly frog is able to master complex formation tasks if only skilfully conditioned.

The hardware approach offers some advantages. We know from neurocytology that the basic elements of the central nervous system are the same in all species regardless of whether fishes or humans are studied. Of course this does not mean that we can compare, say, the forebrain of a goldfish with that of a parrot with respect to its presumed functional capacity. The differences in the organization of the nervous system of these two species are too large to allow meaningful comparisons. The situation is different for comparisons between mammalian species. In different mammals studied, the number of cells in a standard cortical volume is equal, with the sole exception of area 17 in primates (Rockel et al. 1980). The proportion of cell types is also identical regardless of whether cats, rats, monkeys, or humans are examined (Powell 1981; Winfield et al. 1980). These similarities are present to some extent even in the internal connectional patterns of the cortical modules and their basic patterns of lamina-specific afferents and efferents (Powell 1981).

These are results of great importance since they show that the neocortex seems to be a rather conservative structure phylogenetically. This enables us to make comparisons between different mammalian species with respect to the relative extent of their neocortex. For example, it is commonly found that brain/body and neocortex/body ratios rise in moving from insectivores to monkeys and apes to humans (Stephan et al. 1981; Stephan 1972). Some mammals have more of the same basic cortex units relative to their body weight than others – they have the morphological substrate for the surplus capacity. I do not want to suggest that the extent of the neocortex relative to body weight is related one-to-one with intelligence. This would obviously be wrong. But it is clear that thinking needs neuronal capacity and that an increase in neuronal capacity has effects on the complexity of behavior and cognition. This relation has been demonstrated by correlating the volume of functionally defined neuronal substructures with the performance in a part of the animal's behavioral repertoire which is controlled by these structures (Nottebohm et al. 1981). I wonder how Macphail would explain the increased neocortical space of advanced mammalian orders. Would he conclude that these extra capacities are *l'art pour l'art?*

The second criticism is concerned with the assumption that human intelligence is generally at the same basic level as that of other vertebrates and is only differentiated by an additional species-specific language-acquisition device. This hypothesis would imply that the problem-solving capacity of man is lowered to a subhuman level if this device is removed. Probably the most elegant demonstrations that this is not the case come from split-brain studies in which the nonspeaking right hemisphere can for example exhibit nonverbal memory which is superior to that of nonhuman vertebrates tested in similar experiments (e.g., Milner & Taylor 1972). [See also Denenberg: "Hemispheric Laterality in Animals" *BBS* 4(1) 1981.]

We must think about the evolution of brain and intelligence not as a process with qualitative jumps but as a continuation of small quantitative improvements which develop in different directions depending on the ecology of the living system. It is true that detecting causality is the unifying topic of association formation, but links which are causally related are different depending on whether the animal flies or swims, is visually active or entirely blind. An animal is confronted with only a small fraction of all possible causal contingencies and his brain will be specialized primarily for those. The quantity and the internal organization of this brain will then limit the complexity of the animal's cognition and memory.

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From null hypothesis to null dogma

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Although most of what Macphail says is controversial (no doubt intentionally), with much of it I am in complete agreement. It will be more entertaining, however, and possibly more instructive, if I concentrate on a single point of disagreement, specifically, Macphail's claim that no differences in intelligence, either qualitative or quantitative, have yet been demonstrated amongst nonhuman vertebrates.

It will hardly be appropriate to review the earlier book which documented this claim (Macphail 1982). Nor will it be necessary, for the target article provides sufficient insight into the way Macphail attempts to establish it. But it is worth acknowledging that the book provides a valuable corrective to the view that such differences are self-evident and have been proved beyond cavil. The parallel with Kamin's attack on the data said to demonstrate the heritability of IQ (Kamin 1974) is close: Both challenge received wisdom and show that much of it rests on shaky empirical foundations. But the parallel extends further; in the end, both are surely wrong.

Macphail devotes most attention to the successive negative contrast effect (SNCE) produced by a decrease in the value of reward, a phenomenon routinely observed in rats, but not in goldfish. He acknowledges, indeed, that it is "an elusive phenomenon in goldfish," although he gives little feeling for just how elusive it is. By my count, some eight published papers have reported nine experiments from five different laboratories, not one of which obtained a statistically significant contrast effect (Macphail 1982; Couvillon & Bitterman 1985). Experiments from different laboratories inevitably introduce minor differences in procedure, but in these studies the differences have been substantial. The apparatus has included alleyways and small chambers; the responses studied have ranged from consummatory responses, through swimming down an alley, to striking an illuminated target; the rewards have included live or freeze-dried Tubifex worms, pellets, and liquid food, and shifts in their value have been produced by adulteration with quinine as well as reduction in quantity. Of course it is always possible that future studies, using different procedures, will reveal unambiguous evidence of a contrast effect in goldfish. But it can hardly be denied that we already have a long series of attempts to demonstrate contrast in fish, which have involved significant systematic variation. Equally important, there is converging evidence, from other experiments (e.g., Bitterman 1975; Couvillon 1984) that the absence of contrast in goldfish is not an isolated phenomenon but forms part of a larger pattern indicating, perhaps, the insensitivity of their behavior to control by the memory of preceding conditions of reinforcement.

How then does Macphail dismiss this evidence? I shall ignore his appeal to two reports by Breuning and Wolach (1977; 1979) which, he rightly acknowledges, "leave much to be desired." He has two further arguments. The first is, simply, a red herring. The discussion of contrast in goldfish is introduced by reference to one interpretation which Bitterman has put on these data, namely, that goldfish do not form expectancies (Bitterman 1975). Macphail points to data, provided by Bitterman himself (1984b), which suggest that goldfish do, after all, form S-S associations (one form of expectancy). No doubt this provides some reason for questioning this particular theoretical analysis of the causes of the difference between the behavior of rat and goldfish in contrast experiments, but it provides no reason whatever for supposing that the difference is illusory, or that it can be explained away as an artifact of a failure to control for contextual variables.

Macphail's second argument is that "the effects of reward reduction in rats vary with type of reward, response measure, and age. Failures to obtain the SNCE are not yet well understood. . . . Until they are, it will be premature to rest theoretical speculation on failures to obtain the SNCE in goldfish, since such failures could very well be due to inappropriateness of one of the contextual variables critical to the appearance of the effect." If he could persuade us to accept this argument, Macphail would run no risk of ever having to abandon his position; it amounts to saying that even if a particular phenomenon is routinely found in experiments with rats, and never (so far) convincingly demonstrated in goldfish, we could still not conclude that we had evidence of any difference between rats and goldfish, so long as there are *some* conditions under which the phenomenon is not found in rats, and there is no theoretical consensus as to the interpretation of these conditions. But of what phenomenon could this not be said? How can Macphail expect one to take seriously his suggestion that comparative studies may illuminate the structure of animal intelligence if their results can be dismissed in the absence of complete theoretical understanding of any particular phenomenon?

Later on, Macphail briefly turns to other "proposals for species differences in intellect which enjoy experimental support," including our own work on differences between pigeons and crows in the transfer of relational (matching or oddity) rules (Wilson et al. 1985). But these too can be dismissed, because "their experimental support inevitably consists of reports of failures by a species to master some problem," and he wishes to see "a series of such failures . . . involving systematic variation" before he would have any confidence in the proposal.

Our case, as we were at pains to make clear, did not rest on proving that pigeons *cannot* transfer matching or oddity rules. We showed, in three experiments differing significantly in task and procedure, that three different corvid species gave unambiguous evidence of such transfer, and pigeons gave none. We concluded that, whatever the mechanisms underlying such transfer, they were more readily available to, or better developed in, corvids than pigeons. We did not claim that pigeons would never show evidence of such transfer, and we explicitly referred to one published study (Wright et al. 1983) which suggests that, after very lengthy training, pigeons may show some evidence of transfer on a related task. As a matter of fact, however, there have been some 20 or more published experiments purporting or attempting to show transfer of matching or oddity in pigeons over the past 25 years, and the evidence they have provided for such transfer has been singularly unimpressive. D'Amato et al. (1985) have argued in a thorough review of these studies, and we have demonstrated experimentally, that the most systematic series of such experiments, that by Zentall and his colleagues (Zentall 1983), provides no evidence of transfer.

Once again, the range of studies from different laboratories makes nonsense of Macphail's suggestion that there has been no serious attempt at systematic replication of this failure; and recent attempts to provide more favorable conditions for transfer – by increasing the amount of training, the number of exemplars, or the number of negative comparison stimuli on each trial – have proved no more successful than earlier studies (e.g., Holmes 1979; Prisacreta et al. 1985). Finally, as was true for the contrast experiments in rats and goldfish, so here there is converging evidence from a quite different comparison of matching and nonrelational conditional discriminations in cebus monkeys and pigeons, that although monkeys solve matching discriminations by using the relationship between sample and comparison stimuli, pigeons do not (D'Amato et al. 1986).

There is an air of superficial reasonableness to Macphail's argument. We have no proof that animals differ in intellect. We do know, however, that they differ in sensory and motor capacity, the organization of their motivational states, dietary requirements, and the like. We also know that no behavioral phenomenon of any interest that has appeared in experiments with rats or pigeons is totally unaffected by variations in experimental procedure. It is always possible, therefore, to argue that apparent differences in behavior between species should be attributed to differences in contextual variables or in sensory and motivational factors, rather than to any difference in mechanisms of learning or intellect. Of course it is possible. But is it reasonable? The evidence of his target article suggests that Macphail is so wedded to his null hypothesis that he has made it impervious to disproof. At this point, it ceases to be a salutary reminder of the difficulties of doing good comparative research. It is empty dogma.

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