

Rapid #: -8271134

CROSS REF ID: **196498**

LENDER: **ORE :: Main Library**

BORROWER: **YRM :: Main Library**

TYPE: Article CC:CCL

JOURNAL TITLE: Investigations on cetacea

USER JOURNAL TITLE: Investigations on Cetacea

ARTICLE TITLE: The cybernetics of Cetacea

ARTICLE AUTHOR:

VOLUME: 16

ISSUE:

MONTH:

YEAR: 1984

PAGES: 151-197

ISSN: 1010-3635

OCLC #:

Processed by RapidX: 8/19/2014 12:54:59 PM



RAPID

This material may be protected by copyright law (Title 17 U.S. Code)

The Cybernetics of Cetacea

RON EGLASH

Biotechnology laboratory, University of California
Los Angeles 90024 (U.S.A.)

CONTENTS

	Page
Hypothesis of neural evolution in cetacea	150
Evolution of the brain and manipulatory feedback	155
Sexual selection and cetacean vocalizations	162
The analog/digital dualism	168
Application of the analog/digital dualism to cetaceans	177
Conclusions and future research	184
Postscript	189
Acknowledgement	190
Bibliography	190

HYPOTHESIS OF NEURAL EVOLUTION ON CETACEA

*But the limitation then is still there . . . and because we're familiar
with it we forget its mystery. Just as you never think of the
fabulousness of the infinite images — the reflections — of a rain-
washed pavement, the number and the position of the images
being entirely a function of the number and positions of
the observers.*

Edward F. Ricketts
(Hedgpeth, 1978)

1.1 Introduction

Although the mystique of dolphins and whales dates back at least to ARISTOTLE (MONTAGU and LILLY, 1963), their modern status as counter-culture heroes of superior intelligence began with recognition of the large and complex cetacean brain. In his whaling classic *Moby Dick*, HERMAN MELVILLE, a naturalist as well as novelist, points out the great size of the sperm whale brain, and writes:

»Genius in the sperm whale? Has the sperm whale ever written a book, spoken a speech? No, his great genius is declared in doing nothing in particular to prove it. . . . If then, Sir William Jones, who read in thirty languages, could

not read the simplest peasant's face in its profounder and more subtle meanings, how may unlettered Ishmael hope to read the awful Chaldee of the sperm whale's brow? I but put that brow before you. Read it if you can.»

Probably the first modern expression of the problem was in an extensive review of brain-body weight relations by VON BONIN (1937). VON BONIN was aware of the logarithmic relation between brain and body weight, and that certain species were exceptional in this ratio, but notes that, »Whether or not this is an indication of the intelligence of the animals must be left to the psychologists to answer.»

LILLY (1961, 1963, 1967) was the first, and is still the most adamant advocate of a human-like cetacean intelligence and language as the primary cause of the exceptional size and complexity to the cetacean brain. No one takes this anatomical basis for cetacean intelligence to be conclusive evidence, and even LILLY has recently stated that »convincing scientific evidence of cetacean intelligence remains to be established, and arguments comparing levels of human and dolphin are philosophical, not scientific» (LILLY, 1978). Yet it was, at the time of its first suggestion, a very compelling hypothesis.

It is possible to compute an encephalization quotient (EQ) to compare brain/body ratios of different animals (JERISON, 1973). This is based on the actual size of the brain divided by its expected size for an »average» mammal of that weight. The expected size is determined by the 2/3 power ratio of brain to body (suggested by Jerison to be due to square units of motor and sensory surfaces mapping on cubic units of brain volume) and an empirically determined multiplicative constant of .12. Thus, the average mammal has an EQ of 1; very few range above 2.0, while humans average about 7.5. Well established as a statistical measure of relative brain size, the EQ shows cetacea as the only group including species with a relative brain size comparable to that of humans.

In addition to the suprisingly high relative brain size, the intricate fissurization and subsequent increase in neocortex, along with a high degree of regional specialization, have prompted several investigators to place the cetacean brain at a comparable level of advancement to that of higher primates (PILLERI and BUSNEL, 1969; PILLERI, KRAUS, and GIHR, 1969; JANSEN and JANSEN, 1969; MORGANE and JACOBS, 1972; MORGANE, 1974).

Note: Common names used in the text

bottlenosed dolphin	<i>Tursiops</i> sp. (usually <i>truncatus</i>)
common dolphin	<i>Delphinus delphis</i>
harbor porpoise	<i>Phocoena phocoena</i>
Hawaiian spinner dolphin	<i>Stenella longirostris</i>
humpback whale	<i>Megaptera novaeangliae</i>
killer whale	<i>Orcinus orca</i>
narwhal	<i>Monodon monoceros</i>

This is not without controversy. LADYGINA and SUPIN (1970, 1974, 1975, 1977) regard some portions of the large areas labeled as association cortex by MORGANE and JACOBS (1972) to be sensory projection areas, although BULLOCK and GUREVICH (1979) note some inconsistency in their use of homologies concerning these cortical areas. Similar confusion exists in cytoarchitectonic studies. While KESAREV (1969) feels that the differences in lamination of the cetacean cortex (e.g., absence of the granule cell layer) indicates a more primitive cortical organization than that of higher primates, both MORGANE (1974) and ENTIN (1973) report that cortical microstructures are completely comparable to those features in primates.

The general consensus is that the cetacean brain is too dissimilar to other mammalian brains for any strong conclusions, and that the question of intelligence in cetacea must be determined by behavioral study. But while current studies have left open the question of neural and cognitive capacity, the language hypothesis is now very doubtful. LILLY (1967) attempted to keep a researcher and dolphin in constant proximity for 2½ months. Although a great deal of daily interaction occurred, little was accomplished in teaching human sounds to the dolphin or in interpreting its vocalizations.

A more basic attempt was made by BASTIAN (1967), where a dolphin was required to acoustically transmit the state of a cue light to allow another dolphin to respond correctly. Although the responses were made successfully, it was later determined that the »sender» was assuming a posture detectable by echolocation of the »receiver», and that the dolphin made no attempt to transmit information (EVANS and BASTIAN, 1969).

There has been some discussion of attempting to demonstrate the existence of a language in cetacea by evidence of language properties, e.g., openness (c.f. THORPE, 1972). True language is, by definition, a code organized by flexible syntactic structure. While syntax is an elusive entity, the presence of an arbitrary code is in some ways a straight-forward characteristic.

Contrast between communication with arbitrary encoding and that of »emphatic» coding has previously been made in primates. While vervet monkeys (CHANEY and SEYFORTH, 1981) have a set of discrete alarm calls, each signifying a different predator, the macaque monkey (ROWELL and HINDS, 1962; GREEN, 1975) has a graded communication where emphasis given to a single cry ranged on a continuum from pleasure to alarm.

It is commonly thought that many cetacean signals are best characterized as a graded or emphatic system. This has been shown in whistle contours of pilot whales (TARUSKI, 1976), in whistles of bottlenosed dolphins (BASTIAN, 1967), and in the restriction of differing vocal responses to emphatic variations of the same »signature whistle» by dolphins (CALDWELL and CALDWELL, 1967, 1971, 1972). This topic will be discussed further in Chapter Five.

Most convincing is the lack of evidence for natural language in the familiar bottlenosed dolphin of »Flipper» fame, a species which has been under close behavioral and acoustic observation for more than twenty years (CALDWELL and

CALDWELL, 1976). This includes experiments with isolated animals exchanging vocalizations over an electro-acoustic link (LANG and SMITH, 1965), greatly varying degrees of social and environmental interaction (LILLY and MILLER, 1961; BULLOCK and GUREVICH, 1979), and behavioral contingencies ranging from complex acoustic cues (HERMAN, 1980) to direct brain stimulation (LILLY and MILLER, 1962).

The problem with the natural language hypothesis is that one cannot conclusively prove the absence of language; it is only possible to list experiments which have failed to show its presence. But the large list of such failures, particularly for the bottlenosed dolphin, considered to be one of the most intelligent of all cetaceans, has made the hypothesis of natural language a very unlikely possibility.

1.2 The Echolocation Hypothesis

The only other explanation that has been well formulated is that the echolocation system of cetaceans requires an extraordinarily large neural capacity. TOMILIN (1968) suggests that »The use of echolocation and the echolocation apparatus may have played as important a role in the formation of the dolphin brain as did the hands, work, and articulate speech in the development of the human brain.« A similar inference has been made by several others (e.g., WOOD, 1973; CALDWELL and CALDWELL, 1976; GASKIN, 1982; KELLOGG, 1961; WOOD and EVANS, 1979).

WOOD and EVANS (1979) are the only researchers who provide evidence for this idea. Their argument is based mainly on ecological correlates, noting that species with a smaller EQ, such as river dolphins, tend to have much less sophisticated (flexible) echolocation than large-brained species. But river dolphins are also much less social than their large-brained relatives (KASUYA and AMINUL HAGUE, 1972; LAYNE, 1958). This difference in sociality holds for many of the midrange EQ species as well, e.g., the harbor porpoise (AMUNDIN and AMUNDIN, 1973). In addition, these smaller-brained species have fewer communicative sounds; river dolphins and the harbor porpoise are both non-whistling species. WOOD and EVANS (1979) also note that the larger-brained species tend to be generalists, able to adapt their behavior to several niches. However, citing behavioral plasticity as a cause of high relative brain size is equivalent to citing intelligence, and does not, in particular, support the echolocation hypothesis.

A major criticism of the echolocation hypothesis has been its comparison with bat echolocation abilities. Several researchers have noted that the highly skilled echolocation performance of insect-catching bats is accomplished with brains weighing less than a gram, and that the size of the cetacean cortex greatly exceeds that expected for the moderate echolocation superiority they have over bats (HERMAN, 1980; JERISON, 1978; PILLERI and GIHR, 1970). WOOD and EVANS (1979) observed that, while bats use a more specialized FM sweep, cetaceans use a finely controlled transient broadband click, thus requiring a more versatile production and processing capacity.

Although it is true that large-brained cetaceans, such as the bottlenosed dolphin, tend to have very wide bandwidth echolocation, this is not a consistent correlation. For example, when adjusted for the allometric characteristics of large body size, the EQ of the killer whale is probably close to that of the bottlenosed dolphin (WOOD and EVANS, 1979). Killer whales are also very highly rated in behavioral abilities (DEFRAN and PRYOR, 1980). Yet the bandwidth for the killer whale is only 30 kHz, far less than the 100 kHz bandwidth of the bottlenosed dolphin or the 130 kHz bandwidth of the much smaller-brained harbor porpoises.

In addition, the echolocation hypothesis does not explain the large brains of the mysticetes (the huge whales with baleen plankton strainers instead of teeth). While the EQ's for these whales are not above average, the weightless environment and large amounts of poorly innervated tissue, such as blubber and bone, have resulted in a different brain-body weight relationship than that of other mammals; JERISON (1973) estimated that the power ratio of their increase in brain size relative to body size is closer to 1/3 than 2/3. Considering these factors and the behaviorally established reduction of EQ in the killer whale due to its size, it is likely that a high EQ exists for the mysticetes as well. Yet the existence of broad band echolocation in mysticetes is very unlikely.

While the low frequency sounds of mysticetes are almost certainly used in some low resolution tasks, such as echonavigation (NORRIS and DOHL, 1980; PAYNE and WEBB, 1976), detection of other whales (WINN and PERKINS, 1976) and of large food masses (FISH et al., 1974; KINNE, 1975), none of these vocalizations resemble the high resolution pulses required by the echolocation hypothesis. Nor would there be a need for it, since no individual prey items such as those hunted by odontocetes (toothed whales) are taken, only larger aggregations such as planktonic masses, best detected by the long-distance carrying low frequencies. The few experiments carried out on mysticetes (BEAMISH, 1977; DREHER and EVANS, 1964) have failed to demonstrate echolocation of small obstacles. Thus, the large mysticete brains also bring the echolocation hypothesis into doubt.

1.3 Mimicry and Cognition

Another hypothesis which has been suggested is that vocal and motor mimicry is so well developed in cetaceans that it requires an extensive neural capacity (WILSON, 1975). While this has often been dismissed on the grounds that comparable mimicry can be seen in small-brained mammals and birds (WURSIG, 1979; ANDREWS, 1962), it is still interesting in its comparison to the echolocation hypothesis. Each is limited in accounting for the extensive neural development (with echolocation in small-brained bats and mimicry in small-brained birds), and perhaps more importantly, neither would predict the advanced cognitive characteristics indicated for several cetaceans.

These characteristics have been demonstrated primarily in the bottlenosed dolphin and include second-order relational learning, often described as »learning how to learn» (HARLOW, 1949). This occurs for generalized matching to sample, where a

matching rule is applied to sounds never heard before (HERMAN, 1980). Also noted by HERMAN is second order relational learning in multiple discrimination, reversal tasks, and »novelty» learning. Based on these and other cognitive characteristics, HERMAN concludes »Dolphins and many of the simians appear to share levels of information-processing skills not attainable by other taxa.»

This is in contradiction to both the echolocation and mimicry hypotheses since they are predicting neural increase by passive sensory reception, while primate cognitive abilities have evolved from a sensory feedback of manipulation with the environment. The following chapter will examine the differences between these two types of data acquisition and their consequences for the evolution of nervous systems and intelligence.

EVOLUTION OF THE BRAIN AND MANIPULATORY FEEDBACK

2.1 Introduction

The term 'manipulatory feedback' refers to the channel of interactive information between organism and environment arising from a biological manipulator such as the primate hand. This definition may be extended to non-biological systems as well. In considering the place of manipulatory feedback in the evolution of intelligence, it is important to recognize that the presence of a good manipulatory system itself does not require complex computational abilities (i.e. a large brain). This is probably best illustrated by the finely controlled and complex manipulations of certain insects. These are fixed-action patterns and can be accomplished with very small amounts of neural tissue. Thus control of the manipulator does not require much computation.

Manipulators do play an important part in neural evolution. It is well known that brain size is very dependent on the complexity of interaction with the environment. As the number and complexity of the contingencies for behaviors increase, the computational requirements increase. A clear example of this can be seen in the general evolutionary EQ increase that accompanies an increase in the number of predators in the environment (JERISON, 1973). But the complexity of the interaction depends not only on the environmental complexity but on the complexity of the behavioral response as well. Thus the ability to participate in environmental interactions becomes a delimiting factor for evolutionary neural advancement.

At one extreme are sessile organisms. If environmental complexity is increased, e.g., predators are introduced, a sessile organism can only hope to adapt by retracting a little faster or evolving some passive defense, such as a toxin. As the behavioral repertoire increases, the potential for behavioral plasticity increases as well. With a manipulator there is a huge jump in the behavioral potential of the organism; it can now participate in highly complex environmental interactions in response to adaptational requirements.

One might criticize this on the grounds that it is confusing cause with effect; ecological generalists tend to have a high behavioral plasticity and naturally have a more general purpose motor effector than do specialists. But this is precisely the point being made here; there is a coevolution of the neurological basis for behavioral plasticity with an anatomy capable of more plastic behavior.

This can be seen even in very simple manipulators. The bills of the more behaviorally plastic birds such as jays are capable of a much wider range of use than that of the highly specialized birds such as spoonbills. The more behaviorally flexible manipulator is both the cause and effect of behavioral plasticity.

The link in this coevolutionary coupling is the functioning of the manipulator in sensory reception. Manipulatory sensing (i.e., manipulatory feedback) is dynamic and interactive. It operates by disturbing the environment and allows (or forces) the discovery of contingencies; it literally uncovers new information and new environmental characteristics.

Sensory reception exists along a continuum of involvement with environmental interaction. Purely passive sensory reception, such as vision, makes no changes in the environment. Echolocation is a very weak form of active sensory reception. While echolocation does add acoustic energy to the environment, it is a comparatively negligible change. The primate hand is at the extreme of true manipulatory feedback. By mechanical interaction and accompanying sensory reception the hand creates new information, changing the environment as it helps the organism understand it. »As we grasp hold of things, so do we of ideas« (ALBERT EGLASH).

2.2 *Theoretical Analysis of Manipulatory Feedback*

In the case of many information processing systems — finite state automata, production systems, mathematical logic, etc. — a formalization exists which allows comparative assessment of the computational power of the system. No such formalization exists for feedback systems however, although the behavior of simple feedback systems have been fully described in analog mathematical modeling. Thus the computational assessment of manipulatory feedback must be approached indirectly, by demonstration of its characteristics in different fields, rather than by the complete characterization which discrete systems enjoy.

The use of a finite state machine to model biological systems began with the Church-Turing thesis, a philosophically oriented attempt to delimit the computational power of the human mind (cf. HOFSTADTER, 1979). Modeling of an organism in both passive and manipulatory sensing configurations is illustrated in the diagram on the opposite page.

The organism is shown as an automaton comparable to a Turing machine with two read heads on the input tape, which is actually the input and output tape of another automaton representing the environment of the organism. This local environment receives input (e.g., a fire, a movement in the local environment, etc.) and reacts to it in some probabilistically determined manner. This reaction is represented by the output tape.

The goal of the organism is to predict the reaction of the environment to its input; this is representative of the general adaptive nature of all organisms and can be considered equivalent to the establishment of behavioral contingencies. Thus the organism simply keeps track of the i/o relationships observed. It is here that the manipulatory-passive difference emerges. In the manipulatory configuration, read head one becomes read-write head; the organism may manipulate the environment input (just as biological manipulators do).

This gives two different advantages to the manipulatory case. First, while the passive sensing configuration may take an arbitrarily long time before a particular input arises, the manipulatory system can test inputs as fast as each step occurs. Redundant testing can be eliminated and i/o patterns can be taken advantage of. Thus the rate of data acquisition is potentially much faster for manipulatory sensing.

Second, a symbol or sequence of symbols may never arise for the passive case, but given an arbitrarily long time the manipulatory case will eventually be able to

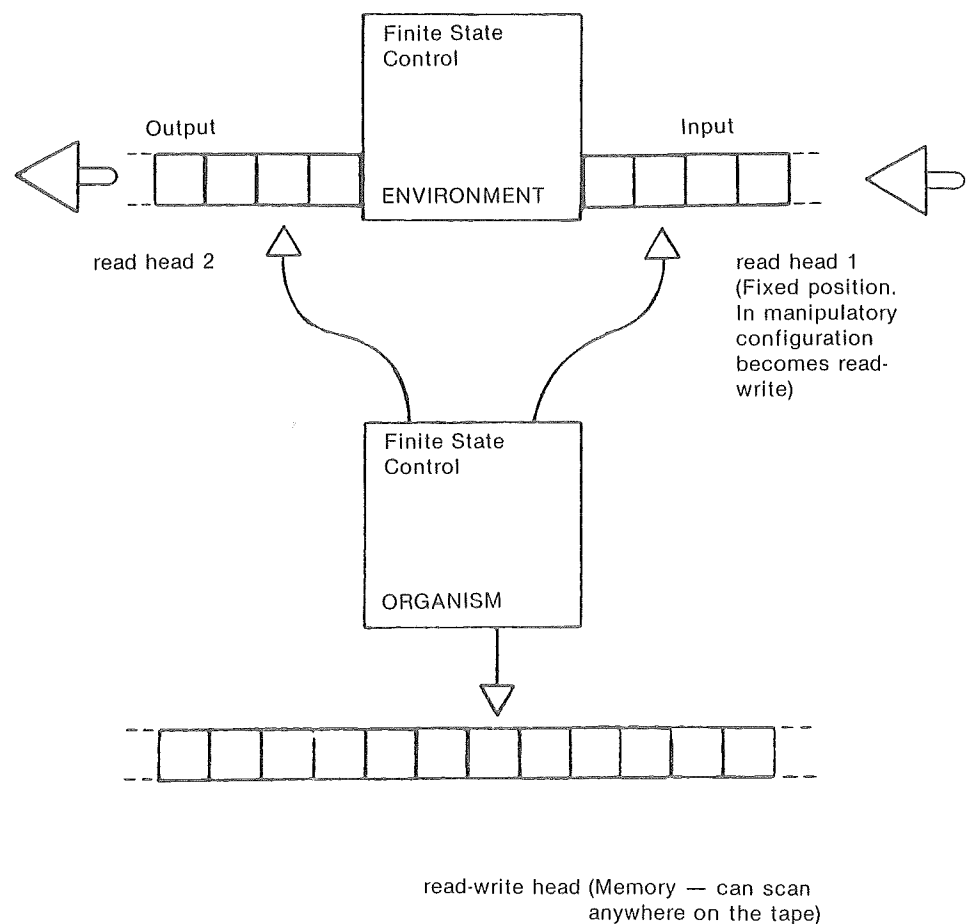


Fig. 1: Computational model of manipulatory and passive sensing configurations.

completely »decide« the environment, thus demonstrating greater computing power for the manipulatory configuration.

A second formulation which has had application to biological systems is that of information theory (c.f. JARISCH, ALLEN, and HSU, 1982). Characterization of feedback control loops in information theory terms was made by WEIDEMANN (1967). Weidemann uses the uncertainty of the output signal (this can be viewed as the mutual information between the output signal and the feedback error signal) as a measure of system performance.

This entropy error vector can be used in modeling the organism/environment interaction as a vector in the multi-dimensional behavioral space of the organism. This is similar to the multidimensional space of physical characteristics used in the definition of an ecological niche. The niche has dimensions of temperature, soil acidity, sunlight, etc.; similarly one could consider behavior to shift through different regions of behavioral state space. The feedback regulatory problem then becomes the stabilization of behavior in the appropriate region of the behavioral space, despite environmental »noise«. The nervous system of the organism plays the part of the error detector or sensor.

It is interesting to compare this to JERISON's (1973) definition of intelligence. In addition to sensory integration, Jerison defines biological intelligence as »the extent to which behavior in response to information is flexible and adjustable to inconsistencies in that information«, precisely the error detection modeling used here.

Obviously feedback improves the behavioral abilities in this model; the interesting result is in Weidemann's demonstration that the improvement in system performance due to feedback is limited by the sensor channel transmittance (the channel capacity of the sensor, i.e. mutual information between sensor input and output). A very poor sensor channel transmittance causes the error entropy (system performance, or behavioral ability of the organism) to approach that of an open loop system. Since the sensor of this model is the nervous system of the organism, this indicates that the information processing ability of the organism (its sensor channel transmittance) must directly increase with a greater feedback dependence.

2.3 Manipulatory Feedback in Robotic Systems

A supplement to theoretical analysis is physical modeling. Manipulatory feedback first became a concern of engineering design when problems arose in teleoperator and prosthesis performance. SOLOMONOW (1976) notes that the lack of sensory feedback in artificial limbs has universally limited their functionality. By the addition of »handbased sensors« BEJCZY (1975) reports that teleoperators are able to execute tasks which are »very difficult or near impossible« under passive visual sensing. More recently, CURLY and BACHRACH (1981) have shown that the presence of tactile feedback in the mechanical manipulator of an armored diving suit is crucial to functionality in many work environments.

There is a close analogy between behavioral plasticity and the kind of improvements attributed to manipulatory feedback in the previous examples. An increase

in behavioral plasticity of an organism, operationally equivalent to intelligence, usually refers to an animal's ability to perform a wider repertoire of tasks and to accomplish behaviors in a greater variation of niche. This is equivalent to engineering assessments of increased functionality and greater applicability in differing work environments.

One problem with these examples of teleoperators and related devices is the intimate involvement of human operators; it is not entirely clear that the dependence on manipulatory feedback is not due to some quirk of human performance. A way of controlling for this is to consider the relationship of manipulatory feedback to behavioral plasticity in automatus systems.

The major design problem in robotics has been that of precision tasks. At first this was met by a purely brute force method in attempting a corresponding precision ability of the robotic system. But mechanical wear and other factors made this a poor solution. It soon became apparent that the need for task adaption and the precision ability itself (as well as other performance measures) were directly dependent on the adaptive, interactive ability of robots.

Perhaps the clearest example of manipulatory feedback in automatus systems involves the use of shaking bins, plates, or belts. By vibrating or jolting the work space, parts are uncovered, separated for visual discrimination and made more accessible for pick-up. In a sense this is manipulatory feedback without the manipulator; the environment causes its own disturbance. But it is a clear demonstration of the crucial role that perturbation of the environment plays in sensory based behavior of automatus systems.

Simply initiating a random disturbance of the environment is only a very crude form of manipulatory feedback, and as such allows a very limited adaptability for the system. Increased manipulatory feedback capability shows a corresponding improvement of the system's abilities.

The problem of precision has been successfully approached in this manner. For example T. GOTO and others (1980) used «a comprehensive study of man's superior functions from a bioengineering standpoint» to solve the problem of micro order precision in insertion operations. The result was a tactile, compliant manipulator, using interactive sensory feedback with the environment. In a more general study, COLLEEN (1981) reviewed pilot studies of feedback sensory based control, and demonstrated increases in practical performance measures. BR10T (1978) has demonstrated that robots can rely entirely on manipulatory feedback (in this case by angle measurement) for recognition of solid objects.

The need for manipulatory feedback in increasing robotic behavioral plasticity becomes most apparent in comparisons of visual sensing, the highest capability passive sensor, with manipulator data acquisition. This has been studied by BEJCZY (1969) who notes:

Specific manipulation-related key events are not contained in visual data at all, or can only be obtained from visual data sources indirectly and incompletely at high cost. These key events include the dynamics of interaction between the mechanical hand and objects.

IHNATOWICZ and DAVIES (1977), concentrating on disordered environments, also conclude that information crucial to robotic abilities »can be obtained solely through the physical interaction of manipulative investigation,» and provide an experimental confirmation.

2.4 *Comparative Neurobiology of Manipulatory Feedback*

The phylum mollusca, which includes snails, bivalves, and cephalopods, is characterized by a very low degree of neural complexity, even for those with well developed sensory capabilities. The Pectinidae (scallops), for example have sensory tentacles, chemoreceptors, and a sophisticated system of eyes comparable to those of advanced arthropods. Yet the nervous system is extremely simple, consisting only of ganglia controlling valve openings and a few other reflexes (WILBUR and YOUNG, 1966).

The octopus, however, endowed with a very sophisticated manipulatory system, has not only the highest neural organization of the mollusks, but the highest organization for any invertebrate. The »brain» to body weight ratio is greater than that of most fish and reptiles (PACKARD, 1972). WELLS (1978) suggests that their intelligence is comparable (although of a very different nature) to that of many birds and mammals.

One problem with citing brain size is that one would expect greater neural complexity to occur in controlling a complex system such as the octopus arms. But the arms are actually a fairly automatus system. WELLS notes that ganglionated cords in the arms of the octopus contain three times as many neurons as the brain itself does, and compares the manipulatory system in the octopus with a human controlling a robot. The octopus brain need only send out the higher command to take in an object; the arms can pass an object to the mouth even when the brain has been removed (ALTMAN, 1971).

Interestingly, PURCHON (1977), noting that »manipulative ability has played a significant part in the development of intelligence in man,» suggests that the separation of control between the CNS and the motor system in octopods »sets a limit to the potential development of intelligence in the groups,» since relinquishing motor control to the arms has diminished the proprioceptive feedback needed for advanced manipulatory skills.

Thus, the evolution of intelligence in octopods has been primarily determined by its system of manipulatory feedback. While the complex, dynamic interaction with the environment has allowed the development of a highly advanced CNS, the peripheral control solution prevents the octopus from further advancement.

Few mammals, aside from the primates, have good manipulators. An exception to this is the raccoon with its excellent grasping paws. The EQ of the raccoon is 1.3 (from data in JERISON, 1973), and the raccoon is known for its high degree of behavioral plasticity (RUE, 1964). It is interesting that in accessing the use of the paws, WELKER and SEIDENSTEIN (1959) conclude that »the manner in which the raccoon uses its forepaws suggest that they function largely as tactile sense organs,»

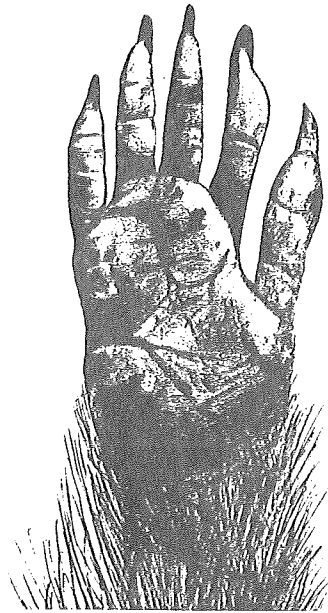


Fig. 2: Right forepaw of the raccoon. Drawing by the author, based on photograph in RUE (1964).

and confirm this in descriptions of the manipulatory behavior and somatic sensory cortex.

Another example in which the effect of manipulatory feedback on intelligence is easily discerned occurs in the large grazing mammals. While all of these have noticeably low EQ's (e.g., .50 for rhinoceros, .87 for the giraffe), the elephants have EQ's in the range of 2.0 (data from JERISON). Although researchers have suggested the large brain is due to the large surface area and number of muscle fibers to be innervated (e.g., LAUER, 1982), the existence of fossil mammals with larger body size than elephants but below average EQ's (JERISON) discounts that possibility.

As noted for mysticetes in the previous chapter, the case is actually just the opposite. JERISON observes that »when selection pressures toward enlargement of the body result in body size above about 1000 kg, they can act more or less independently of those toward enlargement of the brain.« This is very true for the elephant, whose heavy tusks add body weight without corresponding neural increase.

As the previous observations of this chapter have indicated, the suprisingly high EQ of the elephant suggests the presence of a channel of manipulatory feedback, and indeed the highly manipulative trunk serves exactly that purpose, with the sensitive double process at the end able to perform operations as delicate as transferring a coin into a keeper's pocket (CARRINGTON, 1959).

In considering the brains of whales and elephants, Jerison concludes that »For some presently unknown reason, these groups, at least in their living representatives, live in niches to which they respond characteristically by brain enlargement beyond the degree required of an enlarged body.« Finding this reason to be the manipulatory system in elephants poses the question of a manipulatory feedback channel in cetaceans.

The most familiar example of manipulatory feedback in evolution is that of primate evolution leading to *Homo sapiens*; evidence suggests a continual coevolution of both hand and brain (NAPIER, 1962). A more primitive illustration of this occurs in the comparison of higher Lemuroidea on Madagascar with their ecological (and ancestrally related) counter parts in the Old World, the Cercopithecoid genera. In considering the lower brain size and intelligence of the Madagascan Lemuroidea, ANDREW (1962) has noted that specialized incisors used for grooming in this group have reduced the manipulatory abilities, and proposed this reduction as a major hindrance in the evolution of their intelligence.

The two major selective pressures in the brain size are generally agreed to be tool-making and symbolic language. In tool-making, the physical manipulator is central to the process, and it is common to refer to the development of tools in a »feedback relation with the evolution of the brain« (WASHBURN, 1978).

It is not difficult to see language as an acoustic version of a manipulator; it probes the environment (specifically the social environment, but actually there is no distinction) and manipulates it, changing it, and uncovering new information in the process. Language is simultaneously an effector and a sensor, it is exactly the interactive information exchange which defines manipulatory feedback.

It has been demonstrated that high EQ's arise from a channel of manipulatory feedback, whether mechanical as in the elephant's trunk or acoustic as for human symbolic language. Yet the highly encephalized cetaceans have neither mechanical manipulators nor symbolic language. Nor does the passive sensory channel of echolocation meet this requirement. The following chapter will propose the existence of a third type of manipulatory feedback in cetaceans.

SEXUAL SELECTION AND CETACEAN VOCALIZATIONS

3.1 Sexual Selection and Echolocation

The previous chapters presented evidence indicating that cetacean neurobiology and cognition both suggest an information channel of highly interactive feedback between the cetacean and its environment. It was also indicated that previous hypotheses of formal language, echolocation and mimicry do not meet the feedback requirement and, particularly in the case of the language hypothesis, have evidence to the contrary. This chapter proposes the existence of an interactive acoustic channel in cetacea based on sexual selection of vocalizations.

Sexual selection has long been controversial in its distinction from natural selection. Zahavi (1981) has circumvented this problem by redefining sexual selection as a special case of signal selection, i.e., the selection of signals which attract mates or intimidate rivals. The emphasis on signaling (reliability and information content) has had a great impact on the explanatory power of selection. For instance, rather than postulate a female attraction for »beauty» to account for the colorful male plumage in certain species of birds (POULTON, 1890), ZAHAVI (1975) notes that, due to high predation pressure, the surviving birds with conspicuous plumage will be of higher quality than inconspicuous ones. CLUTTON-BROCH and ALBON (1979) suggest that the roaring of the red deer evolved because the same muscles are used in both roaring and fighting, thus making roaring a reliable signal. It is likely that the large, decorated bowers of bower birds, often construed as evidence of a female esthetic sense, are simply signaling that the owner has the time, energy and searching ability to waste on these intricate structures. Long established examples of sexual selection for a reliable demonstration of the individual's quality occur in the ritual courtship flights of birds and insects, in territorial defense and selection, and in the aggression displays of intrasexual competition.

If similar demonstrations of an individual's quality occur in cetacea, an obvious characteristic to be selected for is echolocation ability. The adaptive significance of echolocation is well known for cetaceans. It is the primary sense for several species and has been identified as a significant factor in everything from social integration (NORRIS and DOHL, 1980) to feeding and navigation (GASKIN, 1982).

Demonstration of echolocation ability would have to be of a very different nature than that of other abilities. While the competitive horns of a ram or the visual display of a bird's plumage are limited by physical and biological constraints, echolocation signals may be continually refined both in complexity and duration of the display. Such selection for acoustic behavioral plasticity would have to be met with a complementary increase in neural capacity.

A second, and more important characteristic that demonstration of echolocation ability requires is that of exchange. While all other qualities are overt behaviors or displays, the vast majority of echolocation ability lies in internal information processing. Demonstration of such processing requires an exchange of signals. This includes manipulation of time and frequency characteristics of exchanged signals, with manipulations in accordance with a patterning which demonstrates the information processing ability. Simpler manipulatory feedback would include acoustic — behavioral exchanges, e.g., sexual posturing in response to a signal of proper patterning and complexity.

Thus sexual selection for echolocation ability would create a channel of manipulatory feedback, providing both the impetus for increasing complexity and the source of interactive exchange.

3.2 Evidence for Sexual Selection in Vocalizations

A sexual display of acoustic ability has already been well demonstrated in the mys-

ticetes by humpback whale vocalizations (PAYNE and McVAY, 1971; PAYNE, 1978; WINN and WINN, 1978). Although the interaction is not fully understood, all the observations — preponderance of male singers during the mating season, sexual activity associated with the vocalizations, etc. — are clear indications of a courtship role for the humpback whale song. Particularly striking is its immense complexity; WILSON (1975) describes it as »the most elaborate single display known in any animal species.« The songs may be over 30 minutes, with variation introduced among successive renditions of the same song by the same individual. Although no underlying causal mechanism (i.e., demonstration of echolocation or echonavigation ability) is proposed, a study by TYACK (1981) concludes:

The complexity of humpback song might have arisen through a process of sexual selection. . . . If female humpbacks choose to mate with those male humpbacks that sing the most complex songs, then a powerful process of sexual selection is established.

In the odontocetes (toothed whales), click trains and signals with similarities to echolocation clicks have been shown to occur in contexts and with characteristics that suggest emotional/social significance rather than echolocation. Some of these characteristics include non-overlap of signals during lengthy exchanges, lack of timing variation with distance to possible targets and an increase in signal complexity during exchanges.

In the narwhal FORD and FISHER (1978) report that in addition to typical echolocation signals, pulsed tones of greater complexity than clicks (more variation in frequency and time characteristics, higher emission rate) were present and that »Although the pulses making up these signals are related to echolocation-type pulses, most appear to serve primarily as social signals.«

WATKINS and SCHEVILL (1974), using a three-dimensional hydrophone array to localize the sound sources, observed apparent exchanges of pulse-bursts among wild Hawaiian spinner dolphins. The exchanges were usually 3 to 5 pulse-bursts between two or more porpoises, with a few sequences extending to more than 12 signals exchanged. Pulse-bursts were usually answered within one-half second from nearby porpoises, and appeared to be ignored by more distant animals.

Social exchanges of signals with some similarities to echolocation clicks have also been shown for sperm whales (WATKINS and SCHEVILL, 1977), killer whales (POULTER, 1968), common dolphins (TITOV, 1971, and co-workers, 1971; WOOD and EVANS, 1979), and bottlenosed dolphins (LILLY and MILLER, 1961; BURDIN et al., 1974). WATKINS (1979) suggests that the characteristics of click sounds from most odontocetes (Delphinidae, Phocoenidae, etc.) encountered at sea indicate that »the clicks may be used primarily in social contexts.«

It is significant that researchers initially assumed all clicks were echolocation signals and that whistles and a few other simple phonations (e.g., a 'yelp') were the only signals of communicative significance. This was a logical assumption to make; it seems that whistles and other simple signals could meet all the communication requirements of the cetacean social systems, and this is supported by the low degree of gregariousness in many nonwhistling species (HERMAN and TAVOLGA, 1980).

The use of communicative signals which could cause confusion with the echolocation system is also paradoxical. An acoustic sexual display for echolocation ability would resolve both these problems.

Other support comes from the observations of spontaneous mimicry of artificial pulses sounds. This has been observed for sperm whales in the wild (WATKINS and SCHEVILL, 1975) and for captive bottlenosed dolphins (HERMAN, 1980).

There is almost no data on high frequency recording of sounds accompanying precopulatory behavior. A general problem in this would be in differentiating communicative and echolocation clicks. Complex pulsed sounds accompanying mating were reported for bottlenosed and common dolphins by TITOV (1971, and co-workers, 1971). BUSNEL and DZIEDZIC (1966) report pulsed sounds in the precopulatory behavior of *Phocoena phocoena*. These were described as a »grinding» sound rather than the »creaking» sound of echolocation clicks.

Also relevant are reports by DREHER (1966) of bottlenosed dolphin reactions to recorded vocalizations. In one case sexual posturing appeared, with four or five dolphins orienting toward the speaker. In another playback a sexual response (and what appeared to be bewilderment at the loudspeaker) occurred with a single male. Only the contour of the whistle components were noted.

Another association of sex and vocalization has been shown to occur in the killer whale. DAHLHEIM and AWBREY (1982) demonstrated that the sex of the killer whales could be discriminated by their sounds. The hypothesis of sexual selection for echolocation ability would predict that sounds which best discriminate sex would be most similar to echolocation click bursts. As shown by the diagram on the opposite page, this is indeed the case; there is a decrease of the average discrimination for classes of sounds with a decreased similarity to click bursts. These three classes

Table I: Discrimination of sex by sound type for three classes of varying similarity to echolocation click bursts.

(Data from DAHLHEIM and AUBREY (1982). Order within classes is arbitrary).

Class	Sound Types	% Discrimination of Sex by Sound Type	
		Individual	Class Average
<i>Broad band Pulses</i> (high similarity to click bursts)	Creek	100	94.2
	Buzz	91.4	
	Chatter	100	
	Ricochet	85.4	
<i>Pulsed Signals</i> with strong Harmonic Stress (low similarity to click bursts)	Upscream	68.9	78.6
	Downscream	65.1	
	Whine	96.6	
	Tone	71.4	
	Seesaw	90.9	
<i>Non-pulsed</i> (no similarity to click bursts)	Whistle	60.9	60.9

were based on the description and visual inspection of the sonograms for 10 of 11 sound types given in the Dahlheim and Awbrey study. The click bursts themselves were not included here because many of them are presumably actual echolocation clicks, not communicative.

An earlier study of exchanged signals by POULTER (1968) indicated that a much greater variation in signals occurred for a male killer whale's vocalization with females than with other males.

Also related is the finding by GUREVICH (1972) of a sexual size dimorphism of nasal air sacs in the common dolphin. Nasal air sacs may be involved in sound production and GUREVICH showed that they are larger in the males. This is particularly interesting for the common dolphin since no general size dimorphism is noted for this species (although a difference in fin shape does exist).

3.3 *Sexual Selection in Cetacea*

The evidence for sexual selection itself in cetacea is very good. As previously mentioned, humpback whale vocalizations are related to courtship. Many of their natural history characteristics point to a lekking system, a mating system with a high degree of sexual selection (HERMAN and TAVOLGA, 1980). Other types of polygyny or polyandry, also indicating a high intensity of sexual selection (EMLEN and ORING, 1977) have been indicated for many odontocetes, with a great deal of evidence occurring for the sperm whale (GASKIN, 1982).

Secondary sexual characteristics such as sexual dimorphism and coloring have also been noted for many odontocetes. Sexually related intraspecific scarring and sexual segregation in schools are also widespread (NORRIS and DOHL, 1980). The narwhal is a particularly interesting example; in addition to sexually segregated schools the male narwhal is endowed with a single seven foot ivory tusk protruding from its upper lip. While it is generally agreed that this is a secondary sexual characteristic, its functioning in that respect is unknown. Experimental and anatomical evidence suggest it is involved in propagation of vocal emissions (PILLERI, 1983); BEAMISH (in REEVES, 1977) has suggested that the tusk allows higher energy sound transmission in »acoustic jousting» between competing males. Enhancement of a sexual acoustic display for females is also likely, but either one could originate in a sexual display of echolocation ability.

A high degree of sexual play has been noted for several odontocetes (DEFRAN and PRYOR, 1980), and may be expressed without regard to age, sex or species of partner; masturbation is also common. If vocal behavior is related to sex then it too may be »played» with from an early age. Non-functional echolocation sounds in dolphins calves have been reported (HERMAN and TAVOLGA, 1980), and for the bottlenosed dolphin Caldwell and Caldwell (1966) specifically note that »In an animal as playful as Tursiops, the possibility of their playing with vocalizations should not be overlooked, particularly in the juveniles.» Such behavior would greatly contribute to the interactive acoustic exchange.

3.4 *Consequences for Intelligence*

In the evolution of human intelligence, our physical manipulator (hands) and our acoustic manipulator (symbolic language) have worked together to create a characteristic style of cognition. The extensive need for manipulation of separate objects, the basis of language in naming, objectification by ostensive communication, and the use of discrete mental entities (e.g., archetypes) in higher cognitive processes such as logic have all led to an intelligence which operates mainly by analytic reasoning, that is, by logical relations between discrete items.

Based on contrasting characteristics of the cerebral hemispheres, this has been characterized as »left hemisphere dominant« cognition, and is evidenced by gross anatomical characteristics (greater size of the left hemisphere and right-handedness) as well as by a vast amount of psychological data.

It is interesting to note that from about 1900 until the 1940's the prevailing viewpoint was that the right cerebral hemisphere served only as a »back-up« function. It is now acknowledged that the right has a functional ability comparable (but in an opposite or complementary way) to that of the left; yet we are still quite left-dominant in the sense that the majority of our behavior is controlled by the left hemisphere (ZAIDEL, 1981).

The proposed evolution of cetacean intelligence, that of sexual selection for complexity of signals and interactive exchange, predicts exactly the complementary style of cognition for cetaceans, that of the right hemisphere cognitive style. This is due to the nature of detecting continuous ordered patterns; it is a gestalt process rather than a sequence of discrete operations.

It is appropriate here to mention a similar conclusion arrived at in a largely intuitive manner by BATESON (1966). Noting that cetaceans lack much of the expressive anatomy of other mammals (facial hairs, ears, flaring nostrils, mobile limbs, shifting eyes, etc.), BATESON proposed that vocalizations have taken over the emotive expressions of kinesthetics. This is not incompatible with the sexual selection hypothesis presented here, and, in fact, a complex system for sexual selection of acoustic signals might be expected to have some spill over into other emotive signals as well.

Though acknowledging that such signals are generally in a gestalt or »analog« patterning, BATESON confused the gestalt/analytic or right brain/left brain dichotomy, which he properly termed analog/digital, with the mathematical (and hence information theoretic) distinction of continuous/discrete. BATESON termed the emotive information usually carried by analog signals as »mu functions,« and felt that dolphins used a »digital system whose primary subject matter would be mu functions.« This is an erroneous use of the analog/digital dichotomy; a digital system which can communicate information of emotive relationships is exactly the case of human language.

The following chapter will clarify this analog/digital dichotomy in its relation to cerebral lateralization, information and computational theory, and natural biological communication.

THE ANALOG/DIGITAL DUALISM

4.1 Introduction

The distinction between analog and digital, both in signal patterning and the associated information processing, is common to many disciplines. Yet there exists no underlying formalization of this dualism, particularly in terms of a common mathematical representation. This chapter will develop the dualism in an interdisciplinary sense, using mathematically defined concepts whenever possible.

In its current mathematical sense, analog and digital are differentiated solely on the basis of a continuous/discrete distinction. This common understanding of the analog/digital (A/D) dualism is usually conveyed by an instrumentation example. A mercury thermometer, for instance, is a continuous (real number) representation of the temperature, while a digital thermometer presents temperature in a discrete symbolism. In addition to the obvious distinction of continuous/discrete, a second property shown here is the literally analogous representation of the analog display to the information it represents. This is in contrast to the completely arbitrary symbolism of a digital representation. As BATESON and JACKSON (1964) point out, there is nothing »sevenish« about the numeral seven; yet even an extraterrestrial could deduce intensity variation in the relative fluctuation of an analog display.

A third property is the relationship between the first and second; if the representation of temperature is to be truly analogous, then it is constrained by the continuous nature of temperature. This property is due only to our particular physical world. If we existed at the level of probabilistic quanta, our analog measurements would be discrete. This emphasizes how the second property, that of proportionality between the analog signal and the information it represents, is actually more fundamental to the nature of analog processes than that of the usual continuous/discrete differentiation.

In clarifying this, it is useful to consider a comparison of discrete analog communication with digital communication (see diagram on opposite page). In this illustration the information is transmitted to control a valve opening. The digital system simply specifies the valve position by an arbitrary encoding, shown by a binary word. The analog communication sends a discrete but ongoing signal proportionate to the relative change of position for the valve. The fact that the signals are discrete does not change the analog character of the communication (although changing other features, such as a numeric representation or arbitrary reference point, does change the communication in this respect). In decoding the analog information each signal is defined relative to the previous signal, that is, the information is decoded by a rule of proportionality rather than matching to a pre-existing template.

A more digital (and hence easier to verbalize) explanation of the analog decoding procedure is to view the proportionality as a recursive algorithm. The meaning of the current signal is a function of the meaning of the last signal (in this case the position of the valve) and the current signal value. Thus no signal has an arbitrary

meaning; the meaning of a signal is only defined in its relation to other signals of the communication pattern. This is the definition of a gestalt perception, and thus provides a formal tie between holistic or gestalt patterning and the decoding of analog communication.

In a more familiar example there is the contrast between language and music. For the most part language contains code words which need only be matched to their template to be decoded. Music is just the opposite; the chord G has no meaning by itself and may portray anything from heart-rending misery to ecstatic joy. Its meaning is entirely dependent on the other discrete signals in the communication; they must be perceived as a whole. In addition, the sound of the words (though not their intonation) is completely arbitrary; there is nothing sorrowful about the word »sad». The signals of music are proportionate or analogous to the information they represent. Sad music is slow and deep, while joyful music is fast and high. Thus, music, although made up of discrete signals, is both a gestalt patterning and has information proportionate representation.

A well known example of a very simple analog language is the waggle dance of bees. The straight run of the waggle dance (oriented by the sun's position) gives the

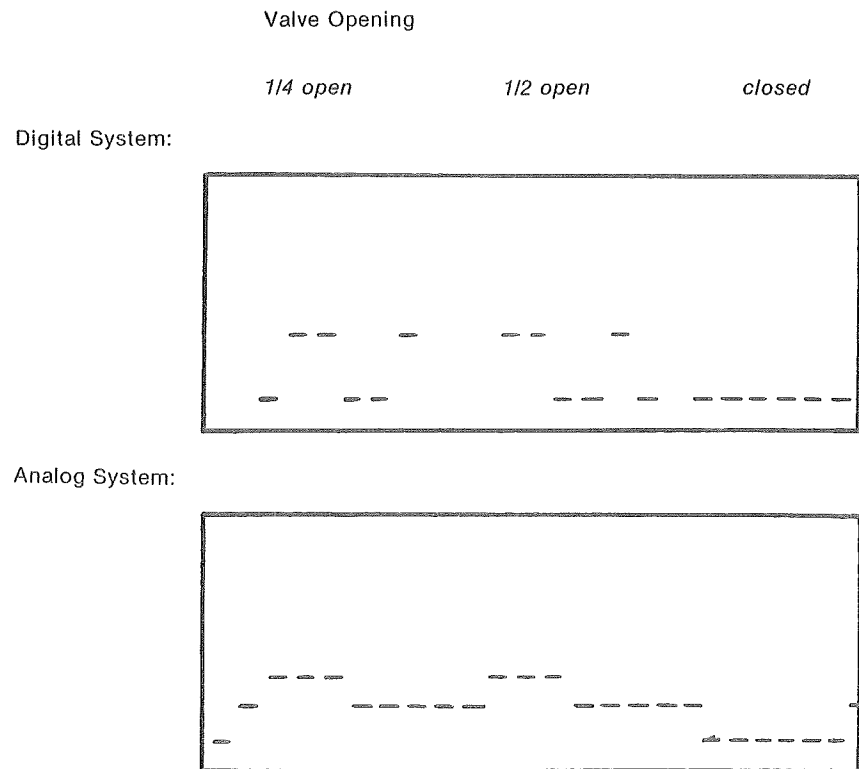


Fig. 3. Comparison of digital and analog communication system for valve control.

surface azimuth angle of the discovered food source, thus setting a continuous proportionality between the angle danced and the angle of the food's location. The distance to the food source is proportionate to the duration of the run. Because these are not complex successions of signals (as in music) but are single signals which vary along a gradient, there is not a strong connection to gestalt patterning, but the information proportionality of the signal is apparant.

Thus the major difference can be summed up as follows: In digital communication decoding is a trivial operation; it is simply the matching of pre-existing templates to the signals. The complex processing in a digital system takes place after decoding (as in human linguistics).

In analog communication, decoding may be a very complex process; a musical phrase has no pre-existing template (unless it is extremely familiar music) and the decoding of the entire gestalt pattern can be very involved when the proportionalities are complex. Once decoded, however, the analogy is complete.

As will be discussed later in this chapter, this is just the case for digital and analog computers. A digital computer performs very complex manipulations of simple symbols. The analog computer may have great difficulty in being set up for a complex proportionality, but once the signal has been decoded by the proportionality, the computation is complete.

4.2 *Interdisciplinary Concept*

Among the many fields which incorporate it, the A/D dualism emerges both in analytic style, as the holism/reductionism distinction, and in general information mechanisms. In biology for example, there is alternation between discrete, symbolic coding of the genes and the continuous features of phenotype. Wave/particle duality is one of many A/D distinctions in modern physics. While the amplitude and frequency of a wave is proportionate to its energy, a particle might be described as a more symbolic energy representation.

The terminology of analog and digital in the sense used here was first formulated in communication studies (RUESCH and KEES, 1956; BATESON and JACKSON, 1964), with language as the prototypical digital coding and paralinguistic features as analog. In the field of animal communication the current terms are graded versus discrete vocal signals. Vervet monkeys for example have a set of discrete alarm calls, each signifying a different predator (CHENY and SEYFARTH, 1981). The disastrous results of confusing an alarm call for eagles with that for leopards gives an obvious selective advantage for making signals as disparate as possible. In mathematical communication theory a set of signals with zero correlation between members are termed orthogonal since their vectors in signal space are at right angles.

The previous example of the waggle dance illustrates a graded system. WILSON (1975) has noted the information proportionate representation of such graded systems but errs in his information theory comparison of digital and analog. WILSON claims that »All other circumstances being equal, graded messages convey more information than equivalent discrete messages,» and bases this on considering

that, if only a single message exists, the discrete encoding can only provide one bit, but a single analog signal can vary infinitely along a gradient as discrimination and variability allows.

The problem here is that Wilson is restricting a digital characteristic (the number of code words or signals of the signal alphabet) but not restricting the complementary analog characteristic, the number of discriminable points along the gradient. WILSON notes that, due to noise (errors of the bees in communicating), the waggle dance is equivalent to specifying one of 16 compass directions; and he suggests that, if a digital system was giving one of 16 directions, the same reduction due to noise would provide less information. But this is subtracting the information lost in noise twice for the digital system; once in arriving at 16 discriminations and then a second time starting from 16 discriminations. For any communication channel both analog and digital encodings have a maximum potential equal to the channel capacity.

The examples of digital communication in vervet monkeys and analog communication in bees also illustrate the influence of the information itself on the communication system. In vervet monkeys the presence or absence of (discrete) predators is indicated. In bees a continuous spatial mapping is specified, as well as the degree of food quality. Thus analog systems evolve for continuous, graded information, while digital systems develop to communicate information about discrete entities or events.

The application of mathematical communication and information theory to the A/D dualism was first suggested by BATESON (1968), who noted that analog information (in the A/D sense) has no counterpart in formal information theory. This is because mathematical information theory distinguished analog and digital signals solely on a continuous versus discrete basis, with no concept of the »second property» of proportionality of signal to information. It is possible, however, to delimit information theory for those aspects which will apply to the A/D distinction.

All digital formulations of information theory assume that symbols and their signal representations are discrete and essentially arbitrary. Since this in no way conflicts with digital in A/D dualism sense, all digital formulations, including encoding and decoding schema, transmission and the classical probabilistic theory of SHANNON (1948, 1949), are applicable. The major problem in applying analog information theory can be seen in decoding operations. Although the signals termed »analog» are indeed continuous, in decoding it is generally assumed that they comprise an »alphabet of transmission signals» (RAISBECK, 1963) and that the process of decoding involves some type of correlation of the continuous wave form with a set of possible transmitted signals. This is generally associated with the correlation factor

$$\frac{\int_{-\infty}^{\infty} f_a(t) \cdot f_i(t) dt}{[\int_{-\infty}^{\infty} f_a^2(t) dt \cdot \int_{-\infty}^{\infty} f_i^2(t) dt]^{1/2}},$$

mathematically equivalent to a matched filter (ROSIE, 1973).

This operation of matching received waveforms with fixed templates is precisely the opposite of the A/D dualism sense of analog. In analog communication the

decoding process takes place by application of a continuous proportionality, not by template matching (actually it is possible to use a huge number of slightly varying templates, each representing the next degree of discriminable difference along the gradient, but the more the communication becomes purely analog, the less efficient the method becomes).

Thus none of information theory assuming a correlational or template coding, despite the continuous waveform restriction, can automatically be applied to the A/D formulation of analog. Cases where a limiting information quantity is considered can generally be adapted since both analog and digital encodings have equivalent capabilities.

In channel capacity, for example, the continuous waveforms considered are actually a set comprising some finite signal alphabet (as in the case of spoken words). But one can also view this as the number of discriminable grades of a truly analog signal varying over the real numbers; the information transmission rate ceiling would be the same for each.

A similar situation exists for the reception of continuous signals. As HYVARI-NEN (1968) notes:

Characteristics of the correlation reception is that it is necessary to know the transmitted set of waveforms $X_i(t)$ and their a priori possibilities p_i .

While this is true for continuous parameter estimation of waveform, the equivalent process of continuous parameter estimation of magnitude needs no predetermined waveform templates and is completely applicable to the truly analog case.

Computation theory also provides a mathematical representation of information processes. The mechanisms of analog and digital computers are not just metaphors of the A/D dualism, but are physical embodiments of it in every sense. While digital computers use logic relations on arbitrary symbols, analog computers provide a continuous mapping between input and output signals based on the functions under investigation. It is literally analogous in that the output is in a (complex) proportion to the input, as well as the functions themselves being analogous to the physical system the computer emulates. Again, it should be noted that the analog system could operate in discrete steps, as does an analog computer using gears; the important characteristic is the information proportionate representation.

Since one function may have several simultaneous inputs, and since the functions themselves are in simultaneous operation, analog computers are parallel information processors. Digital computers presently use Von Neumann architecture, and are entirely sequential in operation. It is theoretically possible to construct digital computers which are parallel processors, but this is difficult to achieve and has so far only been accomplished with very simple circuits of low computational power. Conversely, it is easy to use sequential inputs for analog computers, but this would merely negate one of the main advantages of analog communication.

As in communication, real world computation provides a complete embodiment of the A/D dualism, but its theoretical formulation covers primarily the digital case, with little implication for analog processes. Since analog computers operate over the

real numbers, there is a relevance for computation on infinite sets. Weidmer (1980) showed that these types of computations required a network of parallel processors. This suggests that parallel processing is not simply due to the physical or technical character of analog computers, but it is a mathematical consequence of analog information processing.

4.3 *Application to Neuroscience: Cerebral Lateralization*

Science itself can be seen as an A/D dualism. There is interplay between rule-based inferences within paradigms and interparadigm periods of intuitive, analog-like thinking (KUHN, 1962). Within neuroscience, modes of holistic analysis, empirically founded by LASHLEY's (1960) »engram« results, contrast with reductionistic analysis (e.g., HUBEL and WIESEL, 1965). While reductionist methods have been far more successful, the connectivist schema tend to point toward the paradoxes of a 'grandmother cell' perception or homunculus-like control cells. The presence of both diffusive and connectivist characters of the nervous system is now commonly acknowledged. Grandmother cells can easily exist at lower levels (e.g., line detector cell in the visual cortex) but only very simple command cells can be based on these generalities (e.g., the bug catching reflex in frogs). Ascending to higher cognitive levels, object specific cells become successively difficult to realize, but command output easier. Straight forward connectivist characteristics are combined with a diffuse distribution.

Complimentary A/D characteristics such as this occur at all levels of the nervous system. Individual neurons combine an analog threshold with discrete action potentials. The rate of firing is in a proportionality to the stimulus intensity but the information arises from discrete receptors. Similarly the tongue uses four discrete taste encodings but each sends continuous information of concentration. Cells of the visual cortex perform distributed parallel processing by acting as spatial frequency filters (ALBRECHT, DeVALOIS and THORELL, 1980), but also respond to absolute length of line (HUBEL and WIESEL, 1965), thus functioning in discrete template matching.

4.4 *Cerebral Lateralization: Proposed Dichotomies*

The terminology of analog and digital has been previously mentioned in characterizing cerebral lateralization by PRIBRAM (1962) and BOGEN (1969), but only at an informal level, and as terms synonymous with the usual analytic/holistic distinction. While it is true that analytic/holistic or propositional/appositional distinctions are closely related to the meaning of the A/D dualism, they have none of its ties to mathematical formalism or existing computational devices. They also lack a formal connection between the gestalt process and information proportionate representation (often referred to as imagery coding). Furthermore, the analog counterpart is often defined only in contrast to the digital process; thus, it is not a true functional dichotomy (BRADSHAW and NETTLETON, 1981).

While these dichotomies are too generalized, others cover only certain attributes of the A/D dualism. Dichotomies using the information proportionate representation property of the A/D dualism include matching by physical identity versus matching by name (GEFFEN, BRADSHAW and NETTLETON, 1972), verbally coded versus imagery coded (LEAMON and GAZZANIGA, 1973), and symbolic versus imaginal (ROBERTSON and INGLIS, 1978). In all of these, researchers have characterized the right hemisphere as cognition by a proportionate analogy and the left as using arbitrary symbolic coding. A great deal of supporting evidence for this exists (c.f. BRADSHAW and NETTLETON, 1981), most notably the lateralization of *Kana*, the Japanese syllabic-phonological script, and *Kanji*, an ideographic-pictorial script (SASANUMA, 1975, SASANUMA, ITOH, MORI and KOBAYASHI, 1977, HATTA, 1981). SEMMES (1968) develops a dichotomy of focal/diffuse, noting that left hemisphere damage may lead to specific function loss (suggesting discrete assignment) while damage great enough to disrupt a specific function in the right hemisphere tends to disrupt other functions as well, indicating a continuum based distribution.

It was previously shown that parallel processing is an advantageous attribute of analog functioning, and that digital communication is generally sequential, although parallel processing is not difficult for problems of low complexity. The parallel/serial dichotomy follows this closely. COHEN (1973) found that, for a visual matching task with letters, reaction time (RT) increased as a linear function of set size for the left hemisphere, indicating sequential processing, while the right hemisphere showed the flat response expected for parallel processing. In A/D terms the letters are represented by discrete templates in the left hemisphere. For configurational stimuli (i.e., for which no prior templates are expected) both hemispheres operate in a parallel mode. OHGISHI (1978) and POLICH (1980) both confirm these results, although WHITE and WHITE (1975) do not show an increase in RT for nominal stimuli, indicating that an additional factor is involved. Finally, POLICH (1982) demonstrated that the serial processing is due to an initial transient effect, and the unstressed steady-state response for left hemisphere nominal stimuli was also flat. Thus the right hemisphere works as a parallel processor, while the left may operate in parallel if the task complexity is not increased by initial stress and digital encoding. It may be that the transient stress itself is due to an initial assumption of sequential processing for template (digital) stimuli by the left hemisphere.

Just as the discrete/continuous nature of A/D was shown to be a constraint of our particular physical world, the spatial/temporal dichotomy (e.g., DAVIS and WADA, 1977) is similarly a consequence of physics, acting upon the parallel/serial distinction. Though our primary conception of space is the simultaneous, parallel representation of the visual system, it is simple to sequence spatial information, as in symbolic writing (a primarily left hemisphere task). One may also imagine a simultaneous view of time (e.g., VONNEGUT, 1968). Most importantly, continuous time dependent signals are a common data type for analog computers, e.g., integration. The most important distinction is between sequenced, template matched signals and data represented as a continuous, information-proportionate patterning.

4.5 Functional Specificity

In general, the left hemisphere is specialized for functions of rule based relations between discrete matched patterns, such as linguistic systems; and the right for continuous representation-proportionate information, typical for affect. This is most evident for language. Although the discrete, rule based understanding of language is entirely left hemisphere, the right hemisphere is capable of understanding speech as continuous acoustic patterns, with no phonetic encoding or grapheme-to-phoneme correspondence rules (ZAIDEL, 1978). Related to this is a well established left ear advantage (LEA) for emotional tones and intonation patterns (BLUMSTEIN and COOPER, 1974; CARMON and NACHSHON, 1973; DARWIN, 1969; HAGGARD and PARKINSON, 1977).

Although speech lateralization is comparatively clearcut, lateralization for music, which has been proposed as the right hemisphere counterpart of speech, is still in controversy. Part of the problem has been the lack of distinction between music as an information source, which concerns right hemisphere processing of analog information (e.g., emotion), and components of music as acoustic stimuli. In a recent survey of music lateralization, BRADSHAW and NETTLETON (1981) conclude:

Thus, varying degrees of right-hemisphere mediation (of music) may appear . . . particularly perhaps for the more complex, structured, tuneful melodious combinations.

Viewing music as an information source gives reversal of this conclusion: as the sounds become more structured, tuneful and melodious, the stimulus approaches music, which conveys analog information perceived by the right hemisphere. Acoustic components of music will have lateralizations based on physical characteristics and context (e.g., task requirements). A high degree of familiarity with a musical component will allow a left hemisphere template for that component to arise.

SIDTIS (1980) shows that the magnitude of the LEA increased as the number of harmonics increased. Thus the right hemisphere was more involved for stimuli patterned in simultaneous, spatial-like distribution. Sidtis notes that the inconsistent results for other components such as melody may be due to variations in the harmonic content of test stimuli. Chords are harmonically complex and are generally associated with an LEA (DOEHRING and LING, 1971; GORDON, 1970; TAUB, TANUARY, DOUBLEDAY, and CLARKSON, 1976; GORDON, 1978) although chord lateralization has other influences as well. GORDON (1980) and MORAIS, PERETZ, and GUDANSKI (1982) show that while an LEA appears for naive listeners, experienced musicians show bimodal distribution of lateralization, indicating that some musicians have developed left hemisphere templates for chords. This is a similar result to that of JOHNSON, BOWERS, GAMBLE, LYONS, PRESBREY and VETTER (1977), showing an REA for melody only for musicians able to transcribe music, thus associating template representation of music with left hemisphere processing. Also related are Morse tasks, where skilled operators display

and REA, but inexperienced operators only show an REA for short patterns. When sequences become too complex, the inexperienced subjects are no longer able to utilize left hemisphere templates (presumably more developed in skilled operators), but depend on continuous pattern recognition by the right hemisphere (PAPCUN et al., 1974).

While the lateralization of music components as acoustic phenomena are subject to a great many variables, its association with emotion shows consistent right hemisphere specialization. GROSSMAN, SHAPIRO, and GARDNER (1981) show that damage to the right hemisphere increases errors in discriminating songs of similar mood, but left hemisphere damage only changes errors in linear sequence discrimination. An unusually high LEA (in comparison to general lateralization experiments) was found for identifying the emotional quality of tonal sequences, and this increased further when target and competing stimuli were of different affect. Most importantly, the primary function of music in carrying emotive information (COKER, 1972), the right hemisphere specialization for emotion (e.g., SAFER and LEVANTHAL, 1977), and the lack of evidence of left hemisphere participation in intact music are compelling evidence for this interpretation.

Right hemisphere function in visuospatial process originated as a contrast to the language function of the left hemisphere, and contains a mixture of informational aspects. Right hemisphere function in mapping of exteroceptive body space (LE DOUX, et al., 1977; WITAKE and OJEMANN, 1977) has been contrasted with left hemisphere control of sequential movements (SUMMERS and SHARP, 1979). The evidence for sequencing by the left hemisphere is not consistent, however (JASON, 1983). It may be that the left hemisphere is more specialized for discrete motor movements (a control counterpart to template reception). SUSSMAN and WESTBURY (1978) conclude that the left controls change of oral-facial configuration from one target position to another. Sequencing in general refers to discrete partition as well as ordering in time; Jason (1963) indicates that, when these are separated, the left hemisphere shows control of specific motor acts, but not necessarily their temporal order.

The human face has been the best studied visual pattern for right hemisphere processing. In addition to conveying emotion, a prototypical example of analog information, the face displays information on a continuum, with the signal in a representational proportion to the information (e.g., when one is feeling »down«, the expressive features turn down). This agrees with the considerable evidence for right hemisphere processing of faces. Despite the great potential, relatively little has been done on the lateralization of optical illusions. HOULARD, FRAISSE and HECAEN (1983) show that the Ponzo illusion is less susceptible for right hemisphere damaged subjects (although this is yet to be verified for normals: BERTELSON and MORAIS, 1983). Length matching, as in the Ponzo illusion, versus the more gestalt spatial frequency function was noted earlier as an A/D distinction of the visual cortex. This suggests that the Ponzo illusion is a similar discrimination at the cerebral level.

4.6 Summary

1. Analog information processing characterizes both graded communication systems and right cerebral hemisphere cognition. The complementary systems are characterized by digital information processing.
2. Digital systems decode information by matching the perceived signal to pre-existing templates. Analog systems decode information by a rule of proportionality.
3. Because the signals of analog communication are decoded by a proportionality, the signals are physically representative of the information they convey. A simple proportionality will make the representation obvious; our species can easily interpret the analog kinesthetics (e.g., the gradient from peace to rage) occurring in other species.
4. Complex analog patternings must be processed as a whole rather than as a succession of individual signals. This was previously demonstrated in the discrete characterization of analog decoding as a recursive algorithm, and provides the link between the idea of information proportionate representation and gestalt or holistic processing.
5. The A/D dichotomy is a better characterization of cerebral lateralization than those of »holistic/analytic« or »imagerial/symbolic« since it formally incorporates both gestalt processing and information proportionate representation, as well as providing the physical example of analog computers in specifying the information processing of the right hemisphere.

APPLICATION OF THE ANALOG/DIGITAL DUALISM TO CETACEANS

5.1 Review of Hominid and Cetacean Comparison

In reiterating the comparison of hominid and cetacean evolution of intelligence, it should now be more apparent that, assuming the mechanism of acoustic sexual selection in cetaceans, the differences in these two groups are very similar to the A/D dichotomy.

For hominids, there is speech and the mental processes arising from object manipulation. These are primarily digital information processes, using arbitrary symbolic coding (as in speech) and sequences of discrete operations. We sort objects, name them and perform logical operations with collections of them. In our fundamental conceptions of human intelligence, such as the IQ tests, we stress verbal, symbolic and analytical abilities. Category matching tasks are a typical example; these are fundamentally a discrete template matching and have been shown to be a left hemisphere function (BLACKSTOCK, 1978; GOLDBERG, VAUGHAN, and GERSTMAN, 1978; LEVY, TREVARTHEN, and SPERRY, 1972; VEROFF, 1978; WICKELGREN, 1975).

That the predominance of digital processing in human cognition results in a general left brain dominance has already been mentioned in chapter three. The presence of left-advantaged brain asymmetries in nonhuman primates (GALABURDA et al., 1978) supports the idea that manipulation, and not speech alone, is involved in these asymmetries.

The proposed mechanism for the evolution of intelligence in cetaceans predicts a predominance of analog information processing ability. The detection of continuous, complex patternings, demonstrating vocal abilities for echolocation, echonavigation, and possible other related functions (e.g., auditory memory ability for echolocation patterns of prey or echonavigation mapping) is a purely analog function. This is emphasized by the spatially arranged information in pulsed sounds; the information is presented in a simultaneous frequency spectrum rather than sequentially in time. As mentioned in the previous chapter, such parallel processing of spatially (frequency) arranged sounds in humans is a right hemisphere function, and increases in lateralization as the amount of simultaneous information (number of harmonics) increases.

The analogy to music is useful and holds true in many ways. While our music is predominantly sequential, it is still a »complex patterning« without arbitrary symbolic encoding (except for its visual representations). It is information which is not based on objects or names, yet may reliably demonstrate an individual's cognitive ability, i.e., a subtle and detailed control of the acoustic signal.

As mentioned previously, music is highly representation proportionate, conveying emotionally related information by graded variations, such as tempo and other more complex qualities. A musical composition must be listened to as a whole; one cannot stop in the middle and pick it up later as with written material. The chords and notes are individually without any meaning, it is only in their continuous relationships that they express information. All of this points to a communication that is archetypically analog information.

Because odontocete pulses are simultaneous, frequency distributed signals, they bear little resemblance to the sequential displays of music. But the mysticete sounds suspected for low resolution echolocation (e.g., echonavigation) are temporally distributed and hence may be more familiar to our musical conceptions. The characteristics of both gestalt comprehension and coding by graded variations in a mysticete vocalization were found by TYACK (1981). In reviewing the compositions and variations in humpback whale songs, TYACK concludes:

It is thus unlikely that humpback song is made up of many individual sounds each of which qualifies as a signal in its own right, for each sound is gradually modified into a completely different form or disappears from the song. It is only the rules of the song structure that do not drift, implying that the song itself is the functional unit of this complex string of sounds.

If cetacean intelligence is based on analog information processing, then it should be evidenced in ways similar (although complementary) to the left hemisphere dominance of human cognition. The following sections will discuss this comparative evidence.

5.2 Cerebral Lateralization in Cetaceans

Research with chicks, song birds, rodents, and nonhuman primates has indicated that the brain is lateralized in a similar way across species, with the left hemisphere involved with discrete functions such as matching of auditory signals and the right functioning in spatial and affective information (DEUENBURG, 1981). Because of this consistency, it is possible to consider the indication of analog cognition by right hemisphere dominance in cetaceans, just as humans indicate a predominance of digital processing in the anatomical and neuropsychological character of our left hemisphere.

The skull of odontocete cetaceans is unique in that it is always found to be larger on the right side, with no reversals of this ever reported (WOOD and EVANS, 1979). But there is not a corresponding endocranial asymmetry to any obvious extent. It is interesting, however, to consider the origins for such asymmetry.

Several observations of cerebral asymmetry have been reported. KOJIMA (1951) found that the weight ratio between the right and left hemisphere of a sperm whale was 1 : 0.9; volumetric measurements also indicated a larger right hemisphere. Greater development of the right frontal lobe in the same species was also reported by POUCHET and BEAUREGARD (1889). In the mysticeti, GOLDBERG (1896) and RAWITZ (1910) both report a larger right cerebral hemisphere. More recently, RIDGEWAY (1982) has found larger right cerebral hemispheres in statistical samples of the bottlenosed dolphin and the common dolphin. A sample of the dolphin genus *Stenella* also gave a larger right hemisphere but this did not achieve statistical significance (sample size was 11).

No reports of a larger left hemisphere are found in the literature. POUCHET and BEAUREGARD report that the right temporal region appears less developed in the sperm whale, but apparently the greater asymmetry of the frontal lobes more than compensates for this.

Thus while not completely conclusive, there is definite evidence for greater development of the right cerebral hemisphere in cetaceans. Of course, such gross anatomical features must be supported by evidence in other fields before the question of cerebral dominance can be answered.

5.3 Cognitive Aspects of Analog Information Processing in Cetaceans

The cognitive characteristics which best define the lateralization of the human brain are generally complex and often depend on semantic capabilities (e.g. the lateralization of *Kana* and *Kanji* script). Discernment of analog dominant information processing in cetaceans does not have these lateralization experiments to rely upon; they have not been performed and in most cases would not be directly applicable. But it is the predominance of the analog cognitive style, and not lateralization, which is in question. Thus it is then possible to utilize the results for general cetacean psychophysical experiments in looking at cetacean cognitive style.

The majority of experimentation concerns the auditory memory ability of the bottlenosed dolphin, and this has been almost exclusively in matching tasks. Reviewing the results of these, HERMAN (1981) notes that while the extensive auditory memory capabilities of the dolphin have been well demonstrated, there is little evidence on how this information processing takes place. In comparison to human abilities, known to be supported by the verbally based active rehearsal process, Herman suggest that »analogic eidetic auditory imagery» may be responsible for dolphin memory process. HERMAN notes that »Eidetic perceptual processes may in fact govern human memory for nonverbal items, such as tones, colors, or motor movements (MASSARO, 1970; PEPPER and HERMAN, 1970), and seem a tempting alternate model to animal 'rehearsal' mechanisms.»

A more clear-cut comparison of analog and digital information processing occurred serendipitously for an attempted frequency discrimination experiment, and is reported by JOHNSON (1979) in a survey on anomalies in cetacean auditory studies. The test was in discriminating between an intermittently pulsed tone of constant frequency and a series of alternating tones. As JOHNSON onomatopoeically described it, »In the one case the animal was presented with a da da da da etc. signal and the other is a da dee da dee etc. signal.» The purpose was to reduce the separation in the alternating signal until the dolphins could not tell it from the constant frequency signal, thus providing the just noticeable frequency difference.

It is worthwhile to reproduce JOHNSON's description of this attempt.

This procedure was tried for several weeks using two different animals and no matter how different we made the frequencies of the two tones, neither animal performed above the chance level in making the discrimination. Many different pulse lengths and overall stimulus durations were tried to no avail. Finally, in desperation, the signals were changed from pulsed tones of equal or different frequencies to a constant frequency tone versus a sine wave modulated FM signal. By the end of the first day following the change in signals, the animal was performing the discriminations with near perfection!

Although the information encoded here is simply a binary value, it is still a striking example of ability to process information in analog form and failure to process the same information in digital form.

The bulk of non-auditory experiments, also primarily concerning the bottlenosed dolphin, are visual tasks. In reviewing these, HERMAN (1980) notes that while tasks such as motor mimicry through observation, which »would seem to require the use of analogic imagery», are easily accomplished, other tasks which are certainly not more complex visually (i.e., the visual matching to sample tasks) are extremely difficult for the dolphin. He concludes that »There seems to be a paradox here in that what appear to be sophisticated imitative behaviors are dependent on visual imagery, while in some other cognitive tasks that seem equally dependent on visual imagery information processing capabilities were found to be very limited.» A greater ability to perform gestalt comprehension tasks, such as those of the continuous dynamic stimuli that dolphins excel at, and subsequent poor performance at discrete matching tasks is exactly that predicted by a hypothesis of analog-dominant cognition.

It is well understood that the dolphin is not a visually dominant animal, and that requiring visual information greatly increases task difficulty. This may be the reason for the more obvious emergence of the analogic bias in visual tasks; a similar emphasis of analogical processing in cerebral lateralization due to task difficulty was noted for the serial/parallel dichotomy.

5.4 Cetacean Communication as an Analog Information System

Almost all previous applications of cybernetics to cetaceans have been in cetacean communication, and it is useful to examine these studies in light of the implications of analog information processing.

DREHER (1966) attempted to delimit the channel capacity of the bottlenosed dolphin whistles by the rate of whistles produced (number of whistles per second). A large number of similar studies on various species have been carried out by Russian researchers (BULLOCK and GUREVICH, 1979). Most of these included other sounds beside whistles, and attempts to identify syntactic patterns and association of sounds with behavioral states were sometimes made. Always at question in these experiments is the number of different signals.

Thus all such analyses have assumed an alphabet of code signals, i.e., a digital language. The empirical data, however, suggests the opposite. As previously noted, the signal characteristics alone have suggested a graded system to several researchers. TARUSKI (1976) showed that whistles of wild short-finned pilot whales formed a continuous series, each connected to the next by a subtle variation. BASTIAN (1967) recognized the same graded character in the whistles of captive bottlenosed dolphins. Assessment of humpback whale vocalizations as a graded system has already been mentioned, and in dolphins CALDWELL and CALDWELL (1976) note that »Most pulsed sounds seem to intergrade when large numbers of them are considered.» A graded character is very evident within the spectrogram groupings of killer whale vocalizations made by POULTER (1968).

More importantly, most researchers have suggested that the nature of the information system, and not simply the physical characteristics of the signals is similar to the sense of analog used here. Terms used to describe the representation proportionate characteristics include »emphatic» and »intuitive». CALDWELL and CALDWELL (1976), concentrating on the idea of signature whistle, note that communication of the emotional state seems to be conveyed by emphatic variation of the whistle.

When we examined data presented by other researchers that intended to demonstrate a distress signal, we have found evidence only of the signature whistle of an individual that happened to be recorded in a very stressful situation.

HERMAN and TAVOLGA note evidence for spotted dolphins in the wild showing that alarm was conveyed by »a typical variations» of an individual's whistle. A similar suggestion for pulsed sounds is made by GASKIN (1982), noting that »It is quite possible that the pulsed sounds of dolphins also convey significant informa-

tion through modulation, perhaps giving shades of emotional intensity through variation in emission intensity.»

It is possible to approach the delimiting of the information potential of cetacean vocalizations from an analog information perspective. For the transmission channel the maximum rate of information transfer (channel capacity) is only limited by the signal to noise ratio and the bandwidth. For the bottlenosed dolphins transmitting echolocation clicks in open waters, AU et al. (1974) estimate a minimum of signal to noise ratio of 30 dB at a range of 80 yards (73.2 m); this was confirmed by empirical measurements. Peak frequency bandwidth for this species is given by WOODS and EVANS (1979) as 115 kHz. Using channel capacity as defined by SHANNON (1959):

$$C = W \log (1 + P/N) = 1, 146, 231 \text{ bits/sec}$$

By comparison the human audio channel capacity is about 50,000 bits/sec and the actual upper limit for human information transmission (in reading) is about 43 bits/sec (PIERCE and KARLIN, 1957).

In the reception of signals there is an equally high information potential. MURCHISON (1979) demonstrates that the bottlenosed dolphin has voluntary control over the click interval, and shows a temporal resolution for 10 micro-seconds; thus each click interval can potentially carry 20 discriminations or about 4.3 bits. Although this is certainly an underestimate (the range of 10 micro-seconds is limited by the maximum tested distance of 7 meters; actual echolocation limits are about 10 times that distance), the lowest repetition rate of 10 micro-seconds would give 430 bits/second.

Reception of information by frequency can be delimited by the frequency resolution ability as determined by THOMPSON and HERMAN (1975) for the bottlenosed dolphin. Relative frequency discrimination limens of less than 1 % from 15 to 130 kHz indicate a potential of greater than 100 discriminations, i.e., at least 6.6 bits per signal, greater than that estimated for click intervals.

The most important aspect in delimiting the information potential of cetacean communication is that of signal production. This is limited by the diversity (variance) and by the precision of control for transmitted signals (i.e., whether the variations are controlled or just statistical fluctuations).

While no direct measurements have been made, the results of AU et al. (1974) show that dolphins can greatly vary the peak frequency of a pulse within a click train (the sample shown included a peak frequency difference of 79 kHz between two of the consecutive clicks) and can also maintain the peak frequency to a single value for large numbers of consecutive clicks. This precision is only reported to 1 kHz; the actual precision capability for frequency control may be much greater. Even so, with a 1 kHz precision the peak frequency bandwidth of more than 100 kHz would again give a maximum potential of at least 6.6 bits per click, or a transmission rate of 600 bits/second using a low repetition rate.

The precision of click interval transmission is indicated by the range of resolution experiments and thus is about equal to the reception limits.

Thus all three components of the cetacean communication system — signal production, transmission, and reception — show the capability for a high rate of information transfer. All are very conservative estimates, and other information encodings, such as intensity discrimination, could also be included.

While these limitation estimates are based on echolocation click trains, it should be noted that the click trains assigned a communicative value are generally of higher pulse rate and show greater variation than that of echolocation signals (FORD and FISHER, 1978; NORRIS, 1969; CALDWELL and CALDWELL, 1976). An advantage of using echolocation signals is that the measurements are derived from behaviorally based experiments and thus provide values involving actual use of information. The limits estimated reflect the maximum for a demonstrated information potential, not an arbitrary designation of how many different signals are present.

5.5 *Other Behaviors*

It has been noted that analog information can cross species barriers without prior explanation (that is, without knowing an arbitrary code or prior conditioning to the contingencies of the signals). This is due to the representation proportionate nature of the information; the weak insistent mewling of a juvenile of any species is obvious and is distinct from a threatening roar. Both signals are proportionate to the actual information they represent. Body language is similarly analog. The criticism of anthropomorphism is so often given precisely because the antropomorphic interpretation is so commonly correct that one must train to avoid using it automatically.

Evidence in cetaceans for a heightened perceptive ability of such analog signals has occasionally been misinterpreted as indicating high intelligence. In teaching a dolphin to mimic English words, LILLY (1967) claims that dolphins were able to discriminate metalanguage from language; the dolphin Peter does not mimic »Now listen, Peter,» but does mimic the target phrase that follows. Rather than an understanding of the discrete encoding of the words, it is much more likely that the dolphin was responding to the analog information of tone, expression and gesture. While words are arbitrarily encoded, the paralinguistic signals are proportionate representations of the information, as in the sensory receptive expression (eyes wide open, head swung into direct alignment with partner's) used when one expects an answer.

Care giving (epimeletic) behavior in cetaceans has been controversial due to the many well established cases of intergeneric altruism. This occurs even in the wild, as evidenced by NORRIS (1974) report of striped dolphins attempting to aid a captured pacific pilot whale. As NORRIS and DOHL (1980) note, except for the cetaceans »no wild animal other than man will come to the assistance of a distressed member of another taxon.» While the usual mechanism of kin selection in altruism cannot be applied to such distant genetic relatives, the ability to perceive the representation proportionate signals of distress depends on analog information processing, and thus suggests that a high degree of such cognitive abilities results in a more general (i.e., intergeneric or interfamilial) application to the related epimeletic behavior.

An important aspect of epimeletic behavior is evidenced by the arguments against a cognitive role in cetacean altruism (e.g., GASKIN, 1982). Researchers have noted two characteristics of cetacean epimeletic behavior which they have suggested to be evidence for a lack of reasoning. One is the case where epimeletic behavior is selective, that is, where females are aided but males are often abandoned. The other is the fact that altruistic behavior is often non-selective, e.g., the previous cases of intergeneric or interfamilial altruism, suggested to be a fixed action pattern.

The tautology here is evident; if epimeletic behavior is selective, then it is not rational, and if it is non-selective, then it is not rational. The problem is not in the circularity itself but in the underlying assumption that analytic cognition has anything to do with compassion, caring, or other motivations of sincere human altruism. Of course some human »altruistic« behavior may be only an insidious simulation, with purely calculated, analytic scheming as its only motivation; operationally there is no difference. But, in general, human altruism is derived from complex, highly emotive cognition.

It is in fact analytic thought which generally opposes care-giving behavior in people, with rationales extending from »you must paddle your own canoe« to »I was just following orders.« In this respect it is interesting to consider some of the extreme forms of epimeletic behavior as resulting from a predominance of analogic, emotive cognition. While the mass stranding and death of an entire school due to a single moribund individual is not a logical behavior, it certainly is not a particularly adaptive one either. The high degree of empathetic perception and cognition accompanying analog information processing (as seen in the highly emotive associations of the human right cerebral hemisphere) could be the primary causal factor.

If a predominance of analogic cognition plays a direct role in mass strandings, then (assuming the acoustic sexual selection hypothesis) there should be a correlation between the degree of sexual selection and stranding activity. This is evidenced by the observation that »pronounced sexual dimorphism is almost confined to odontocete species that regularly strand as schools« (NORRIS and DOHL, 1980).

As to the level of intelligence involved, there is nothing in the epimeletic behavior of cetaceans to determine whether it is an activity of high or low cognitive complexity. We only know of the cognitive complexity of human altruistic behavior by our self-experience and by communication from other people; their music, art, and other emotive expressions. Until an experiment can be devised to test for similar communicative behaviors (that is, acoustic expressions of emotive analogical cognition) in cetaceans, the question of cognitive complexity in cetacean altruism must remain posed.

CONCLUSIONS AND FUTURE RESEARCH

6.1 Hypothesis Confirmation

The most fundamental research for confirming the hypothesis presented here is that concerning sexual selection for acoustic signals. This is currently being accomplished

in a very direct way for humpback whales, but these vocalizations are very apparent as displays. They are lengthy arrangements in time rather than simultaneous frequency distribution, thus giving a recognizable acoustic patterning (in its similarity to our music, bird songs, etc.). Particularly apparent is the association with courtship behavior; the seasonal localization of a mating site in the clear tropical waters has been instrumental to the success of the studies.

On the other hand, we may be reaching the limit of our ability to understand the informational content of these vocalizations. Without knowledge of the contingencies of the vocalizations (behavioral/acoustic responses to females, significance of individual variations in song production, and particularly the basis of analysis) there is little available data to advance our comprehension.

The situation with odontocetes is just the opposite. The connection with courtship is obscured by the lack of a single overt display, by the constant sexual and vocal behavior of both sexes, and by the distribution of information in frequency rather than in time varying signals. Yet the potential for advancing our understanding may be much greater than that for humpback whale vocalizations. Because there is an exchange of pulsed sounds (rather than a lengthy solo), the basis for production and analysis of the sounds is made visible. Possibilities for such direct investigation of the informational content of the signals will be discussed in the following section.

Less direct but more easily obtained evidence than the ethological-acoustic data, such as that supporting sexual selection for signals in humpbacks, are found in a variety of sources. Sexual dimorphism of the vocal apparatus was found in the common dolphin; this could be investigated for other species as well. The confirmation of sexual dimorphism in killer whale vocalizations should also be attempted for other species, particularly the relation between signal similarity to echolocation signals and the strength of the acoustic dimorphism.

While lateralization with right hemisphere dominance may be the most unusual aspect of the analog hypothesis, its empirical confirmation is in some ways more standardized, thanks to its grounding in physiological phenomena and the extensive experimental background provided by human lateralization. It is hoped that experiments would be confined to non-invasive techniques.

Cognitive based evidence must accompany this to allow any real conclusions, but transforming the currently controversial human experiments into other forms suitable to dolphins may be extremely difficult. A fundamental experiment would be an acoustic version of the visual experiments comparing discrete matching with dynamic stimuli tasks.

6.2 *Communication Research*

No aspect of cetaceans has captured the imagination more than the prospect of understanding and participating in their communications. But the popular notion of a »dolphinese« translation is not possible if the analog hypothesis is correct; it suggests that our fundamental cognitive processes are so different that only a few communication forms (such as music) have any similarity.

In addition, the proposed origins of cetacean communication in purely emotive information suggests that devising contingencies to motivate them into natural communication will be very different from the object/action basis of hominid communication (although it may be possible to impose a simple artificial digital language in this manner; c.f. HERMAN, 1980).

This does not eliminate the possibility of human-cetacean communication; if there is actually a high information content in their communications (in the sense of meaningful exchange) then our participation is probably the only method for understanding that information. But it does suggest that other analyses will have to take place before useful attempts can be made in that area.

A first approach to this should be in strengthening and exploring the isomorphism to music. One of the best defined mathematical models for music is its relation to »1/f noise,» and evidence suggests that it is the analog aspects of music which are responsible for this relation.

The term 1/f noise refers to any changing property with a spectral density which varies as $1/f^\gamma$, where f is the frequency and $0.5 \leq \gamma \leq 1.5$. The spectral density (power spectrum) is related to the autocorrelation function; a 1/f power spectrum implies a correlation of the variable's value at any time with the previous values over all time scales for which the 1/f relations holds. In more familiar acoustic terms, a white noise (e.g., the hissing static of a radio or a succession of completely random strikes at a keyboard) is not correlated at all; it has a $1/f^0$ spectral density. A noise based on a random walk sequence (»brown noise«, where the value at any time is simply the sum of all preceeding vectors) is highly correlated, with a spectral density of $1/f^2$. Brown noise can be simulated by literally letting one's fingers take a random walk on a keyboard; starting at the center notes you would drift up and down the scale, eventually drifting off one end.

Thus, noise with a $1/f^1$ (from here on written 1/f) spectral density will be a balance between the chaos of $1/f^0$ and the monotony of $1/f^2$. Music is often described as just such a balance between order and chance, and indeed listeners rate stochastic note sequences »most music like« when it is 1/f based, with $1/f^0$ sounding too random and $1/f^2$ too predictable (VOSS and CLARKE, 1978).

In addition, the empirical measurements show a 1/f spectral density for a great variety of music, including classical, jazz, blues, and rock (VOSS and CLARKE). This occurs for fluctuations in audio power (loudness) as well as for pitch. While there is no statistical relation for the frequencies of individual sounds in English speech, the spectral density of audio power fluctuations in speech does show the 1/f dependence.

Thus 1/f noise shows a strong relation to analog information signals. The »correlation over all time« defines a gestalt patterning; the signal values are not arbitrary codings but form a continuous relationship, with the meaning of each signal partially defined by previous signals. Such a recursive construction of 1/f noise has been previously noted by MANDELROT (1977) in its relation to the recursive construction of fractal curves, a spatial version of 1/f noise.

While the subjective and mathematical associations to music give an empirical basis for the relationship of $1/f$ noise to analog signals, the gestalt patterning and recursive construction indicate the mechanisms responsible for the relationship. More evidence for this is provided by the spectral densities for speech qualities. While the emotive, analog information conveyed by changes in the loudness (the intonation, inflection, etc., previously noted as a right hemisphere activity) gave a good $1/f$ correlation, the frequencies of the speech sounds gave no such statistical relation. As VOSS and CLARKE note:

In English speech . . . the communication is not directly related to the frequencies of the individual sounds: Successive sounds may convey related ideas even though their frequencies are statistically uncorrelated. In other words, the ideas communicated may have long time correlations even though the frequencies of successive sounds are unrelated.

The converse of this is that music has a correlation among its successive sounds which does vary with the ideas communicated. Thus the representation proportionate patterning in music and the arbitrary encoding of speech are also indicated by the spectral density.

These relations to analog information, along with the objective mathematical basis make the spectral approach an excellent starting point for the analysis of cetacean vocalizations. The humpback whale songs are the easiest in this respect; they are already well established as a mating display, are of low frequency, and vary in time. In addition they already appear to have some of the »fractal« structuring. As MANDELBROT (1977) notes, music is recursively composed from long time scales of movements down to the shortest meaningful subdivisions. Analysis of humpback whale songs has indicated a similar natural hierarchy of time scales (PAYNE and McVAY, 1971), with the levels (from smallest to largest) termed subunit, unit, phrase, theme, song, and song session.

Just as important as finding the correlation with $1/f$ noise is discovering the ways in which humpback vocalizations deviate from that model; in music those deviations comprise crucial rhythmic and compositional structures of various time scale levels (as evidenced by experiments in stochastic music; see VOSS and CLARKE, 1978). For odontocetes the structural rules are more likely to be exchange based and the information itself is distributed in frequency rather than time, thus making even the simple $1/f$ correlation difficult to observe. It should be possible, however, to develop a »spatial« analog of the time-based spectral density correlation.

It was noted that the next step after investigation of the natural communication system is to attempt a human-cetacean »dialogue.« The use of music has been hinted at and has already been attempted several times in semi-scientific contexts (e.g., SPONG, 1974). There is no reason why such objectively based events cannot occur under a testable paradigm. Spontaneous mimicry of artificial sounds has already been demonstrated; extending the exchange to more complex relationships may be possible as a gradual progression, thus providing a usable record of vocal exchange. By »more complex relationships«, no linguistic exchange is implied, just the purely subjective relationship similar to dueting jazz musicians exchanging a complex, sub-

jectively related, yet meaningful sounds. A major problem here may be in providing humans with an i/o translation for the frequency distributed information odontocete pulsed sounds.

6.3 Conclusions

The following conclusions have been reached.

1. The hypothesis of a digital language in cetaceans, in light of the extensive negative findings, is very doubtful.
2. Evidence of extensive cognitive and neural development in cetaceans suggests an evolutionary source other than echolocation or mimicry.
3. The characteristics of manipulatory feedback indicate that such a channel of interactive information exchange will be found in advanced neural systems.
4. There is evidence in cetaceans for such an exchange based on sexual selection for acoustic signal processing ability.
5. An intelligence evolved by selection for complexity of signal patternings predicts a predominance of analogical information processing, in contrast to the digital (left hemisphere) dominance in hominid evolution.
6. Evidence for an analog-dominant cognitive style in cetaceans includes the graded (emphatic) character of their communicative signals and certain results of psychophysical and behavioral studies. There is anatomical evidence for an actual shift to right hemisphere dominance.

The two major consequences not yet discussed are the implications as analyzed by the two branches of cybernetics; computation and communication. Digital forms are predominant in our scientific descriptions. The lack of analog computational theory, the initial assumption by many neurobiologists of right cerebral hemisphere serving only a »back-up» function, and the extreme difficulty which researchers have had in specifying the mechanism for information processing in the right cerebral hemisphere are all cases of an inability to ascertain the analog nature of a system whose digital nature is easily understood. This is not a coincidence; it is related to our own left hemisphere dominance. Even within our brain, neglect and denial of right hemisphere experience by the left hemisphere has been well demonstrated experimentally (ZAIDEL, 1978). The following suggests that this has occurred when we have considered cetacean intelligence and communication.

In cetacean communication, it was noted that cybernetic analyses have only considered the digital formulation, even though an analog communication system has been empirically indicated. Part of the answer for this lies in an idea well articulated by WOOD and EVANS (1979).

The development of communication signals may have contributed to neural control and processing capabilities, but the meager evidence for vocalizations have apparent communication significance in delphinids . . . suggests that they are of an »intuitive» nature, rather than having the characteristics of formal language (the difference between »ouch» and »Fire is hot»). But this issue must remain open.

Although not always explicitly stated, this typifies an underlying assumption that analog communication is restricted to being a simple, closed communication system. While it may be difficult to musically express »place the square onto the blue box«, there are certainly equivalent problems in verbal descriptions of music, or of emotive information in general.

It is ironic that LILLY, who has designated the majority of his writings as »a plea for open-mindedness« and decries the »interfering presumptions« of researchers, has been the most insistent on digital communication and cognition (c.f. »Experimental Definitions for Intellectual Capacity« in LILLY, 1975). Interestingly, BATESON was director of Lilly's research laboratory at the time he developed his ideas on analog communication in dolphins.

One of the few refutations to the assumption of a digital communication requirement for advanced intelligence is that of HERMAN (1980).

A failure of the dolphin to demonstrate linguistic skill, assuming adequacy of procedure, could not therefore be easily explained as a lack of general information-processing capacity but would seem to lie in some cognitive specializations within the Hominoidea not extant in other taxa.

Taking this one step further, it can be seen that just as a lack of digital communication does not (in light of analog possibilities) put any constraints on the amount of information exchanged, a paucity of digital cognition would not preclude a high degree of information processing capability. This has been demonstrated in many different scientific disciplines. The ethnocentrism in early anthropological designations of »primitive« to non-analytically oriented cultures (c.f. TENHOUTEN and KAPLAN, 1973) is now commonly recognized. The use of intelligence tests not biased by left hemisphere tasks has shown an equivalent competence between the information processing abilities of the cerebral hemispheres. It is entirely possible (though by no means yet indicated) that a cetacean mind will be found to have superior information processing ability to our own, just as analog computers had superior computing power over digital computers until the 1940's.

6.4 Ethical Considerations

A final note is appropriate concerning the much discussed problem of ethics of cetacean research. I cannot think of any reason, research or otherwise, which would justify the lengthy captivity which many cetaceans have been subject to. Field research and specimens from natural mortality should provide enough data to allow our understanding to progress; if not, then ignorance seems to me the best alternative.

POSTSCRIPT

Since the completion of this manuscript in the summer of 1983 there have been many developments, both in newly published research well as in my own mind. Morgane (personal communication) has revised many of his earlier conclusions on cetacean neurology. Views on mammalian brain-body weight ratios

have also changed (cf. 'Nature' vol. 306 #24, pp. 314—315). Many other areas, particularly that of cerebral lateralization, have had pertinent new developments.

My own research has centered on a better definition of the bewildering issues raised in chapter four (The Analog/Digital Dualism), particularly those of AI, neurocybernetics and metamathematics. Both the new research developments as well as my own findings will be covered in a forthcoming text, 'The Cybernetics of Cetacea'.

ACKNOWLEDGEMENT

I am very grateful for the help I have recieved from Richard Dickey, Margot Flowers, John Lyman, Peter Narins, Steve Strand, Jacques Vidal, Eran Zaidel, my family, and fy friends.

BIBLIOGRAPHY

Due to the large number of references in Chapter Four (about one-third the total number) they are listed separately below.

References for Chapter Four

- ALBRECHT, D.G.; DeVALOIS, R.L. and THORELL, L.G. (1980): Visual cortical neurons: Are bars or gratings the optical stimuli. *Science* 207: 88—90.
- BATESON, G. (1968): Logical categories of learning and communication. *Conference on World Views* Wenner-Gren Foundation 1968 reprinted in *Steps to an Ecology of Mind*, Ballantine Books, N.Y. 1972.
- BATESON, G. and JACKSON, D.: Some varieties of pathogenic organization. *Res. Pub. Assn. Res. Nerv. Ment. Dis* 42: 207—283, 1968.
- BERTELSON, P. and MORAIS, J. (1983): The Ponzo Illusion *Neuropsychologia* 21: 105—110.
- BLUMSTEIN, S. and COOPER, W.E. (1974): Hemispheric processing of intonation contours. *Cortex* 10: 146—58.
- BOGEN, J.E. (1969): The other side of the brain II. An appositional mind. *Bulletin of the Los Angeles Neurological Society* 34: 73—105.
- BRADSHAW, J.L. and NETTLETON, N.C. (1981): The nature of hemispheric specialization in man. *The Brain and Behavioral Sciences* 4: 51—91.
- CARMON, A. and NACHSHON, I. (1973): Ear asymmetry in perception of emotional nonverbal stimuli. *Acta Psychologica* 37: 351—57.
- CHENEY, D.L. and SEYFARTH, R.M. (1981): Selective forces affecting the predator alarm calls of vervet monkeys. *Behavior* 76: 25—60.
- COHEN, G. (1973): Hemispheric differences in serial versus parallel processing. *Journal of Experimental Psychology* 97: 347—56.
- COKER, W. (1972): *Music and Meaning*. The Free Press N.Y.
- DARWIN, C.J. (1969): Auditory perception and cerebral dominance. Cited in BRADSHAW and NETTLETON (1981).
- DAVIS, A.E. and WADA, J.A. (1977): Hemispheric asymmetries of visual and auditory information processing. *Neuropsychologia* 15: 799.
- DOEHRING, D.G. and LING, D. (1971): Matching to sound of three tone simultaneous and successive sounds, by musical and nonmusical subjects. *Psychonomic Science* 25: 103—105.
- GEFFEN, G., BRADSHAW, J.L. and NETTLETON, N.C. (1972). Hemispheric asymmetry: Verbal and spatial encoding of visual stimuli. *Journal of Experimental Psychology* 95: 25—31.
- GORDON, H.W. (1970): Hemispheric asymmetries in the perception of musical chords. *Cortex* 6: 387—98.

- (1978): Hemispheric asymmetry for dichotically presented chords in musicians and nonmusicians. *Acta Psychologica* 42: 383—95.
- (1980): Degree of ear asymmetries for perception of dichotic chords and for illusionary chord localization in musicians of different levels of competence. *Journal of Experimental Psychology: Human Perception and Performance* 6: 516—27.
- GROSSMAN, M., SHAPIRO, B.E. and GARDNER, H. (1981): Dissociable musical processing strategies after localized brain damage. *Neuropsychologia* 9: 425—33.
- HAGGARD, M.P. and PARKINSON, A.M. (1971): Stimulus and task factors as determinants of ear advantages. *Quarterly Journal of Experimental Psychology* 234: 168—77.
- HATTA, T. (1981): Differential processing of Kanji and Kana stimuli in Japanese people. *Neuropsychologia* 19: 87—93.
- HOULARD N.; FRAISSE, P. and HECAEN, H.: Effects of unilateral hemispheric lesion on two types of optico-geometric illusions. Cited in BETELSON and MORAIS (1983).
- HUBEL, D.H. and WIESEL, T.N. (1965): Receptive fields and functional architecture in two nonstriate visual areas (81 and 19) of the cat. *Journal of Neurophysiology* 28: 229—225.
- JASON, G.W. (1983): Hemispheric asymmetries in motor function: Left hemisphere specialization for memory but not performance. *Neuropsychologia* 21: 35—45, 1983.
- JOHNSON, R.C.; BOWERS, J.K.; GAMBLE, M.; LYONS, F.M.; PRESBEY, T.W. and VETTER, R.R. (1977): Ability to transcribe music and ear superiority for tone sequences. *Cortex* 13: 299—35.
- KUHN, T.S. (1962): *The Structure of Scientific Revolutions*. University of Chicago Press: Chicago.
- LASHLEY, K. (1960): In search of the engram. In *The Neuropsychology of Lashley*, McGraw Hill, N.Y.
- LE DOUX, J.E.; WILSON, D.H. and GAZZANIGA, M.S. (1977): Manipulo-spatial aspects of cerebral lateralization: clues to the origin of lateralization. *Neuropsychologia* 15: 743—50.
- MORAIS, J.; PERETZ, I.; GUDANSKI, M. (1982): Ear asymmetry for chord recognition in musicians and nonmusicians *Neuropsychologia* 20: 351—54.
- OHGISHI, M. (1978): Hemispheric differences in the mode of information processing. *Japanese Journal of Psychology* 49: 257—64.
- PAPCUN, G.; KRASHEN, S.; TERBEEK, D.; REMINGTON, R. and HARSHMAN, R. (1974): Is the left hemisphere specialized for speech, language and/or something else? *Journal of the Acoustical Society of America* 55: 319—27.
- POLICH, J.M. (1980): Left hemisphere superiority for visual search. *Cortex* 16: 39—50.
- (1982): Hemispheric differences for visual search: serial versus parallel processing revisited. *Neuropsychologia* 20: 297—307.
- PRIEBRAM, K.H. (1962): In *Interhemispheric Relations and Cerebral Dominance* ed. by MOUNTCASTLE.
- RAISBECK, G. (1963): *Information theory* MIT press: Cambridge Mass.
- ROBERTSON, A.D. and INGLIS, J. (1978): Memory deficits after ECT: cerebral asymmetry and dual encoding. *Neuropsychologia* 16: 179—87.
- ROSIE, A.M. (1973): *Information and communication theory* Van Nostrand Reidhold Co. London.
- RUESCH and KEES (1956): *Nonverbal Communication* □.
- SAFER, M.A. and LEVENTHAL, H. (1977): Ear differences in evaluating emotional tones of voice and verbal content. *Journal of Experimental Psychology: Human Perception and Performance* 3: 75—82.
- SASANUMA, S. (1975): Kana and Kanji processing in Japanese aphasics. *Brain and Language* 2: 369—83.
- (1977): with ITOH, M.; MORI, K. and KOBAYASHI, Y. Tachistoscopic recognition of Kana and Kanji words. *Neuropsychologia* 15: 547—53.
- SEAMON, J.G. and GAZZANIGA, M.S. (1973): Coding strategies and cerebral laterality effects. *Cognitive Psychology* 5: 249—56.
- SEMMES, J. (1968): Hemispheric specialization: A possible clue to mechanism. *Neuropsychologia* 6: 11—26.
- SHANNON, C.E. (1948): A mathematical theory of communication, *Bell System Technical Journal* 27: 379.
- (1949): Communication in the presence of noise. *Proc. IRE* 37: 10.

- SIDTIS, J.: On the nature of the cortical function underlying right hemisphere auditory perception. *Neuropsychologia* 18: 321.
- SUMMERS, J.J. and SHARP, C.A. (1979): Bilateral effects of concurrent verbal and spatial rehearsal on complex motor sequencing. *Neuropsychologia* 17: 331—43.
- SUSSMAN, H.M. and WESTBURY, J.R. (1978): A laterality effect in isometric and isotonic labial tracking. *Journal of Speech and Hearing Research* 21: 563—79.
- TAUB, J.M.; TANGUAY, P.E.; DOUBLEDAY, C.N. and CLARKSON, D. (1976): Hemisphere and ear asymmetry in the auditory evoked response to musical chord stimuli. *Physiological Psychology* 4: 11—17.
- VONNEGUT, K.: *Slaughter-House 5* Dell, N.Y. 1968.
- WIEDMER: Computation on sets containing infinite objects. *Theoretical Computer Science* 10: 133—155.
- WHITAKER, H.A. and OJEMANN, G.A. (1977): Lateralization of higher cortical functions as a critique. *Annals of the New York Academy of Sciences* 299: 459—73.
- WHITE, M.J. and WHITE, K.G. (1975): Parallel-serial processing and hemispheric function. *Neuropsychologia* 13: 377—81.
- ZAIDEL, E. (1978): Concepts of cerebral dominance in the split brain. In *Cerebral Correlates of Conscious Experience*, ed. P.A. BUSER and A. ROUGEUL-BUSER 263—84.
- (1978): Lexical organization in the right hemisphere. *Ibid.*

GENERAL REFERENCES

- ALTMAN, J.S. (1971): Control of accept and reject reflexes in the Octopus. *Nature* 229: 204—206.
- AMUNDIN, M. and AMUNDIN, B. (1973): On the behavior and study of the harbor porpoise, *Phocoena phocoena*, in the wild. In *Investigations on Cetacea* Vol. V (G. PILLERI, Ed.), pp. 317—328. Berna, Switzerland: Institute of Brain Anatomy, University of Berne.
- ANDREW, R.J. (1962): Evolution of intelligence and vocal mimicking. *Science* 137: 585—589.
- AU, W.W.L., FLOYD, R.W., PENNER, R.H. and MURCHISON, A.E. (1974): Measurement of echolocation signals of the Atlantic bottlenosed dolphin, *Tursiops truncatus* Montagu, in open waters. *J. Acoust. Soc. Am.* 56: 1280—1290.
- BATESON, G. (1966): Problems in cetacean and other mammalian communication. In *Whales, Dolphins and Porpoises* (K.S. NORRIS, Ed.) Berkeley: University of California Press.
- BASTIAN, J. (1967): The transmission of arbitrary environmental information between bottlenosed dolphins. In *Animal Sonar Systems*, Vol II (R.G. BUSNEL Ed.), pp. 803—873. Jouy-en-Josas, France: Laboratoire de Physiologie Acoustique.
- BEAMISH, P. (1977): Evidence that baleen whales do not use food-finding sonar. *Proc. 2nd Conf. Biol. Mar. Mammals*, San Diego, California, Dec. 1977, p. 72.
- BEJCZY, A.K. (1975): Effect of hand-based sensors on manipulator control performance. *Second Conference on RMS*, NASA.
- (1979): Manipulator control autonomy using smart sensors. *Electro/79 Convention*. New York, N.Y.
- BROIT, M., RENARD, M. and STOJILJKOVIC, Z. (1978): An approach to spatial pattern recognition of solid objects. *IEEE Transactions on Systems, Man and Cybernetics*, vol. 8.
- BULLOCK, T.H. and GUREVICH, V.S. (1979): Soviet literature on the nervous system and psychobiology of cetacea. *Int. Rev. Neurobiol.* 21: 47—127.
- BURDIN, V.I., REZNIK, A.M., SKORNYAKOV, V.M. and CHUPAKOV, A.G. (1974): Study of Communicative Signals in Black Sea dolphins. *Akusti Cheskiy Zhurnal*, 20: 518—525.
- BUSNEL, R.G. and DZIEDZIC, A. (1966): Acoustic signals of the pilot whale *Globicephala melaena* and of the porpoises *Delphinus, delphis* and *Phocoena phocoena*. In *Whales, Dolphins and Porpoises* (K.S. NORRIS, Ed.) pp. 544—568 Berkeley: University of California Press.
- CALDWELL, M.C. and CALDWELL, D.K. (1965): Individualized whistle contours in bottlenosed dolphins, *Tursiops truncatus*. *Nature* 207: 434—435.

- (1971): Statistical evidence for individual signature whistles in Pacific white-sided dolphins, *Lagenorhynchus obliquidens*. *Cetology* 3: 1—9.
- (1972): Behavior of marine mammals. In *Mammals of the Sea* (S.H. RIDGEWAY, Ed.) pp. 409—465. Springfield, Ill.: Thomas.
- (1976): Cetaceans. In *How Animals Communicate* (T.A. SEBEOK, Ed.), pp. 794—808 Bloomington: Indiana University Press.
- CARRINGTON, R. (1959) *Elephants*: New York: Basic Books Inc.
- CHENEY, D.L. and SEYFARTH, R.M. (1981): Selective forces affecting the predator alarm calls of vervet monkeys. *Behavior* 76: 25—60.
- CLUTTON-BROCK, T.H. and ALBON, S.D. (1979): The roaring of the red deer and the evolution of honest advertisement. *Behavior* 69: 145—170.
- COLLEEN, H. (1981): Giving robots the power to cope. *Robotics Today*, Sp. 81: 32—34.
- CURLEY, M.D. and BACHRACH, A.J. (1981): Tactile sensitivity in the one-atmosphere diving system JIM. *Human Factors* 23 (3): 291—297.
- DAHLHEIM, M.E. and AWBREY, F. (1982): A classification and comparison of vocalizations of captive killer whales (*Orcinus orca*). *J. Acoust. Soc. Am* 72 (3) 661—670.
- DEFRAN, R.H. and PRYOR, K. (1980): The behavior and training of cetaceans in captivity. In *Cetacean Behavior* (L.M. HERMAN, Ed.), pp. 319—362 New York: John Wiley and Son.
- DENENBURG, V.H. (1981): Hemispheric laterality in animals and the effects of early experience. *The Brain and Behavioral Sciences* 4: 1—49.
- DREHER, J.J. (1966): Cetacean communication: small group experiment. In *Whales, Dolphins and Porpoises* (K.S. NORRIS, Ed.), pp. 529—543 Berkeley: University of California Press.
- DREHER, J.J. and EVANS, W.E. (1964): Cetacean communication. In *Marine Bio-acoustics* (W.N. TAVOLGA, Ed.) pp. 373—393 Oxford: Pergamon.
- EMLIN, S.T. and ORING, L.W. (1977): Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215—223.
- EVANS, W.E. and BASTIAN, J. (1969): Marine mammal communication: Social and ecological factors. In *The Biology of Marine Mammals* (H.T. ANDERSON, Ed.) pp. 425—475. New York: Academic Press.
- ENTIN, T.I. (1973): Histological study of the occipital cortex in the dolphin brain. *Arch. Anat. Histol. Embryol.*, 65: 92—100.
- FISH, J.F., SUMICH, J.L. and LINGLE, G.L. (1974): Sounds Produced by the gray whale *Eschrichtius robustus*. In *The California Gray Whale* (W.E. EVANS, Ed.) pp. 38—45 *Mar. Fish Rev.* 36: 38—45.
- FORD, J.K. and FISHER, H.D. (1978): Underwater acoustic signals of the narwhal (*Monodon monoceros*). *Can J. Zool.* 56: 552—560.
- GASKIN, D.E. (1982): *The Ecology of Whales and Dolphins*, London: Heinemann Educational Books Ltd.
- GOTO, T. and TAKEYASU, K. (1981): Control algorithm for precision insert operation robots. *IEEE Transactions on Systems, Man and Cybernetics* 11: 151—160.
- GREEN, S. (1975): Variation of vocal pattern with sound situation in the Japanese macaque (*Macaca fuscata*): A Field Study. In *Primate Behavior* Vol. 4 (L.A. ROSENBLUM, Ed.) pp. 1—102. New York: Academic Press.
- GULDBERG, F.Q. (1896): Über die Zirkularbewegung als tierische Grundbewegung, ihre Ursache, Phenomanalitat und Bedeutung. *Biol.* 16: 779—783 as cited in ARVY (1977) Asymmetry in cetaceans. In *Investigations on Cetacea*, (G. PILLERI, Ed. Vol. 8: 183—201).
- GUREVICH, V.S. (1972): Morpho-functional investigation of supercranial respiratory passages of common dolphin (*Delphinus delphis*). *Konf. Primen. Mat. Metodov Vychisl. Tekhn. Med. Bionike*. Leningrad, pp. 19—21.
- HARLOW, H.E. (1949): The formation of learning sets., *Psychol. Rev.* 56: 51—65.
- HEDGPETH, J.W. (1978): *The Outer Shores*. Eureka: Mad River Press.
- HERMAN, L.M. (1980): Cognitive characteristics of dolphins. In *Cetacean Behavior* (L.M. HERMAN, Ed.) pp. 363—429 New York: John Wiley and Sons.
- HERMAN, L.M. and TAVOLGA, W.N. (1980): The communication systems of cetaceans. In *Cetacean*

- Behavior* (L.M. HERMAN, Ed.) pp. 149—209 New York: John Wiley and Sons.
- HOFSTADTER, D.R. (1980): *Godel, Escher, Bach: An Eternal Golden Braid*. New York: Vintage Books.
- HYVARINEN, L.P. (1968): *Information Theory for Systems Engineers*. Berlin: Springer-Verlag.
- IHNATOWICZ, E. and DAVIES, B. (1977): Mechanical Manipulation for the Investigation on Disordered Environments. *7th Internat. Symp. on Industrial Robots* Tokyo: JIRA.
- JANSEN, J. and JANSEN, J.K.S. (1969): The nervous system of cetacea. In *The Biology of Marine Mammals* (H.T. ANDERSON, Ed.) pp. 176—252 New York: Academic Press.
- JERISON, H.J. (1973): *Evolution of the Brain and Intelligence*. New York: Academic Press.
- JOHNSON, C.S. (1979): Important areas for future cetacean auditory study. In *Animal Sonar Systems* (R.G. BUSNEL and J.F. FISH, Ed.) pp. 515—518 New York: Plenum Press.
- KASUYA, T. and AMINUL HAGUE, A.K.M. (1972): Some information on distribution and seasonal movement of the Ganges dolphin. *Sci. Rep. Whales Res. Inst.*, 24: 109—115.
- KELLOGG, W.N. (1961): *Porpoises and Sonar* Chicago: University of Chicago Press.
- KESAREV, V.S. (1969): Structural organization of the limbic cortex of the dolphin brain. *Arch. Anat. Histol. Embryol.* 56: 28—35.
- KINNE, O. (1975): Orientation in space: Animals: Mammals. In *Marine Ecology* vol. II (O. KINNE, Ed.) pp. 702—855 London: Wiley.
- KOJIMA, T. (1951): On the brain of the sperm whale (*Physeter catodon* L.). *Sci Rep. Whales Res. Inst. Tokyo* 6: 49—72.
- LADYGINA, T.F. and SUPIN, A.Y. (1970): The Acoustic projection in the dolphin cerebral cortex. *Fiziol. Zh. SSSR im. I.M. Sechenova*, 56: 1554—1560.
- (1974): Evolution of cortical areas of the brain of terrestrial and marine mammals. In *Morfologiya, Fizilogiya i Akustika Morskikh Mlekopitayushchikh*.
- (1975): Sensory projections into the cerebral cortex of the bottlenosed dolphin (*Tursiops truncatus*). In *Marskiye Mlekopitayushchiye* (G.B. AGARKOV, Ed.) pp. 172—173 Kieve: Izd. Naukova.
- (1977): Localization of the projection sensory areas in the cortex of the Atlantic bottlenosed dolphin (*Tursiops truncatus*). *Zh. Evol. Biokh. Fiziol.* 13: 172—178.
- LANG, T.G. and SMITH, H.A.P. (1965): Communication between dolphins in separate tanks by way of an acoustic link. *Science* 150: 1839—1843.
- LAUER, E. (1982): The telencephalon of ungulates. In *Comparative Correlative Anatomy of the Vertebrate Telencephalon* (E.C. CROSBY and H.N. SCHNITZLEIN, Ed.) New York: MacMillan.
- LAYNE, J.J. (1958): Observations on freshwater dolphins in the upper Amazon. *J. Mammalogy*, 39: 1—22.
- LILLY, J.C. (1961): *Man and dolphin* New York: Doubleday.
- (1963): Distress call of the bottlenosed dolphin: Stimuli and evoked behavioral responses. *Science* 139: 116—118.
- (1967): *The Mind of the Dolphin*. New York: Doubleday.
- (1975): *Lilly on Dolphins*. New York: Doubleday.
- (1978): Dolphin and the law, Ltr. to the Honolulu (Hawaii) Advertiser, 31 Jan. as cited WOOD, F.G. and EVANS, W.E.
- (1979): Adaptiveness and ecology of echolocation in whales. In *Animal Sonar Systems* (R.G. BUSNEL and J.F. FISH, Ed.) pp. 381—426. New York: Plenum Press.
- LILLY, J.C. and MILLER, A.M. (1961): Vocal exchanges between dolphins. *Science* 134: 1873—1876.
- (1962): Operant conditioning of the bottlenosed dolphin with electrical stimulation of the brain. *J. Comp. and Physiol. Psychol.* 55: 73—79.
- MANDELBROT, B.B. (1977): *The fractal geometry of nature* San Francisco: W.H. Freeman and Co.
- MASSARO, D.M. (1970): Perceptual processes and forgetting in memory tasks. *Psychological Rev.* 77: 537—567.
- MONTAGU, A. and LILLY, J.C. (1963): *The Dolphin History*. Los Angeles: University of California.
- MORGANE, P.J. (1974): The whale brain: The anatomical basis of intelligence. In *Mind in the Waters* (J. McINTYRE, Ed.) pp. 84—93 New York: Charles Scribner's Sons.
- MORGANE, P.M. and JACOBS, N.S. (1972): Comparative anatomy of the cetacean nervous system.

- In *Functional Anatomy of Marine Mammals* (R.J. HARRISON, Ed.) pp. 117—244 New York: Academic Press.
- MURCHISON, A.E. (1979): Detection and range resolution of echolocating bottlenosed porpoise. In *Animal Sonar Systems* (R.G. BUSNEL and J.F. FISH, Ed.) pp. 43—70 New York: Plenum Press.
- NAPIER, J. (1962): Evolution of the hand. *Scientific American* 207 (6): 56—62.
- NORRIS, K.S. (1969): The echolocation of marine mammals. In *The Biology of Marine Mammals* (H.T. ANDERSON, Ed.) pp. 391—423. New York: Academic Press.
- (1974): *The Porpoise Watcher* New York: Norton.
- NORRIS, K.S. and DOHL, T.P. (1980): The structure and function of cetacean schools. In *Cetacean Behavior* (L.M. HERMAN, Ed.) pp. 211—317. New York: Wiley.
- PACKARD, A. (1972): Cephalopods and fish: the limits of convergence. *Biol. Rev.* 47: 241—307.
- PAYNE, R.S. and McVAY, S. (1971): Songs of humpback whales. *Science* 173: 585—597.
- PAYNE, R.S. and WEBB, D. (1971): Orientation by means of long range acoustic signaling in baleen whales. *Ann. N.Y. Acad. Sci.* 188: 110—141.
- PEPPER, R.L. and HERMAN, L.M. (1970): Decay and interference effects in short-term retention of a discrete motor act. *J. Exp. Psychol.* 83: Pt. 2 1—18.
- PIERCE, J.R. and KARLIN, J.E. (1957): Reading rates and the information rate of a human channel. *The Bell System Technical Journal* 36: 497—516.
- PILLERI, G. (1983): Auf Baffinland zur Erforschung des Narwals (*Monodon monoceros*). 80 p. Hirn-anatomisches Institut, Bern.
- PILLERI, G. and BUSNEL, R.G. (1969): Brain/body weight ratios in Delphinidae. *Acta Anat.* 73: 92—97 (Cited in MORGANE, 1974).
- PILLERI, G. and GIHR, M. (1970): The central nervous system of mysticete and odontocete whales. In *Investigations on Cetacea*, Vol. II (G. PILLERI, Ed.) pp. 89—127, Brain Anatomy Institute, University of Berne.
- PILLERI, G., KRAUS, C. and GIHR, M. (1968): The structure of the cerebral cortex of the ganges dolphin *Susu (Platanista gangetica* Lebeck, 1801. *Z. Mikrosk Anat. Forsch.* 79: 373—388 (Cited in MORGANE, 1974).
- POUCHET, G. and BEAUREGARD, H. (1889): Recherches Sur le Chachalot. *Nouvelles Arch. Mus. H.N., Ze serie, 1*, 1—96 et 4, 1—90 (1892).
- POULTER, T.C. (1968): Marine mammals. In *Animal Communication: Techniques of Study and Results of Research* (T.A. SEBEOK, Ed.) pp. 405—465. Bloomington: Indiana University Press.
- POULTON, E.D. (1890): *The colors of animals: their meaning and use, especially considered in the case of insects*. London: Kegan Paul, Trench Trubner and Co.
- PURCHON, R.D. (1977): *The Biology of the Mollusca*. Oxford: Pergamon Press Ltd.
- RAWITZ, B. (1910): das Zentralnervensystem der cetacean. Die Furchen und Windungen des Grosshirns von *Balaenoptera rostrata* FAB. *Arch. Mikr. Anat.* 75: 225—238 as cited in ARVY (1977) Asymmetry in cetaceans. In *Investigations on Cetacea* (G. PILLERI, Ed.) Vol. 8: 183—201.
- REEVES, R.R. (1977): Hunt for the Narwhal. *Oceans* 10: 50—57.
- RIDGEWAY, S.H. (1982): Relative brain sizes and cortical surface areas in odontocetes. Third International Thereological Congress Helsinki 15—20 Aug. 1982. *Acta. Zool. Fin.* □
- ROWELL, T.E. and HINDE, R.A. (1962): Vocal communication by the Rhesus monkey (*Macaca mulatta*) *Proc. Zool. Soc. Lond.* 8: 91—96.
- RUE, L.L. (1964): *The World of the Raccoon*. New York: J.B. Lippincott.
- SHANNON, C.E. (1959): Communication in the presence of noise. *Proc. IRE* 47: 10—21.
- SPONG, P. (1974): The whale show. In *Mind in the Waters* (J. McINTYRE, Ed.) pp. 170—184. San Francisco: Charles Scribner's Sons.
- SOLOMONOW, M. (1976): Artificial Sensory Communication via the Tactile Sense. Ph.D. dissertation, UCLA.
- TARUSKI, A.G. (1976): Sounds and behavior of the pilot whale *Globicephala* spp. Ph.D. Thesis, University of Rhode Island.
- TENHOUTEN, W.D., and KAPLAN, C.D. (1973): Science and its mirror image: A theory of inquiry. New York: Harper and Row.

- THOMPSON, R.K.R. and HERMAN, L.M. (1975): Underwater frequency discrimination in the bottle-nosed dolphin (1—140 kHz) *J. Acoust. Soc. Am.* 57: 943—948.
- THORPE, W.H. (1972): The comparison of vocal communication in animals and man. In *Non-Verbal Communication* (R.A. HINDE, Ed.) pp. 27—47. Cambridge: Cambridge University Press.
- TITOV, A.A. (1971): Characteristics of sonic signaling of common dolphins (*Delphinus delphis*) under new conditions. *Bionika* 5: 62—67.
- TITOV, A.A., TOMLIN, A.G., BARYSHNIKOV, N.S., YUREVICH, L.I. and LEKOMTSEV, V.M. (1971): Communication-emotional signals of Black Sea dolphins. *Bionika* 5: 67—72.
- TOMILIN, A.G. (1968): Factors promoting powerful development of the brain in odontoceti. *Trudy Vsesoyuznogo Sel'skokhozyaystvennogo Instituta Zaochnogo Obrazovaniya*, No. 31, pp. 191—200. In Russian. JPRS No. 49777 as cited in WOOD, F.G. and EVANS, W.E. (1979) Adaptiveness and ecology of echolocation in whales. In *Animal Sonar Systems* (R.G. BUSNEL and J.F. FISH, Ed.) pp. 381—425. New York: Plenum Press.
- TYACK, P. (1981): Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology* 8: 105—116.
- VON BONIN, G. (1937): Brain weight and body-weight in mammals. *Journ. Gen. Psych.* 16: 379—389.
- VOSS, R.F. and CLARKE, J. (1978): »1/f noise« in music: Music from 1/f noise. *J. Acoust. Soc. Am.* 93 (3): 194—211.
- WASHBURN, S.L. (1978): The Evolution of Man. *Sci. Am.* 93 (3): 194—211.
- WATKINS, W.A. (1979): Click sounds from animals at sea. In *Animal Sonar Systems* (R.G. BUSNEL and J.F. FISH, Ed.) pp. 291—297. New York: Plenum Press.
- WATKINS, W.A. and SCHEVILL, W.E. (1974): Listening to Hawaiian spinner porpoises, *Stenella cf. longirostris*, with a three-dimensional hydrophone array. *J. Mammalogy* 55: 319—328.
- (1978): Sperm whales (*Physeter catodon*) react to pingers. *Deep Sea Res.* 22: 123.
- WEIDEMANN, H.L. (1967): Entropy Analysis of Feedback Control Systems. Ph.D. dissertation, UCLA.
- WELKER, W.I. and SEIDENSTEIN, S. (1959): Physiological significance of succli in the cerebral cortex of the raccoon (*Procyon lotor*). *J. Comp. Neurob.* 11: 469—502.
- WELLS, M.J. (1978): Octopus. New York: Halsted Press.
- WICKELGREN, W.A. (1975): Relations, operators, predicates, and the syntax of (verbal) propositional and (spatial) operational memory. *Bulletin of the Psychonomic Society* 6: 161—64.
- WILBUR, K.M. and YONGE, C.M. (1966): *Physiology of Mollusca*, Vol. II. New York: Academic Press.
- WILSON, E.O. (1975): *Sociobiology: The New Synthesis*. Cambridge Mass: Belknap/Harvard.
- WINN, H.E. and PERKINS, P.F. (1976): Distribution and sounds of the minke whale, with a review of the mysticete sounds. *Cetology* 19: 1—12.
- WINN, H.E. and WINN, L.K. (1978): The song of the humpback whale *Megaptera novaeangliae*, in the West Indies. *Mar. Biol.* 47: 97—114.
- WOOD, F.G. (1973): *Marine Mammals and Man*. Washington D.C.: Luce.
- WOOD, F.G. and EVANS, W.E. (1979): Adaptiveness and ecology of echolocation in whales. In *Animal Sonar Systems* (R.G. BUSNEL and J.F. FISH, Ed.) pp. 381—425. New York: Plenum Press.
- WURSIG, B. (1979): Dolphins. *Sci. Am.* 240 (3).
- ZAHAUI, A. (1981): Natural selection, sexual selection and the selection of signals. In *Evolution Today* (G.G.E. SCUDDER and J.L. REVEAL, Ed.) pp. 133—138.
- ZAIDEL, E. (1978): Concepts of cerebral dominance in the split brain. *Cerebral Correlates of Conscious Experience* (BUSER and ROUSED-BUSER, Ed.) Elsevier/North Holland Biomedical Press.