The elements of the "respiratory zone" may be regarded as randomly distributed in the lung. There are essentially the same number of alveoli (300 million), alveolar ducts (14 million), and capillary segments (280 billion) in all lungs. The dimensions of these architectural elements are shown to depend mainly on the size of the lung. The effect on these dimensions of such functional variables as the degree of inflation of the lung or of the filling of capillaries with blood are discussed.

The alveolar and alveolar-capillary surface areas, which are of importance in the analysis of gas exchange between air and blood, are found to increase with the size of the lung. In our material, both varied in the range of 40 to 80 square meters.

The elements of the conductive zone of the lung show a polar orientation. The airways have, on the average, 23 generations of dichotomous branching; the pulmonary arteries reach the precapillaries after about 28 generations. The average diameters of the airway and blood-vessel elements at each generation appear to follow the laws of "best" dimensions. The functional significance of this finding is discussed.

It is suggested that morphometric studies conducted according to this general model may be useful in the anatomical description of other organs (*16*).

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Evolution of Intelligence and Vocal Mimicking

Studies of large-brained mammals promise to elucidate some problems of human evolution.

R. J. Andrew

Some 20 years ago McBride and Hebb (*1*) pointed out that the brain of the bottlenose dolphin (*Tursiops truncatus*) was comparable to that of man, both in size and in general cortical development, and argued that this species (and presumably other Cetacea) were therefore probably of a very high order of intelligence indeed. This argument has recently been revived and greatly extended by Lilly (*2*, *3*), on the basis of extensive studies on *T. truncatus*. The advanced nature of the structure of the brain in *T. truncatus* appears to be fully established. Not only are cells as densely packed in the thalamus (*4*), for example, as in man, but the cortex shows extensive "silent areas" (*2*). However, it seems unsafe to predict on this anatomical basis alone, as Lilly does (*2*), that *Tursiops* will prove to be as intelligent as man, although perhaps with an intelligence specialized along different lines. Direct evidence for very high intelligence (*5*) in *Tursiops* seems to be lacking. The most striking difference from other mammals appears to be the degree to which dolphin vocalization can be modified; dolphins can be trained to vocalize for a reward, and there is evidence of some degree of mimicking (*2*). However, comparison with birds suggests that a difference in the control of vocalization may be involved rather than a difference in intelligence. Anecdotal evidence from animal trainers and from brain-stimulation studies suggests intelligence of an order anywhere between that of a dog and that of a chimpanzee. Wide interest has rightly been aroused by current discussions of the brain of *Tursiops*. In view of this, and of the fact that the acquisition of high intelligence and the ability of vocal mimicking have been crucial in human evolution, it seems appropriate at this time to consider the factors which seem to have affected the evolution of these two characteristics in the mammals in general.

Let us consider the problem of mimicking first. It appears that *Tursiops truncatus* will answer human laughter, whistles, and Bronx cheers with similar sounds (*2*, p. 201). This however, is not in itself evidence of true mimicking; it is rather the elicitation of a call by sound which resembles it, since these calls are part of the normal repertoire of the species (*3*). Such a condition has evolved at least twice, and probably many times, in the Primates. In the Lemuroidea, *Lemur fulvus* and related species answer any loud, short, deep sound from a social fellow with their contact call, which is loud and deep; *Lemur catta* gives its contact call (a high wail) in response to high-pitched sounds of similar quality (*6*). The gelada baboon (*Theropithecus gelada*) will give the characteristic baboon "segmented grunt" in response to human imitations. *Hylo-*

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bates concolor replies to human grunts with grunts (*7*), while the sound of the gibbon "song" elicits "song" in other species of *Hylobates* (*8*). Species of *Papio* and *Macaca* answer a number of calls of their own species (for example, the "woo" call of *M. mulatta*) with similar calls (*6*).

Comparable instances occur in other social mammals (for example, evocation of the howl of the domestic dog by high-pitched sounds). It appears that the calls involved may serve to reestablish contact with fellows (as in *Lemur*) or may be a greeting (as in *Theropithecus*). The whistle of *Tursiops* is used as a contact call (*2*), and the "laughter" and "Bronx cheers" appear to be the same as the "quacks, blats, and squawks" (*3*) which are emitted by a dolphin during bodily contact when greeting another dolphin. *Tursiops*, in answering sounds with similar calls, thus provides one more instance of what is probably a relatively widespread occurrence among social mammals; such behavior is adaptive—for example, in maintaining contact between members of the same group.

The detailed imitation of human speech which is thought by Lilly (*2*) to occur in *Tursiops* cannot be paralleled in other mammals. The only possible comparison within the mammals is with the human evolutionary line, in which some ability to mimic must have evolved before any form of true language could develop. A particular meaning for a particular pattern of vocalization could hardly be transmitted from one individual to another until the pattern itself could be readily imitated. Reasons for the first appearance of such an ability may be sought by considering birds which mimic. In passerine birds, mimicking, which is sometimes limited to patterns of sounds resembling in tonal quality the normal song of the species (*9*), serves to provide each male with a song repertoire which is characteristic both of the species and, where topographic barriers exist, of a particular small dialect area (*10*).

The selective advantage of dialects is still obscure, and it may well be that song learning has evolved purely as a simple means of insuring the transmission of complex species-specific song, and that the existence of dialects is a functionless by-product. That this method of transmission appears to allow enough variability to permit individuals to be recognized by slight differences in the form of their song (*10*) is probably also important.

The matter is complicated by the fact that it is not yet possible to establish the course of evolution of song learning in any line of passerine evolution. It is even possible that extensive learning is primitive within the group, and that this faculty has been lost in some lines (*11*). However, it is clear that mimicking can be evolved in the absence of any very high level of intelligence when there is a need for the acquisition during development of complex species-specific, group-specific, or individual-specific patterns of vocalization.

Such a need may well have been present in the human line. Thus, it may have been advantageous for an individual to be able to distinguish his own group from others at a distance (*6*). In this way disastrous attempts to join the wrong group could be avoided; such mistakes might be easier to make in a hunting society, in which the group often subdivided or even separated into individuals when in pursuit of prey, than in a foraging society like that of baboons (for example, *Papio*) (*12*). Other factors which may have been involved are an increase in the number of calls which were available for "matching" against external sounds, making possible a gradual approach to true mimicking, and an increase in the ease with which vocalization in general was elicited. This latter change would be no more than a continuation of the facilitation of vocalization which appears to have occurred several times in the primates as a result of the need for better communication between individuals, which followed the development of permanent societies (*6*). Finally, the incipient appearance of language (perhaps the use of contact calls to summon fellows to a prey) would itself greatly increase the advantage conferred by mimicking abilities.

There is no obvious reason why any of these hypothetical effects should have caused the Cetacea, rather than any other major group of mammals, to acquire the ability to mimic sounds. However, so little is known of the causes of the evolution of this ability in birds or man that it would be foolish to assume that cetaceans cannot mimic. It is to be hoped that further data will soon be available.

Information Carried by Mammalian Vocalization

However, it should be emphasized that even if mimicking occurs, this would be no proof that the vocalizations of *Tursiops* are comparable to human language, or even that they carry any more elaborate information than the calls of a bird which is capable of mimicking. In such a species the mimicked sounds are usually given as part of song and convey no more elaborate information than the presence of the individual on a certain territory, or the loss of contact by an individual. The other vocalizations convey simple information such as the likelihood that the caller will perform such acts as fleeing or attacking or attempted copulation (*Fringilla coelebs* exhibits such calls) (*13*).

There is no evidence in mammals that calling depends on any intent on the part of the caller to convey information. Like other displays, calling appears not to be under the same kind of direct control that locomotor or grasping movements are, for example. Evidence has recently been summarized (*14*) which suggests that primate vocalizations are basically evoked by stimuli which contrast with background stimulation. This property of contrast may be intrinsic, as in the case of a sudden noise or movement, or it may be acquired as a result of experience; thus, in a social species, the absence of social fellows is responded to as a persistently conspicuous feature of the environment. To take specific examples, in forms ranging from *Galago* in the Lorisoidea to *Pan* and *Homo*, the same low-intensity calls are elicited by situations as various as obtaining a desired food, establishing bodily contact with a fellow, or perceiving a novel and disturbing object. High-intensity vocalizations, such as screams, can be evoked by intensely disturbing situations such as a threat from a superior or, in infants, loss of contact with the mother; however, they are also produced in tantrums brought on by prolonged exposure to a desired but unobtainable object.

A detailed theoretical treatment of behavior which appears to be caused in this way is presented elsewhere (*15*). The important point for the present argument is that the causation of vocalization appears to be such that any one call occurs only in a limited number of motivational states. As a result, in combination with other display components, calls enable other animals to predict the probable future behavior of the caller, without any *intent* to communicate being involved. A second example, from another group of responses, may make the point clear. In a number of groups of mammals and birds, inferiors threatened by a superior show a marked decrease in locomotion and the activity of postural reflexes. As a result, an animal which shows free locomotion and marked postural reflexes during a social encounter indicates (without any intent to communicate) confidence and lack of any tendency to flee. In some mammals (for example, *Lemur* and *Canis*), at such times the tail is fully elevated, a response which can be regarded as an exaggeration of a postural reflex for purposes of communication.

Situations which evoke vocalizations in *Tursiops* in captivity (contact with other porpoises or with humans or perception of a novel object) (*3, 16*) are precisely analogous to those in which vocalization occurs in other tame social mammals.

Evolution of Intelligence

At first sight it would appear that there is no way of life in mammals in which a slight increase in intelligence would be anything but an advantage for any particular individual. However, if this is so, then equally strong reverse selection pressures, perhaps connected with opposition to changes in the structure and proportions of the brain, must exist. Thus, the American opossum (*Didelphis*), for example, differs little from Lower Eocene mammals in the size and proportions of the brain (*17*) and shows a far worse performance on conditioning tests (*18*) than even such a small placental mammal as the rat. Even without any quantitative comparative data it is clear that the range of problem-solving abilities among the mammals is very wide indeed.

It thus seems likely that intelligence increases rapidly during evolution only when there are some special demands on the species which can be met only in this way. To my knowledge there has been no explicit discussion of what such demands might be, except for the human line of evolution. In that case, it is now generally held (see, for example, *19*), that a way of life in which the manufacture of tools was of crucial importance greatly favored the evolution of increased intelligence. Clearly such an argument can be justified only if other instances of increase in intelligence can be explained along similar lines.

One interesting case is that of the higher Lemuroidea on Madagascar and corresponding cercopithecoid genera in the Old World. Certain species of *Lemur* have the same general way of life as *Cercopithecus* and *Macaca*: *L. fulvus* and related species may be compared with the arboreal species of *Cercopithecus*, and the more terrestrial *L. catta*, with species of *Macaca*. They are as fully social (*6*), and they appear to eat the same kinds of food, which they grasp with the hands. However, they perform much more poorly on choice tests than, say, *Macaca mulatta*. Contrary to results in the earlier study of the subject (*20*), it has proved quite easy, in our laboratory, to train *Lemur fulvus* and *Propithecus ver eauxi* to discriminate between such patterns as a white square with a central black bar of one length and a white square with a longer black bar, and so on. However, this can be done only if the animal is prevented from establishing position preferences; this is accomplished by progressively changing the incorrect pattern from one which matches the background to one which contrasts with it in the same way as the correct pattern. At the same time the position of the correct pattern is continuously alternated between right and left sides. The animal learns first to pick the pattern which contrasts most with the background, and only with later training begins to respond to such features as the central black bar. This may be contrasted with discrimination training in *Macaca mulatta* (Catarrhini), in which Harlow (*21*) found that object discriminations could be established very easily. In the present study, *Cebus albifrons* (Platyrrhini) has been found readily to solve pattern discriminations which, when presented to lemurs with no initial phase of training such as is described above, resulted in rigid and permanent position preferences.

Here, then, are three groups which are derived from a common ancestor and which have come to occupy similar ecological niches but which appear to differ markedly in problem-solving ability. Two different reasons for this may be advanced. It has been argued elsewhere (*22*) that, in the lemurs, lack of any use of the hands to part the fur or pick up fine objects from the skin in grooming has hampered the evolution of manual dexterity. (The lemur spends much of its time, just as Old World monkeys do, in grooming itself and its fellows, but Lemuroidea such as the lemur have specialized lower incisors which they use to scrape objects from the fur in grooming.) The poorer manipulative abilities of the group [*Lemur*, for instance is capable of only one pattern of grasping (*23*)] may in turn have hindered the evolution of intelligence.

The second reason is more important, since it is of more general application. On Madagascar there has been interaction between a far more restricted range of mammalian types than in the main continental land mass; indeed, nearly all the large mammals evolved in Madagascar have been lemuroids. It may be argued that it is such interaction which leads to rapid increase in intelligence. If one group, by entering a new niche, is forced to increase in intelligence, then this very increase in intelligence will enable it to compete with other groups in niches to which it formerly had no access. To take a crude example, the presence of intelligent carnivores will result in the evolution of intelligent ungulates, and vice versa. The Australian fauna appears to provide a parallel case. Anecdotal evidence suggests that marsupials are much less intelligent than placentals which occupy comparable niches (for example, thylacine as compared with wolf).

Edinger (*17*) has provided paleontological evidence of a case which appears to be comparable to that of the lemurs. The ways of life of *Hyracotherium* and of *Orohippus* appear to have had very similar effects on skeletal proportion and structure on body size. However, the cerebrum of *Orohippus* is much expanded backwards and shows more sulci than that of *Hyracotherium*, strongly suggesting marked selection for increased intelligence between the Lower and the Middle Eocene. This trend continued throughout the evolution of the Equidae. Edinger points out that even *Mesohippus* (Oligocene) has a much smaller neocortical area than a modern ungulate of similar size and proportions (for example, a sheep).

It is argued here that such changes depended on interaction with other lines of placental mammals in which similar changes were occurring.

In summary, then, what evidence there is suggests that any increase in intelligence depends on strong selection for such increase. In the two examples discussed, such selection was ascribed to interaction with other intelligent mammals, but the general way of life of a species is probably also important. Thus, lorisoid primates survive in the Old World as crepuscular and nocturnal insectivores. The problem-solving ability even of such a large active lorisoid as *Galago crassicaudatus* appears to be somewhat inferior to that of *Lemur* or *Propithecus* (*24*). Thus, although the Lorisoidea have evolved for as long in the Old World as the Old World monkeys (or man), their way of life appears not to have demanded increased intelligence.

It would seem that, if very high intelligence does exist in the Cetacea, they provide an exception to these tentative conclusions. The only mammalian group with which they interact seriously is the Pinnipedia. At the same time, the way of life of the dolphin appears to be that of a permanently social hunter, and one would predict intelligence comparable to that of *Canis* on such a basis (this is, of course, a relatively high order of intelligence). However, so little is known of cetacean ecology that it would be foolish to disregard the possibility that the way of life of cetaceans may, for as yet unknown reasons, demand more advanced intelligence.

Very Large Brains

The differences in intelligence already discussed are accompanied by differences in brain proportions, in particular by differences in the relative size of the neocortex. The effect of simple increase in brain size due to an increase in body size has not yet been considered at all here. The main experimental evidence is that reported by Rensch (*25*), who compared the learning ability of dwarf and giant strains of house mice and hens. The results were ambiguous in that the dwarf mice appeared to learn more quickly and to remember longer than the giant mice, whereas the dwarf hens learned easy tasks more quickly than their relatives but were slower in learning more difficult tasks; they were also less good at retaining discriminations. A second approach was that of studying very large species and comparing their abilities with those of other mammals. A study of an Indian elephant (*26*) suggested high ability: it could remember 20 different pairs of visual discriminations simultaneously. However, a horse also was able to remember 20 pairs; an ass apparently could retain only 13. The elephant's performance may therefore appear impressive only because data in a comparable form are not available for moderate-size carnivores or primates, for example.

The other group of giant mammals are, of course, the cetaceans. Unfortunately no such data as those of Rensch are yet available even for *Tursiops*. McBride and Hebb (*1*) maintained that the species lay somewhere between the dog and the chimpanzee in "emotional and motivational behavior," on the basis of four lines of evidence. The first was the long duration of visually aroused fear of inanimate objects (24 to 48 hours), which is said to be comparable to that of the chimpanzee. The second, the formation of strong social bonds between individuals, is, of course, paralleled in many dogs by relations formed between master and dog; individual recognition is very marked in the primates, even as low as *Lemur* spp. (*4*). The third, the elaborate chasing play of the porpoise, is again paralleled in the dog, as is the fourth—the direction of copulatory behavior toward members of other species. Thus in these respects, for what they are worth, *Tursiops* is comparable to the dog.

Far more important for any estimate of dolphin intelligence is the wealth of anecdotal evidence assembled by Lilly (*2*). Unfortunately, the evaluation of much of this is made difficult by the lack of any full account of the instinctive behavior patterns of the species. Thus, the behavior of supporting injured animals in such a position that they can breathe is adduced as evidence of intellectual capacity. This behavior, while fascinating in itself, evidently represents the extension to adult social fellows of a response made by the mother to the newly born infant (*1*). One may compare the defense of injured adult fellows in primates (*27*). To assume high intelligence on the basis of such behavior without knowing its ontogeny and causation would be like ascribing high intelligence to a weaver bird because of its nest-building abilities. Elsewhere it is suggested that a special behavior pattern in the dolphin, which involves making sounds like a baby crying, with most of the animal's body out of water, was learned by one dolphin from another. This may be so. However, a third dolphin began to exhibit such behavior in isolation from other dolphins, and it seems equally likely that we have here a behavior pattern which is part of the normal repertoire of the species.

A final example will suffice. Killer whales have been observed to break thick ice in an apparent attempt to seize dogs which were on the surface of the ice. Ice-breaking to obtain prey seems a very likely pattern to have evolved as part of the hunting behavior of such a cold-water species; again, no great intelligence need be postulated.

Evidence from animal trainers of the acquisition of new tricks by their dolphins gives rise, to some extent, to the same doubts. However, some tricks, such as presenting a flipper for a handshake, must certainly be new, and the general testimony of the trainer is that tricks are acquired with ease. It may well be that dolphins are to be compared with macaques, for example, rather than with dogs, in the ease with which they can be trained. This is suggested also by the rapidity (three to 20 trials) with which *Tursiops truncatus* learns self-stimulation in reward areas (*28*). However, Olds (*29*) has pointed out in this connection that even rats may learn self-stimulation in a single trial if the electrode is correctly placed.

It is only in the ability to modify their vocalizations that dolphins appear to differ markedly from other mammals. Trainers have been able to cause dolphins to give one type of call (high wails) in preference to other types of call in the normal repertoire of the species (*2*). The problem of the occurrence to true mimicking has already been discussed, and it has been shown that such mimicking would not necessarily require high intelligence.

Perhaps most interesting of all is the fact that it was apparently easy to train a dolphin to whistle in order to obtain rewarding brain stimulation (*2, 28*). This is in marked contrast to findings in the primates (*30*), but this again need not be directly related to intelligence. The dolphin appears to vocalize much more readily than primates, perhaps because of its frequent use of vocalization as "sonar," and this must make a vocalization response more readily obtainable in conditioning. The point may be stated in these terms: if a primate is trying to solve a problem it does not vocalize (unless it is giving up and going into a tantrum). If it is made to vocalize, then its attention is no longer on the problem, or on the reward that awaits its solution; that it will learn to use vocalization to obtain a reward is therefore most unlikely.

It thus seems fair to say that we have no exact knowledge of the level of intelligence of *Turisops* and can only say that it is probably as great as that of a dog. There is as yet no proof that it is as high as that of a chimpanzee. This in no way makes the brains of this and other cetaceans of less scientific interest. The adult brain of *Tursiops truncatus* weighs about 1600 to 1700 grams, and the cerebrum is relatively very large; this compares well with the weight for the human brain of 1450 grams (*2*). However, the most likely conclusion from this seems to be, not that *Tursiops* is as intelligent as man, but that the size and general proportions of the brain are not always accurate measures of intelligence. This conclusion is reinforced when the enormous size of the brains of large whales (for example, *Physeter catodon*, with a brain weighing as much as 9200 gm) (*2*), or of elephants (with a weight, for example, of 6075 gm) (*2*) is considered.

It seems unlikely that elephants are really considerably more intelligent than human beings, when our long experience with them in zoos and as beasts of burden has revealed no sign of this. If large brains really are not always accompanied by commensurate intelligence, then it must be supposed that an increase in brain size due to increased body size is not very effective in increasing intelligence in the absence of strong selection for increased intelligence.

Two unsolved questions thus arise from this discussion. First, why is the dolphin brain so large? This in part may be due to the large body size of the animal; the high degree of convolution of the cerebrum may also be partly due to this, since convolution increases with body size (*17*). However, this is not a full explanation. Second and more important, why is so large a mass of nervous tissue not as effective as a smaller mass in man? Is it a matter of more wasteful organization, or is it the lack of an effective means of interacting with the environment, such as the human hand provides?

Eventually more specific questions may be asked, relative to the capacity of immediate memory or the accessibility of stored information, for example. It is important, however, that such questions should be viewed always as part of the wider problems of mammalian evolution in general. Such an approach may enable us one day to give firm answers to problems concerning the evolution of human intellectual abilities, which will never be resolved while the human line of evolution is considered in isolation (*31*).

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