

From: ANIMAL SONAR  
Edited by Paul E. Nachtigall and Patrick W. B. Moore  
(Plenum Publishing Corporation, 1988)

## COGNITION AND ECHOLOCATION OF DOLPHINS

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### INTRODUCTION

In this conference, we have already been given several examples of sonar hunting bats relying on an internal representation of some past experience as a basis for action. These include experiments demonstrating the predictive tracking of horizontally moving targets by a fishing bat (Campbell & Suthers, this volume) and the extracting of a species-specific concept from acoustical "glint" cues by greater horseshoe bats (von der Emde, this volume). Internal representation involves the encoding of information about specific features of stimuli as well as about relations among stimuli (Schusterman and Krieger, in press).

The purpose of this paper is to explore some aspects of the interaction between the cognitive skills of dolphins and their echolocation capabilities. I will first discuss the concept of cognition by briefly reviewing the differences between behavioristic psychology and cognitive psychology. I will then review some aspects of dolphin cognition, initially outside the context of echolocation and then within the context of echolocation. Before getting into the text of this paper, the reader should be aware that every time the word "dolphin" appears, I am usually referring to captive studies with the genus of delphinid known as *Tursiops*, the one Wood (1986) calls "the adaptive bottlenose" and the one that we know best from seeing its performances in oceanariums, aquariums and zoos and hearing about experiments dealing with its cognitive skills and its echolocation abilities.

### WHAT IS COGNITION?

The history of cognitive psychology as an interdisciplinary effort, which included not only philosophy, linguistics and artificial intelligence, but the neurosciences and ethology as well, is brilliantly described in Howard Gardner's new book, "The Mind's New Science" (1985). The extreme reductionism, functionalism and operationalism of a stimulus-response (S-R) behavioristic psychology eschewed such topics as mind and thinking, and such concepts as plans, desires or intentions. Moreover, S-R behaviorists never talked about any form of construct related to mental representations. In general, they insisted on the Lockian point of view, that animals are fundamentally blank slates to be written upon

by experience (Roitblat, 1986), and that "laws of learning" could be applied to virtually all organisms in most, if not all, tasks without regard to specific learning skills or cognitive structures tailored by natural selection to a particular task. At any rate, the goal of much of S-R behavioristic psychology was to develop an elaborate machinery detailing how much the triadic contingency of stimulus/response/reinforcement could describe and explain the learning and shaping of any behavior. In general, questions about an organism's umwelt or perceptual world were largely ignored. Only on rare occasions did S-R behaviorists consider questions about language acquisition, planning, reasoning, and intentionality, rule learning and learning sets, concept formation, memory, serial pattern learning, problem solving, etc. in human or nonhuman animals. The relative sterility of many forms of behavioral psychology became most apparent in the late 1950s when several behaviorists like Karl Lashley, Edward Tolman and Harry Harlow spoke of men and animals as behaving not as passive reactors to environmental pushes and pulls, but behaving as they do because of expectancies, plans, hypotheses and strategies about the world around them. [For theory and research in the late 1950s and early 1960s, which has structured much current thinking about strategies and rule learning in animals; see Levine (1959), Restle (1958) and Schusterman (1962)].

During the 1960s, several books were published which called for the abandonment of the constricted conceptual view of stimulus-response in favor of more mentalistic conceptions. The impact of this approach became evident about 20 years ago with the publication of Ulric Neisser's influential textbook "Cognitive Psychology" (1967), in which he refers to cognition as "all processes by which sensory input is transformed, reduced, elaborated, stored, recovered, and used." Although the term "cognition" as originally used by Neisser and other experimental psychologists referred to the processing of information by relatively linguistically sophisticated humans, comparative psychologists also conceptualize nonverbal animals as active processors of environmental information.

As Figure 1 shows, Neisser's definition can be readily viewed within the context of an information processing approach in which the acquisition, storage, retrieval and utilization of information involves a number of different stages. Cognitive theories attempt to identify what happens in each of the stages and to identify interactions between the stages. After a brief exposure to a visual or auditory stimulus (e.g., 5 msec), sensory input may be maintained in a sensory store for a considerably longer time period (e.g. 250 msec). Transformation of the sensory input means that animals or, to be more precise, their CNS's, are not passive recipients of environmental information, but reduce and enhance or elaborate on incoming information. Thus, an animal's representation of the world depends not only on the incoming information, limited by its attention and by its short-term memory (STM), but also on

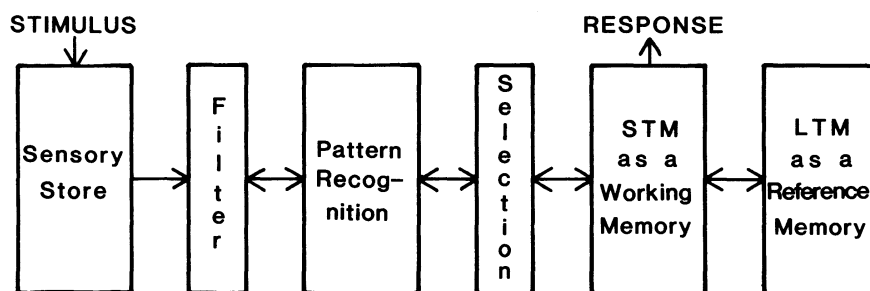


Fig. 1. Stages of an information-processing model (after Reed, 1982).

the elaboration of this new information by previously stored knowledge [which has been momentarily retrieved from long-term memory (LTM)]. According to Jerison (1973; 1986), the construction of perceptual worlds is information processing performed by large and complex neural networks and that such construction accounts for the gross enlargement of the brain in "higher" vertebrates (birds and mammals), enlargement beyond the requirements for controlling the body--the so-called "structural encephalization." An encephalization quotient (EQ), as defined by Jerison (1973), is the ratio between the observed brain weight and the expected brain weight for a defined body weight. Wood and Evans (1980) discussed the relationship between echolocation in odontocete cetaceans, adaptability in "niche" hunting or feeding strategies and EQ at the last Animal Sonar Conference in 1979, and most recently Jerison (1986) has speculated that echolocation in the high EQ dolphin may have resulted in dolphin schools having a shared reality.

In applying an information processing model to dolphin cognition and echolocation, imagine if you will an echolocating dolphin comparing the complex patterns of echoes (and possibly reflected light patterns as well) emanating from objects in its current environment with its stored memory of complex echo patterns (and also possibly reflected light patterns) from previously captured palatable prey. Indeed, the term "hunting by searching image" has been widely adopted in the ethological and behavioral ecology literature (Krebs, 1973) and fits very nicely into an information processing model of foraging behavior. Furthermore, the study of predation behavior in general and specifically hunting by means of echolocation in bats and dolphins may be profitably studied by using a comparative cognitive approach. Hypotheses deriving from ecologically oriented research on hunting behavior are well suited to laboratory manipulation and analysis (i.e., hunting by searching image, hunting by expectation, area-restricted search and even "niche" hunting and optimal foraging).

Returning to Figure 1, note that environmental input appears to be processed in separate sequential stages from sensory input to response output. This is, of course, not the case. Information from the environment enters a sensory buffer, it's filtered and selected, classified, processed in STM, and eventually stored in LTM. Although the stages are arranged discreetly and sequentially, there is a great deal of reciprocal interaction between the processing stages, as indicated by the two-headed arrows, so that an earlier stage can be influenced by information in a later stage and vice versa. Flow from input through sensory store, pattern recognition and memory stages is often called bottom-up or sensory-driven processing. The reverse flow from memory through the pattern recognition stage is often called top-down or concept-driven processing. In top-down processing, sensory information is analyzed in a manner controlled by the animal's knowledge and expectancies.

Getting back to Neisser's definition of cognition, perhaps the final part is the most significant (Reed, 1982). Following the various stages of information processing, the information must be used in an adaptive manner--for example, to make complex decisions about sensory events and to solve problems regarding feeding, reproduction and predator avoidance. (Perhaps in the case of dolphin biosonar, the integration of sensory events from different modalities also includes cross modal transfer between sonar and vision.) At the last Animal Sonar Conference in 1979, Schusterman (1980) reported that on a variety of signal detection tasks (primarily nonecholocating), the decision criteria of dolphins and pinnipeds changed predictably and rapidly as a function of the animal's expectancy of signal occurrence and as a function of knowledge about reinforcement contingencies or the payoff matrix. Recently, some of

these results have been replicated in an experiment in which a dolphin used biosonar (Au and Turl, 1984).

In summarizing about what cognition refers to, or more specifically, what is meant by animal cognition, I will quote from Herb Roitblat's remarkably lucid, rather thorough and brand new textbook, "Introduction to Comparative Cognition" (1986).

"Comparative cognition is the study of the minds of organisms. Mind is the set of cognitive structures, processes, skills, and representations that intervene between experience and behavior. Comparative cognition views animals as intelligent processors of information capable of adapting to their environments through expression of varied cognitive skills. These skills include learning, remembering, problem solving, rule learning, concept formation, perception, pattern recognition, and others. Comparative cognition seeks to explain behavior in terms of the skills, representations, and processes that organisms use as they interact with their environment" (Roitblat, 1986, pp. 1-2).

#### DOLPHIN COGNITION SANS ECHOLOCATION

Although the cognitive skills of dolphins based on anecdotal and naturalistic evidence may be found in Greek and Roman literature, McBride and Hebb (1948) gave the first objective modern account of the cognitive abilities of dolphins albeit in the context of play and motivation and they placed them as high or higher than apes in any comparative ranking (see also Kellogg, 1961). John Lilly (1961) supported this notion, but may have gone overboard in suggesting that dolphins communicate in a sonic language as sophisticated as human language. Nevertheless, Lilly's insights into such potentially significant cognitive/communicative skills as mimicry and intentionality and his special efforts in pointing out the importance of social bonding between these animals and their trainers in the application and formal demonstration of such skills is now recognized by many scientists who have worked closely with dolphins (Jerison, 1986). However, from the standpoint of rigorous experimental methodology, the best demonstration of such cognitive skills as memory and rule learning in dolphins comes from the recent work of Louis Herman and his colleagues (for a summary of these studies, see Herman, 1980; Herman, 1986; Richards, 1986).

#### Working Memory as STM

Given two discriminative stimuli, D1 (a triangle) and D2 (a square), an animal selects D1 if conditional stimulus C1 (a triangle or a white disc) is provided, and selects D2 if the conditional stimulus is C2 (a square or a black disc). The conditional relations are: If C1, then D1; if C2, then D2. When the conditional or "sample" stimuli are physically the same as the discriminative stimuli, the task or performance is called "identity" matching, and when sample and discriminative stimuli are physically different, the performance is called "nonidentity," "arbitrary" or "symbolic" matching (see Sidman and Tailby, 1982 for a more detailed account of the relationship between conditional discriminations and matching to sample). A delay between presentation of the conditional or sample stimulus (e.g., C1) and the availability of the discriminative or choice cues (e.g., D1 and D2) defines a "delayed matching to sample" (DMTS) procedure and is considered a versatile technique for studying STM, or "working" memory, in animals. The DMTS task can be used to illustrate the distinction between working memory and LTM or "reference"

memory. When the animal is given cues (D1 and D2), it has to remember or retain a mental representation of the sample (C1) in order to choose the appropriate discriminative stimulus, and such information need be retained only long enough to complete a particular trial, after which the information is best discarded since it is not needed and it may interfere with the memory requirements of the next trial (e.g., presentation of C2). This is a type of working memory and illustrates retention for a limited time of recently acquired information within the context of enduring knowledge. Memory for C1 or C2 will not work if there is no enduring knowledge of "if C1, then D1; if C2, then D2." In contrast to information in working memory that may be disposed of following each trial, information about the relationship between the conditional stimulus, or sample, and the discriminative stimuli, or choice cues, had to be retained in memory on all trials. Such memory is called "reference" memory or LTM. (For a more detailed description of methodology, comparative results and theory about animal memory, see Honig, 1978; Roitblat, 1986; Domjan and Burkhard, 1986).

A variety of DMTS procedures have been modified for testing the working memory of a single dolphin (Kea) for particular acoustic signals generated electronically and presented under water (Herman, 1980). The most important feature of the acoustical modification of visual DMTS is that following the conditional, or sample, sound, the two choice sonic cues are presented successively with a 0.5 sec interval between the termination of the first cue and the onset of the second cue. The results of these tests showed that the auditory STM of a dolphin compares favorably with the visual STM of monkeys (D'Amato, 1973; Wright, Santiago, Sands & Uruicoli, 1984) and is superior to the visual STM of pigeons (Grant, 1976; Santiago and Wright, 1984). For example, when "novel" sample sounds were played for 2.5 sec, the dolphin had virtually a perfect memory for the sounds, even with delays as long 120 seconds, whereas pigeons have much poorer retention after delays of only 20 seconds--particularly with visual samples having a duration < 4 sec. In other experiments using just two familiar sounds differing in frequency and amplitude modulation, Kea's memory in either identity or symbolic DMTS was stable and accurate out to 50 sec delays. Moreover, identity "matching" remained accurate even when the sample duration was reduced to only 3 msec! However, evidence from several experiments showed that Kea's retention of sounds was degraded by proactive interference--probably because she "confused" the two sample sounds--as well as by retroactive interference--probably because Kea's "rehearsal" of the sample sound was disrupted when a different sound was inserted between the sample and the choice cues for almost the entire 15-sec delay interval. Finally, the dolphin Kea was given a serial probe recognition (SPR) task, i.e., a multiple memory task, in which a list of different sounds (drawn from a pool of 800) was presented as a "multiple" sample with the last or most recent item followed by a single test sound. The dolphin was trained to press either a "Yes" or a "No" paddle to indicate whether or not the test sound was in the list of items. Kea was correct on about 85% to 95% of the trials when list length consisted of three or fewer items, and her performance deteriorated to about 70% correct when a maximum list length of six items was given. The dolphin's serial position curve showed a pronounced recency effect, i.e., there was superior performance on terminal items, suggesting that new items displace or degrade the quality of older items held in a dolphin's working memory.

In summary then, a single dolphin has, thus far, been shown to have memory skills for acoustical signals which converge with the those of monkeys for visual signals and suggest a specialized sonic memory related to social communication and echolocation. The memory of a dolphin is degraded by both proactive and retroactive interference, as has been

shown with all other vertebrates thus far tested. The ability of the dolphin Kea to maintain in memory a 3-msec duration sound for more than 50 seconds also indicates a specialized sonic memory.

### Learning Set and Rule Learning

The initial idea of "learning to learn" or learning set (LS) formation by monkeys was developed by Harry Harlow (1959) in order to explain all kinds of transfer of learning between problems of a single type. These included Pavlovian learning as well as Kohler's "insight" learning (1927), where chimpanzees, after being previously stymied in their attempts to reach food, suddenly hit upon the solution of using a variety of tools to extend their reach. In a typical LS paradigm, monkeys are given a series of two-choice visual discrimination problems and typically they solve the initial ones slowly in "trial and error" fashion before solving novel problems of the same type following a single information trial. It was first shown empirically and unequivocally by Schusterman (1962; 1964) that the solution to such problems by chimpanzees depends on the development of an abstract rule (the same rule sometimes used in solving discrimination-reversal problems); a rule which goes beyond the concrete characteristics of the visual stimuli. Such an abstract rule or strategy has been termed "win-stay, lose-shift" with respect to the discriminative stimuli.

Conceptual abstractions, like win-stay, lose-shift, which are unrelated to specific perceptual relations of immediate experience, are also involved in generalized matching-to-sample and sameness-difference problems. For example, although pigeons can treat the relationship between A and A as the same, or B and B as the same (a first-order relationship), they have difficulty recognizing that the relationship existing between A and A is the same as the relationship existing between B and B, i.e., pigeons may be incapable of conceptualizing a relationship about a relationship (a second-order relationship). However, chimpanzees and some other nonhuman primates appear quite capable of rapidly learning to classify almost any stimulus pair as the same, regardless of whether or not they lie along the same stimulus generalization gradient (Premack, 1978; 1983). [For a summary of different viewpoints on the ability of pigeons and chimpanzees to acquire concepts, see Roitblat (1986)].

The dolphin Kea, much like Schusterman's chimpanzees on visual problem-solving, was also shown to be capable of developing a win-stay, lose-shift strategy, and thus eventually could use a single information trial to solve any one of a number of two-choice auditory discrimination or discrimination reversal problems (Herman, 1980). Furthermore, the same dolphin later learned auditory matching and demonstrated a generalized auditory matching-to-sample capability analogous to that shown by nonhuman primates with visual stimuli (Herman, 1980). A different type of rule learning which emphasized reinforcement training was demonstrated with a rough-toothed dolphin. Only those motor patterns which were novel were selected for reinforcement by the trainers. Following a period of frustration and confusion, the dolphin started performing novel behaviors, such as spitting and swimming in corkscrew patterns, demonstrating rule learning and some degree of creativity (see Pryor, 1986 for a review of reinforcement training and cognition in dolphins). Yet still another example of a dolphin learning set comes from studies of vocal mimicry with the dolphin Ake. She was trained to mimic specific whistle sounds and then tried to mimic any novel sound she heard (Richards, 1986). Such accomplishments by dolphins suggest that, at least within the acoustical modality, they may be capable of coding environmental information or "thinking about the world" in relatively abstract ways unencumbered by perceptions arising from immediate experience.

From a cognitive standpoint, one of the features of animal sonar systems that is particularly intriguing is that, unlike the more passive ways of perceiving the environment, doing it actively with echolocation allows a researcher with the appropriate equipment to monitor changes or adjustments in an animal's echolocating signals and thus look for signs of active information processing prior to overt behavioral decision-making. By designing experiments in animal sonar which seek to determine the nature and causal sequence of the processes operating on representations, we will most certainly advance our current theories of cognition as well as identify the kinds of information conveyed to a given species by the echoes of its sonar emissions (Simmons, 1980). The consequences of such a research program should give us a much better understanding of the types of interactions occurring between concept-driven and sensory-driven processes.

### Concept-Driven Processes

There are several recent examples demonstrating that a dolphin's knowledge and expectancies affected its performance on an echolocation task. In one of the studies, the goal was to induce a cognitive state in the dolphin that can best be described as "failure expectancy" (as reflected in response bias) and then eliminate or "extinguish" the failure expectancy. Details of the study can be found in the original paper (Schusterman, Kersting and Au, 1980). Suffice it to say that in a bio-sonar study of material discrimination, the dolphin, Sven, could distinguish between a small hollow aluminum cylinder and a small glass cylinder with virtually perfect accuracy, but could not distinguish between the same types of large cylinders (twice the size of the small ones). By striking one of two response paddles, the dolphin indicated which of the cylinders was present, aluminum or glass. Throughout the insolvable problem, the animal biased its response, nearly always choosing the paddle associated with glass, suggesting it was echolocating in a perfunctory fashion. We therefore reasoned that, if Sven was given test sessions (consisting of 64 trials) with the solvable problem which were intermittently and unpredictably preceded by sessions with the unsolvable problem, then the dolphin might keep its sonar turned down or off during the initial stages of the solvable problem and thus err in favor of the paddle associated with glass. Figure 2 is a summary of the results which confirmed the hypothesis. The dolphin did indeed make significantly more errors by biasing its choice response during the first half of the sessions with the solvable problem. Interestingly, the failure expectancy was so persistent that it took 20 consecutive sessions of the solvable problem to extinguish it the first time and 10 consecutive sessions of the solvable problem to extinguish failure expectancy the second time. Unfortunately, the dolphin's click trains were only sporadically monitored during a single session of the solvable problem, and with this sparse data we could discern no clear relationship between click trains and performance. We therefore interpreted our results as meaning that the dolphin's failure expectancies diminished its attention for listening to previously established distinctive echoes. This interpretation is similar to one suggesting that bats having learned to rely on spatial memory pay less attention to echoes in an obstacle avoidance task (see Griffin, this volume). However, there is a high likelihood that the dolphin Sven did turn his sonar down when he expected the insolvable problem. Evidence for this effect comes from some recent work on detection tasks.

In experimental studies of echo ranging by dolphins (Au, Penner and Kadane, 1982), click emissions were monitored more assiduously than

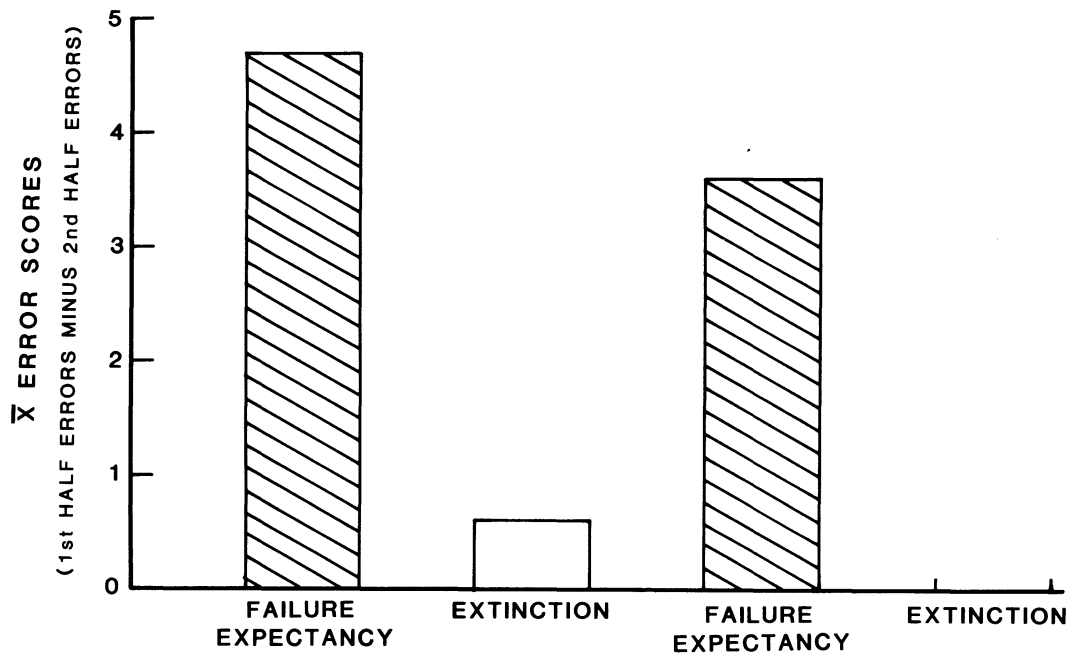


Fig. 2. Summary of results showing a dolphin's errors on a solvable discriminative echolocation task as a function of induced "failure expectancy," extinction of the "failure expectancy," re-induction of "failure expectancy," followed again by extinction.

described above, and click intervals (which were greater than the two-way transit time) were found to be similar during correct detections (target present) and correct rejections (target absent), demonstrating that dolphins clearly expected to hear an echo at a specified time following pulse emission. In fact, like the failure expectancy study, a dolphin may fail to report target presence for a few trials after the range has been changed, even though the dolphin had previously perfected detection at that range. In a psychophysical study on the noise limitations of echo-ranging in two dolphins, Au, Penner and Kadane (1982) continuously monitored click emissions. Among other things, they found that during an insolvable target detection task (masked by noise) in which the animals showed response bias, one dolphin did not emit any detectable clicks on about 30% of the trials while the other dolphin failed to emit clicks on 14% of the trials despite behaving as if they were echolocating. These results do indeed show that when food-motivated, echolocating dolphins have knowledge, they use that knowledge in a global way, they adjust motor output as well as sensory input and they will place themselves on a 50% partial reinforcement schedule rather than refuse to work at a task.

#### Perception and Conception

Recently, Nachtigall and Patterson (1980) in a brief report described training a dolphin on what they called a sameness-difference echolocation problem. The animal was required to report whether or not two simultaneously presented targets were the same or different. The targets were constructed to be aspect independent, and differences between targets were made as obvious as possible by varying the size, shape and material. After the dolphin perfected the original discrimination with two pairs of targets, two novel pairs were introduced and perfect transfer ensued. This work suggests that, perhaps like chimpanzees in the visual modality, dolphins by means of echolocation may be able to conceptualize abstract relationships. However, the evidence in this



report of dolphins forming second-order relationships about targets ensonified by echolocation clicks is not without some ambiguity. For example, it is not clear what stimulus relationships were perceived by the dolphin, i.e., whether the sonar targets belonged to similar or different perceptual classes (see Premack 1978 for a full discussion of the problem of distinguishing between perceptual relations or first-order relations and conceptual relations or second-order relations). There is always a difficulty in understanding the nature of stimulus equivalence. Pattern recognition, stimulus generalization and concept formation in echolocating dolphins have been discussed by Schusterman (1980), who showed that even in a well controlled study of dolphin echo-recognition by Hammer (1978), the animal probably used a simple detection of a single set of features to classify a whole range of targets differing in materials, such as aluminum, bronze, glass and steel. Thus, except for detection tasks like target size, the more complex psychophysics of recognition and classification by dolphin sonar has, as yet, not been clearly elucidated, and the dolphin's world of echo information is still relatively poorly understood. Moreover, the intermodal equivalence of sonar cues and reflected light cues from common objects remains a rich, untapped source for cognitive research with the high EQ dolphins.

#### ACKNOWLEDGMENTS

The writing of this paper was fully supported by Office of Naval Research Contract N00014-85-K-0244. I thank Forrest G. Wood for his cogent and "fussy" comments on the original manuscript. I also thank all the people in Helsingor, Denmark, who almost literally blew my mind at the Animal Sonar Systems Conference, 1986.

#### REFERENCES

- Au, W. W. L. and Turl, C. W., 1984, Dolphin biosonar detection in clutter: Variation in the payoff matrix, J. Acoust. Soc. Am., 76:955.
- Au, W. W. L., Penner, R. H. and Kadane, J., 1982, Acoustic behavior of echolocating Atlantic bottlenose dolphins, J. Acoust. Soc. Am., 71:1269.
- D'Amato, M. R., 1973, Delayed matching and short-term memory in monkeys, in: "The Psychology of Learning and Motivation: Advances in Research and Theory," G.H. Bower, ed., Academic, N.Y.
- Domjan, M. and Burkhard, B., 1986, "The Principles of Learning and Behavior," Brooks/Cole, Monterey.
- Gardner, H., 1985, "The Mind's New Science," Basic Books, N.Y.
- Grant, D. S., 1976, Effect of sample presentation time on long-delay matching in the pigeon, Learning and Motivation, 7:580.
- Hammer, C. E., 1978, Echo-recognition in the porpoise (Tursiops truncatus): An experimental analysis of salient target characteristics, Naval Ocean Systems Center, San Diego, Tech. Rep. 192.
- Harlow, H. F., 1959, Learning set and error factor theory, in: "Psychology: A Study of a Science," S. Koch, ed., McGraw-Hill, N.Y.
- Herman, L. M., 1980, Cognitive characteristics of dolphins, in: "Cetacean Behavior: Mechanisms and Functions," L.M. Herman, ed., Wiley-Interscience, N.Y.
- Herman, L. M., 1986, Cognition and language competencies of bottlenosed dolphins in: "Dolphin Cognition and Behavior: A Comparative Approach," R.J. Schusterman, J.A. Thomas, and F.G. Wood, eds., Lawrence Erlbaum Associates, Hillsdale, N.J.

- Honig, W. K., 1978, Studies of working memory in the pigeon, in: "Cognitive Processes in Animal Behavior," S. H. Hulse, H. Fowler, and W. K. Honig, eds., Erlbaum, Hillsdale, N.Y.
- Jerison, H. J., 1973, "Evolution of the Brain and Intelligence," Academic Press, N.Y.
- Jerison, H. J., 1986, The perceptual worlds of dolphins, in: "Dolphin Cognition and Behavior: A Comparative Approach," R. J. Schusterman, J. A. Thomas and F. G. Wood, eds., Lawrence Erlbaum Associates, Hillsdale, N.J.
- Kellogg, W. N.I., 1961, "Porpoises and Sonar," University of Chicago Press, Chicago.
- Kohler, W., 1927, "The Mentality of Apes," Reprinted by Vintage Books, N.Y.
- Krebs, J. R., 1973, Behavioral aspects of predation, in: "Perspectives in Ethology," P. P. G. Bateson and P. H. Klopfer, eds., Plenum Press, N.Y.
- Levine, M., 1959, A model of hypothesis behavior in discrimination learning set, Psychol. Rev., 66:353.
- Lilly, J. C., 1961, "Man and Dolphin," Doubleday, N.Y.
- McBride, A. F. and Hebb, D. O., 1949, Behavior of the captive bottlenose dolphin, Tursiops truncatus, J. Comp. Physiol. Psychol., 41:111.
- Nachtigall, P. E. and Patterson, S., 1980, Training of a sameness/difference task in the investigation of concept formation in echolocating Tursiops truncatus, in: "Proceedings of the International Marine Animal Trainer Association Conference, October 28-31, 1980," J. Pearson and J. Barry, eds., Boston: New England Aquarium.
- Neisser, J., 1967, "Cognitive Psychology," Appleton-Century-Crofts, N.Y.
- Premack, D., 1978, On the abstractness of human concepts: Why it would be difficult to talk to a pigeon, in: "Cognitive Processes in Animal Behavior," S. H. Hulse, H. Fowler, and W. K. Honig, eds., Erlbaum, Hillsdale, N.J.
- Premack, D., 1983, The codes of man and beasts, The Behavioral and Brain Sciences, 6:125.
- Pryor, K., 1986, Reinforcement training as interspecies communication, in: "Dolphin Cognition and Behavior: A Comparative Approach," R. J. Schusterman, J. A. Thomas and F. G. Wood, eds., Lawrence Erlbaum Associates, Hillsdale, N.J.
- Restle, F., 1958, Toward a quantitative description of learning set data, Psychol. Rev., 65:77.
- Richards, D. G., 1986, Dolphin vocal mimicry and vocal object labelling, in: "Dolphin Cognition and Behavior: A Comparative Approach," R. J. Schusterman, J. A. Thomas and F. G. Wood, eds., Lawrence Erlbaum Associates, Hillsdale, N.J.
- Roitblat, H. L., 1986, "Introduction to Comparative Cognition," W. H. Freeman and Co., San Francisco.
- Schusterman, R. J., 1962, Transfer effects of successive discrimination reversal training in chimpanzees, Science, 137:422.
- Schusterman, R. J., 1964, Successive discrimination-reversal training and multiple discrimination training in one-trial learning by chimpanzee, J. Comp. Physiol. Psychol., 58:153.
- Schusterman, R. J., 1980, Behavioral methodology in echolocation by marine mammals, in: "Animal Sonar Systems," R. G. Busnel and J. F. Fish, eds., Plenum, N.Y.
- Schusterman, R. J., Kersting, D. and Au, W. W. L., 1980, Response bias and attention in discriminative echolocation by Tursiops truncatus, in: "Animal Sonar Systems," R. G. Busnel and J. F. Fish, eds., Plenum Press, N.Y.

- Schusterman, R. J. and Krieger, K., in press, Artificial language comprehension and size transposition by a California sea lion (Zalophus californianus), J. Comparative Psychol.
- Sidman, M. and Tailby, W., 1982, Conditional discrimination vs. matching to sample: An expansion of the testing paradigm, J. Exp. Anal. Behav., 37:5.
- Simmons, J. A., 1980, The processing of sonar echoes by bats, in: "Animal Sonar Systems." R. G. Busnel and J. F. Fish, eds., Plenum Press, N.Y.
- Wood, F. G., 1986, Social behavior and foraging strategies of dolphins, in: "Dolphin Cognition and Behavior: A Comparative Approach," R. J. Schusterman, J. A. Thomas and F. G. Wood, eds., Lawrence Erlbaum Associates, Hillsdale, N.J.
- Wood, F. G. and Evans, W. E., 1980, Adaptiveness and ecology of echolocation in toothed whales, in: "Animals Sonar Systems," R. G. Busnel and J. F. Fish, eds., Plenum Press, N.Y., 381.
- Wright, A. A., Santiago, H. C., Sands, S. F. and Urcuioli, P.J., 1984, Pigeon and monkey serial probe recognition: Acquisition, strategies, and serial position effects, in: "Animal Cognition," H. L. Roitblat, T. G. Bever and H. S. Terrace, eds., Lawrence Erlbaum Associates, Hillsdale, N.J.