What Laboratory Research has Told Us about Dolphin Cognition

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Studies of sensory, cognitive, and communicative skills of bottlenose dolphins (*Tursiops truncatus*) were carried out over a 34-year period at the Kewalo Basin Marine Mammal Laboratory in Honolulu. Findings on sensory skills included fine discrimination of auditory frequency differences and auditory duration, good visual resolution capabilities in water and in air, and sharing of object recognition across the senses of vision and echolocation. Short-term memory for auditory and visual materials was well developed, including memory for lists of items. Concept learning was demonstrated within several paradigms, including discrimination learning sets and matching-to-sample. Dolphins understood novel instructions conveyed within artificial gestural or acoustic language systems using "sentences" as long as five words whose interpretation required processing of both the semantic and syntactic features of the languages. Gestural instructions were understood as reliably when conveyed through television images of trainers as when conveyed by live trainers. The words of these languages were understood referentially, including an ability to report whether a referenced object was present or absent in the dolphin's tank. Both vocal mimicry of novel sounds and behavioral (motor) mimicry of other dolphins and of humans was demonstrated, an extensive and unique dual ability among animals tested, including an understanding of the *concept* of imitate as well as an understanding of the concept of behavioral synchrony. Behavioral synchrony (two dolphins acting together) was carried out effectively for behaviors directed by a trainer and for self-directed behaviors. The dolphins understood the referring function of the human pointing gesture, possibly as a generalization from the referring function of their echolocation beam. Self-awareness was demonstrated in two domains: the dolphin's conscious awareness of its own recent behavior, and its conscious awareness of its own body parts when symbolically referenced. This suite of findings attest to the remarkable flexibility and extensibility of dolphin cognition and reveals cognitive competencies that surely aid the dolphin's effective functioning within its complex social and ecological milieu.

The question of dolphin "intelligence" has long been a subject of intense speculation and dispute, ranging from early zealous affirmations (e.g., Lilly, 1961, 1967) to vigorous denials (e.g., Manger, 2006). Here, I review what has been learned about dolphin cognition through 30+ years (1969-2003) of scientific behavioral research at my laboratory at Kewalo Basin Harbor in Honolulu. There were many who joined me in that research—hordes of graduate and post-doctoral students whose contributions made this research possible and whose names are preserved in many of the publications cited in this paper. My dolphin collaborators were, in order of appearance, Wela, Kea, Nana, Puka, Akeakamai, Phoenix, Hiapo, and Elele. All were bottlenose dolphins, all were from the Atlantic except for Wela, the Pacific variety, and all were female except for Hiapo, whose name in Hawaiian means "older brother". Though all are gone now, their legacy survives through the studies reviewed here that testify to the special cognitive traits and intellectual depth and breadth of this species.

Early Research

Almost 30 years ago I wrote (Herman, 1980, p. 363-364):

Descriptions of the brain of the bottlenosed dolphin (Tursiops truncatus) . . . uniformly remark on its large size, quality, and complexity . . . . These descriptions hint at the intellectual potential of the species, which ultimately depends on brain structure and organization . . . (but) it is behavior, not structure, that measures the intellectual dimensions and range of the species, or what might be called its cognitive characteristics

I followed that text with a review of what was known of those cognitive characteristics at that time, based on the previous nine years of research at my Kewalo Basin Marine Mammal Laboratory in Honolulu. Three areas of research were reviewed: (a) defining selected sensory abilities and constraints that might allow for or limit cognitive processing, (b) the dolphin's ability to process, store, and retrieve items from working memory, based on the evident assertion that memory is the bedrock on which learning must rest, and (c) basic conceptual processes, particularly the ability of the dolphin to uncover and apply an abstract rule for the solution of a class of problem. The principal subjects of these early studies were two female bottlenose dolphins, Keakiko (Kea) and Puka, with an assist also from Nana and Wela.

Sensory studies

Both hearing and vision were studied. The hearing studies mapped out the dolphin Kea's ability to resolve small differences in pitch, i.e. frequency discrimination, across almost the entire frequency range of dolphin hearing (Herman & Arbeit, 1972; Thompson & Herman, 1975) and small differences in the duration of brief sounds (Yunker & Herman, 1974). The results showed that differences in pitch on the order of 0.1% to 0.2% could be detected, a resolution

ability surpassing that of any other species tested with the exception of the human. Differences in sound durations on the order of 8% were resolved, a value surpassing human ability for detecting duration differences of the type given the dolphin. Pitch discrimination was most acute within the frequency range characterizing dolphin whistles and is likely important for resolving differences in the frequency varying characteristics of the whistles of individual dolphins, which appear to be a major communication medium (Herman & Tavolga, 1980; Tyack, 2003). Whistle duration may also have communicative value, for example as an overlay that might inform the listener about the sender's emotional state.

In the early 1970s and before, dolphin vision was often thought of as a "secondary" sense, with hearing (together with echolocation) being the primary and dominant sensory modality through which the social and ecological life of the dolphin was managed. In fact, anatomical and opthalmoscopic observations suggested inferior resolution acuity, particularly in air, where it was supposed that the dolphin was highly myopic (Walls, 1942). These "hard-science" observations contrasted with the every-day observations of dolphins in aquariums catching small objects thrown to them in air, or wild dolphins snagging a fish hurtling itself out of the water in an attempt to escape. At my lab, we tested Puka's vision both underwater and in air at various viewing distances using a graded series of black-and-white gratings as a measure of resolution acuity (Herman, Peacock, Yunker, & Madsen, 1975). We found roughly equivalent acuity across the two mediums, at about the level of measured acuities for dogs and cats, but with best acuity in air occurring at relatively far distances and in water at relatively near distances. These different best-viewing distances seem adaptive to the ecological constraints of the two viewing mediums and the different kinds of targets that might be encountered in each—for example, in water, nearby individual prey fish, and in air, birds circling in the distance as a sign of a fish school beneath. We also tested Puka for color vision and spectral sensitivity (Madsen & Herman, 1980). Color vision was absent; Puka was unable to reliably distinguish between blue, green, or red monochromatic light with brightness levels controlled. The tests showed, though, that under both photopic and scotopic conditions spectral sensitivity was best in the blue end of the visible spectrum and weakest in the red end. This again seemed ecologically adaptive to the spectral composition of oceanic waters. The overall results suggested that we should not regard vision as underdeveloped or as a secondary sense in the bottlenosed dolphin. Rather, vision likely subserves important life functions and, like the auditory system, may route information to higher centers where recognition and interpretation, or other advanced cognitive operations, can take place. Our later studies with other dolphins, as will be reviewed later, in fact established that the visual modality allows for highly complex cognitive tasks to be carried out.

Studies of working memory

We learned a great deal about the characteristics of dolphin memory for sounds. Using variations of the delayed matching-to-sample (DMS) test, we

examined Kea's ability to remember brief (2.5 s) novel sounds, new to her experience, over intervals ranging from 1 to 120 seconds (Herman & Gordon, 1974). Our results showed Kea's short-term memory for sounds to be exceptionally faithful. After a period of initial familiarization with the DMS task, Kea went on a remarkable streak, making only three matching errors over the last 175 novel sounds given her, despite the maximum period over which she had to remember them being stretched to 90 and 120 seconds, the longest lengths tested. Our results for dolphin short-term memory for things heard compared favorably with short-term memory of old-world monkeys for things seen (e.g., D'Amato, 1973). In additional studies we showed that Kea's short-term memory system functioned much like that of monkeys, apes, and humans, showing the classic limiting effects of retroactive and proactive interference (Herman, 1975; cf. Herman & Bailey, 1970). Still later, we extended our findings to show that Kea could not only remember individual sounds but also whole lists of sounds (Thompson & Herman, 1977; Herman, 1980). For this test, Kea listened to a list of as many as eight novel sounds, each of 2 s duration and separated by 0.5 s silent intervals. At the end of the list one additional sound appeared, called the "probe." Kea had to determine whether the probe sound was a member of the list (one of the "old" sounds) or not (a new sound not on the list). Kea showed a classic "recency" effect, able to remember sounds late in the list much better than sounds early in the list. From this result, we determined her memory span to be about 4 to 5 items, a somewhat reduced buffering limit in comparison with human limits of 5 to 7 items (Miller, 1956).

Finally, we demonstrated good spatial memory in Kea—memory for spatial locations signaled by the brief occurrence of a sound from one of four locations (Thompson & Herman, 1981). After a delay that might range to more than a minute, Kea had to indicate the location of the previous sound by approaching the speaker that had produced it. Potential postural cues were controlled by having pairs of speakers positioned in the same direction relative to Kea's position, but at different distances from her. Kea's selection of the correct speaker remained well above chance through to 70 s delays, the longest tested.

Studies of concept learning

In my earliest work on dolphin cognition, I sought to make contact with comparative animal studies seeking measures of "intelligence" that might order species in a way consistent with their brain development. The most popular model for such study in the 1950s through to the early 1970s was the "learning set" task devised by Harry Harlow (Harlow, 1949). This task evaluated a species' efficiency in learning to solve multiple problems of a given type—how rapidly the species could learn how to learn (i.e. to develop what Harlow called a "learning set"). Harlow gave his Rhesus monkey subjects a large number of visual two-choice problems and asked whether there was improvement in the rate at which they solved each new problem. The measure of learning efficiency was the animal's performance on the second trial (Trial 2) of a multi-trial problem over successive

blocks of problems. In theory, the outcome (reward or nonreward) of the animal's "random" choice of object on its first encounter with the pair of objects (Trial 1) should be sufficient for it to identify the correct object thereafter, using the rule, "Win-stay, lose-shift". Studies with a variety of species, ranging from monkeys to rats, yielded results that seemed to fulfill expectations based on brain size (see Warren, 1965 for a review and for exceptions).

Our initial studies with the Pacific bottlenose dolphin Wela (Herman, Beach, Pepper, & Stalling, 1969), or with Kea and Nana (Beach & Herman, 1972), did not demonstrate reliably increasing efficiency over blocks of problems. However, later improved methodology used with Kea did reveal such capability (Herman & Arbeit, 1973). During the final block of two-choice auditory discrimination problems given Kea, she was approximately 93% correct on Trial 2, a level comparable with or exceeding the best levels reported for primate species (see Warren, 1965).

Our learning-set results, together with the diverse findings on memory that I've summarized, began to establish that dolphins were flexible learners with apparent requisite skills necessary for managing even more complex cognitive tasks. We thus began a study of Kea's ability to learn to understand instructions given within the framework of an arbitrary acoustic language we created (Herman, 1980). After initially teaching her acoustic "names" for three objects (*ball, ring, cylinder)* and three actions (*touch, fetch, mouth)*, Kea was able to spontaneously carry out two-word instructions ordered as *object name + action name*, so that, for example, the sequence glossed as *ball + touch* resulted in her touching the ball (and not the other objects). This work with Kea, and ongoing work with Puka on visual capabilities, ended at this point, in May of 1977. As I wrote (Herman, 1980, p. 415, footnote):

> *Kea, along with our second dolphin, Puka . . . was abducted, late at night, by two recently discharged tank cleaners . . . and abandoned in the ocean in remote waters known to have a large shark population . . . . They were never recovered and almost certainly died not long after their abandonment.*

Later Research

Language learning

Our studies began again, after a 14-month hiatus, with two newly arrived, young female bottlenose dolphins, Akeakamai (Ake) and Phoenix. We took up again the issue of dolphin capabilities for understanding instructions given though artificial languages. Ake was tutored in a language in which "words" were represented by the gestures of a trainer's arms and hands, while Phoenix was tutored in a language in which "words" were represented by arbitrary electronic sounds generated by a computer and broadcast into her tank though an underwater speaker (Herman, 1986, 1987; Herman, Morrel-Samuels, & Pack, 1993b; Herman,

Richards, & Wolz, 1984). A major area of investigation was the dolphin's ability to understand strings of words ("sentences") in which both word meaning and word order contributed to the interpretation of an instruction. For example, could the dolphins understand the difference between *take the ball to the hoop* versus *take the hoop to the ball?* The results clearly indicated they could. Sentences as long as five words, and requiring word-order processing, were understood within each language (Herman et al., 1993b). The studies also demonstrated that different grammatical structures could be understood. A linear (left-to-right or S-V-O) grammar was used successfully in Phoenix's acoustic language, and an inverse (O-S-V) grammar was used successfully in Ake's gestural language (Herman et al., 1984). An ability of an animal to process different grammatical formats and to utilize word-order information was first established in these dolphin studies. Since then, Savage-Rumbaugh et al. (1993) have provided examples showing an understanding by the bonobo, Kanzi; word order given him in spoken English instructions affected his interpretation of the instruction.

Reference

A major question in studies examining language competencies is whether the symbols used to refer to objects in the language system come to represent those objects. For example, in English the word *hoop* is understood as representing or referring to a class of objects with certain physical and functional properties. For us, either the written word or the spoken word elicits the mental representation of the object and its properties. To examine whether the gestures we used for objects in Ake's language were understood by her as surrogates for, or as representing those objects, we tested whether she understood a reference to an *absent* object. Understanding a symbolic reference to an absent object is a hallmark indicant of referential understanding (Terrace, 1984). We taught Ake a new grammatical form expressed as *Object + Question.* She understood, for example, that *Hoop + Question* asked whether a hoop was present in her tank (Herman & Forestell, 1985). She could answer *Yes* by pressing a paddle to her right or *No* by pressing a paddle to her left. At each trial there was a single object (one of six possible objects) present in her tank, and either it or one of the other objects not present was referred to. Ake correctly responded *Yes* to 92% of 36 object-present trials and correctly responded *No* to 94% of 18 object-absent trials). With three objects present in the tank, correct performance declined to 72% and 78% respectively for *Yes* and *No* responses, but still significantly well above chance levels. Overall, the results demonstrated that for Ake, the gestures we used for objects were understood referentially as symbolic representations of those objects.

Grammatical understanding

In addition to demonstrating syntactic processing by Ake and Phoenix (Herman, 1986, 1987; Herman et al., 1984; 1993b), we examined the depth of the dolphins' understanding of the grammars of their respective languages by

presenting them with anomalous sentences that violated either the semantic or the syntactic rules of the learned languages (Herman et al., 1993a; Holder, Herman, & Kuczaj, 1993). Anomalous sentences have been used extensively in studies of child language to examine the grammatical systems used by the children, or their competency in adult forms of grammar (e.g., de Villiers & de Villiers, 1972; Kuczaj & Maratsos, 1975). A semantic anomaly was a sentence that was framed correctly syntactically but that instructed the dolphin to carry out an impossible task, such as transporting a window of the tank to a surfboard (*surfboard window fetch)*. The usual response was to reject such anomalous instructions—the dolphin remaining at its station "staring" at its trainer. Less frequently, the dolphin carried out a substitution response as, for example, taking some transportable object to the surfboard. There was never an attempt to retrieve the immovable object.

Some of the syntactic anomalies were constructed so that, as a whole, the sequence of instructions violated the grammatical structure of the learned languages. However, embedded within the sequence were several possible subsets that were consistent with the constraints of the grammatical structure. For example, as a whole, the sequence *Person Ball Hoop Fetch* is syntactically anomalous as there is no grammatical structure that allows for three object names in a row. But embedded in the anomaly are three syntactically correct three-item sequences: *Person Ball Fetch, Person Hoop Fetch,* and *Ball Hoop Fetch (*respectively, *take the ball to the person, take the hoop to the person, take the hoop to the ball).* In sequences of this type, the dolphin (Ake in this case) typically extracted one of the subsets and correctly carried out its instruction. The results of these studies (also see Herman & Uyeyama, 1999) demonstrated that the dolphins had developed an intrinsic understanding of the grammatical structure of their respective languages (i.e. the structure was not explicitly taught), which was the first such demonstration for a language tutored animal.

Interpretation of abstract representations of the real world

For reasons that seem not to be well understood, most animals have difficulty in responding to television scenes as representations of reality. Savage-Rumbaugh (1986) summarized data showing that this constraint even held for chimpanzees, including those that were home or laboratory reared. Thus, it was surprising to find that both Ake and Phoenix were able to interpret television scenes immediately on their first exposure to television (Herman, Morrel-Samuels & Pack, 1990). Each dolphin viewed a small television screen placed behind an underwater window and saw there a live image of a trainer gesturing to them using either sequences from the gestural language (for Ake) or single gestures that normally elicit specific behaviors (for both dolphins). Ake was given 14 different gestural instructions altogether and completed all but two correctly. Phoenix successfully carried out 18 of the 19 different gestural instructions given her. These results were consistent with the high levels of performance achieved by the dolphins when taking instructions from live trainers. We later made the television scenes abstract by gradually "disembodying" the trainer, initially showing only the

trainer's arms and hands on the TV screen, then hands only, and finally only two circles of light moving about the screen (achieved by having the trainer entirely blacked out except for two yellow three-inch diameter sponge balls held in the trainer's hands. On the black-and-white TV screen, the balls appeared as two white circles). The movements of the circles across the screen traced the trainer's movements as she completed various gestures holding the sponge balls. The dolphin tested, Ake, showed either minor performance decrements or none at all in the first two stages. There was a decline in the final stage of moving white circles, but Ake's performance was still significantly well above chance and better than or equal to all of the laboratory staff except for the most senior trainers when they were tested for interpretation of the moving circles. These results gave evidence of exceptional perceptual and cognitive flexibility in the dolphins.

Co-equality of the senses: Integration of vision and echolocation

Our earliest work could not establish conclusively that the visual system allowed a pathway for information to be processed robustly cognitively (e.g., Herman et al., 1969; Beach & Herman, 1972). However, later work made it abundantly clear that the visual system is not only highly functional (Herman et al., 1975), but also allows for complex cognitive operations, including processing of a visual (gestural) language system (Herman, et al., 1984; Herman & Forestell, 1985), the understanding of video representations of reality (Herman et al., 1990), and learning of concepts, in particular generalized match-to-sample (MTS) (Herman, Hovancik, Gory, & Bradshaw, 1989; Herman, Pack, & Wood, 1994). Results from these studies and others, showing complex cognitive operations being performed on visual information, are summarized in Herman (1990). The Herman et al. (1989) MTS study established that the generalized matching *concept* developed fully in both visual and auditory MTS tasks, and that matching abilities were substantially equally proficient whether information arrived through the visual or the auditory sense. One additional dragon that needed to be slayed was the oft-cited viewpoint that vision was a secondary sense of relatively little value in the dolphin's oceanic world, at least relative to the utility of echolocation. Some of the strongest evidence for the functionality of the visual system and its parity with the echolocation system comes from a series of studies we did on cross-modal matching (matching of objects *across* the senses of vision and echolocation) (e.g., Herman & Pack, 1992; Herman, Pack, & Hoffman-Kuhnt, 1998; Pack & Herman, 1995; Pack, Herman, Hoffman-Kuhnt, & Branstetter, 2002; Pack, Herman & Hoffmann-Kuhnt, 2004). In these studies, the dolphin (the primary subject was the female Elele) inspected a "sample" object through one sense, vision or echolocation, and then, using the other sense, sought a match for it among two, three, or four alternatives (the fourth alternative was a press of a paddle to indicate that there was no match, i.e., "none of the above"). For echolocation inspection, objects (random shapes constructed from sand-filled PVC pipe and fittings) were suspended in the water column inside a visually opaque but acoustically transparent box. For visual inspection, these same types of objects were presented

in air, where the dolphin's echolocation system is ineffective. Our results showed that Elele was, in most cases, nearly perfect in her matching performance and was equally proficient whether making a match from vision to echolocation or from echolocation to vision. These results further attest to the flexibility and extensibility of the dolphin's cognitive system. A sensory integrative ability could be functionally valuable in the wild, as our findings suggest that a target detected by the dolphin through echolocation creates a mental representation (an "image") analogous to that formed through vision, such that the dolphin on drawing within visual range of an ensonified object already knows the visual identity of that object. Physiologically, the integration of the senses in the dolphin might be aided by the adjacency of the auditory and visual cortical areas in the dolphin brain (see Fig. 2.7 in Ridgway, 1986) as contrasted, for example, with their relatively wide separation in the human brain.

Vocal mimicry and octave generalization

In an early study (Richards, Wolz, & Herman, 1984) we demonstrated that the dolphin, Ake, was able to faithfully mimic a wide variety of sounds, preserving both the absolute frequencies of pure tones, the modulation characterisitics of FM sounds, and the pulsatile characteristics of pulsed sounds. She also preserved the durations of these sounds. The sounds to be imitated, called "models," were generated by programmable waveform generators under computer control and were broadcast into Ake's tank though an underwater speaker. Ake then produced an imitation of the model, using her whistle mode, by vocalizing into a hydrophone located adjacent to the speaker. The frequency, time, and intensity characteristics of both the model sound and the accompanying imitation were displayed on a two-channel oscilloscope for visual comparisons, and the sounds themselves were routed to headphones. Judgments of mimicry were made in real time using these tools and later verified through the archived record of sounds. Ake was able to imitate a variety of model sounds on their first appearance, although some imitations had to be "shaped" by reinforcing successively closer approximations to the models. No sound we used failed to be imitated. In our published results, there were two sounds whose contours were faithfully reproduced but in one case at an octave above the model sound, and in the second case at an octave below. As this appeared to be a case of octave generalization, well developed in humans but absent or rare among animals, including birds (e.g., Hulse & Cynx, 1985) and rats and monkeys (D'Amato & Salmon, 1982, 1984), we later conducted a test of this capability (Ralston & Herman, 1989, 1995). Octave generalization is what enables us to recognize tunes played in different keys, or sung in different voices, as the same. The important characteristic preserved by octave generalization is the frequency contour or "shape" of the tune, rather than the absolute frequency values of the notes. In contrast, songbirds seem to attend to the absolute values and fail to show octave generalization (Page, Hulse, & Cynx, 1989). We focused on the dolphin Phoenix for these new studies, as she seemed to be particularly attentive to music played for her at tankside. The experiment asked her to discriminate

between two "tunes", one consisting of a series of four descending notes and the other, a series of four notes all of the same frequency, and to continue to do so regardless of octave shifts up or down. Phoenix successfully passed the test. At the time of this study, the dolphin was the only animal to have demonstrated octave generalization reliably, though in a later study, a rhesus monkey also passed the test (Wright, Rivera, Hulse, Shyan, & Neiworth, 2000). Together, the studies of dolphin vocal mimicry and octave generalization suggest considerable vocal flexibility as well as sensitivity to vocal nuance that may be key components of vocal communication among wild dolphins, especially in the recognition of the individualized whistle contours of others in their group. Studies of wild dolphins have in fact corroborated the vocal mimicry ability of dolphins, particularly their ability to imitate the signature whistles of others, possibly as a means of calling to, or referring to, that dolphin (e.g., Janik, 2000; Janik, Sayigh, & Wells, 2006).

Synchrony, behavioral mimicry and innovation

In the wild, dolphins are naturally synchronous; for example, it is common to see pairs of dolphins surfacing and leaping in unison. Such synchrony may index the close social bonding of the pair and also function to strengthen, or reaffirm, that bonding (e.g., Connor, Smolker, & Bejder, 2006). Such synchronous behavior seemingly requires "locking on" to and anticipating the other's behavior and likely also involves the process of imitation, a complex cognitive act. At our lab we carried out formal studies of behavioral imitation, in particular the ability of a dolphin to copy the motor behaviors of another dolphin as well as those of humans (Xitco, 1988; summarized and extended with additional findings in Herman, 2002). The study of dolphin-to-dolphin imitation was carried out with the dolphins Ake and Phoenix and with a newly acquired pair of young dolphins, the female Elele and the male Hiapo. For both pairs, one or the other dolphin acted as demonstrator and the other as imitator. The roles were entirely reversible. The imitator was taught to observe the behavior of the demonstrator and then imitate it if and only if seeing a particular gesture we glossed as "imitate." Otherwise, it was to perform whatever other behavior was directed gesturally by the trainer. For example, instead of giving the imitate sign after the demonstrator's behavior the trainer might sign, "back-swim." All dolphins reliably carried out imitations if given the imitate gesture, or reliably carried out the alternate behavior if so signaled by the trainer. A complete record of the diversity of behaviors imitated can be found in Xitco (1988) and Herman (2002), and included such things as touching an object with the tail, twirling a Frisbee on the rostrum, or slapping the tail on the water surface. All four dolphins were also able to copy the behaviors of a human demonstrator, who was either in the water next to the imitator or at tankside in the trainer's normal location. The dolphin Elele was especially adroit at imitating human motor behaviors including, for example, "walking" in synchrony with a trainer by standing erect, her tail resting on the tank bottom like a foot, and moving forward by pushing off the tank bottom in a succession of small "hops (Herman, 2002)." The dolphins were also able to imitate the behaviors of a trainer

viewed on a television screen —for example, a trainer nodding his head up and down or raising a leg in the air—as reliably as they imitated behaviors demonstrated by live trainers. Television imitation was not trained but occurred spontaneously, giving further evidence of the dolphin's ability to interpret representations of reality.

As a further adjunct to our studies of synchrony we taught the dolphins another gestural sign we glossed as "tandem." The sign instructed a *pair* of dolphins (Ake and Phoenix or Elele and Hiapo) to carry out *together* whatever behavioral instruction followed the tandem sign. For example, the sequence of gestures glossed as *tandem +back-dive* instructed the pair to execute a backward dive together in close synchrony both in timing and characteristics (see reviews in Herman, 2002, 2006). The dolphins were able to execute a wide variety of synchronized behaviors together in response to such sequences. We had also taught the dolphins another gesture we glossed as "create." In response to this gesture, the dolphins were required to create their own behavior (see Herman, 2006; cf. Pryor, Haag, & O'Reilly, 1969). Any behavior would do, and most behaviors offered were not those that had been specifically trained. The only constraint was that if a second *create* sign were given after completion of the response to the previous gestural sign, the behavior chosen must be different from the previous one. Again, in most cases, this rule was followed and some behavior different from the first was executed. We then challenged the dolphins intellectually with the new sequence *tandem + create* that instructed a pair to again execute a behavior together in close synchrony, but it was to be a behavior of their own choosing. The dolphins understood this instruction and carried out a variety of uninstructed behaviors together. Videotape analyses of examples of their performance did not reveal any clear leadership, but it seemed most likely that imitation was again involved, together perhaps with bodily cues that signaled intent. We also searched for acoustic cues that might relate to the behaviors chosen but could not determine any reliable association. It is obvious that such performances by the dolphin involve complex cognitive operations including, in the least, interpretation, memory for signs, social awareness of the other, imitation, and innovation. The dolphins' demonstrated ability for behavioral (motor) mimicry adds to its already demonstrated ability for vocal mimicry, as described earlier (Richards, Wolz, & Herman, 1984). No other animal species tested, other than humans, has revealed this dual capability at such a deep level, although it is likely that some other cetacean species not yet tested may share this suite of mimicry abilities, possibly to the extent that they share social and communicative pressures similar to those of the bottlenose dolphin.

Social awareness

Behavioral imitation is obviously a strong index of social awareness, i.e. the conscious awareness of others. Imitation of motor acts involves not only the perception of the other's behavior but also the realization of the relation of one's own body parts to those of the other. When the imitation is of the same species,

that relation is obvious, but it is far more challenging in cross-species imitations, as when a dolphin imitates human behaviors. In that case, the dolphin must create analogies, where for example, its tail is analogous to the human leg (the dolphin will raise its tail in the air when the human raises a leg in the air), or "hopping" along on its tail flukes while standing erect analogizes a human walking (Herman, 2002). We tested another form of social awareness with the dolphin, Ake—the understanding of the intent of the human pointing gesture as a reference to a remote scene or object and as an attempt to share our attention to that scene or object with the dolphin (Herman et al., 1999; Pack & Herman, 2006). Few animals seem to attend to the referring function of human pointing. Even chimpanzees or other non-human primates do *not* seem to recognize the import of the human pointing gesture when the object of attention is relatively remote, though they can learn to *use* pointing to refer the human to something of interest to them (Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997). Dogs are an exception, in that they do understand the human pointing gesture (Hare, Call, & Tomasello, 1998; Soproni, Miklosi, Topal, & Csanyi, 2001), but their long history of co-evolution with humans and their domestication have surely contributed to that capability (Hare, Brown, Williamson, & Tomasello, 2002). Dolphins, of course, have been on an evolutionary trajectory radically different from that pursued by humans, yet are able to understand the human pointing gesture even without explicit training. For Ake, a pointing movement toward an object can be substituted for the gestural "name" of that object. For example, in her familiar gestural language with multiple objects floating about in her tank, Ake will swim under the hoop in response to a sequence of two gestures glossed as *hoop + under.* If, instead, we point at the hoop and then sign *under,* the same result will obtain; Ake will swim under the hoop. More generally, sequences consisting of *point at object + action name* were acted on as reliably (i.e., virtually without error) as were sequences consisting of *object name + action name.* Herman et al. (1999) speculated that such understanding might be a derivative of the dolphin's ability to understand echolocation "pointing" by another dolphin, in which both the body- line and the echolocation beam extend toward the target of attention. Xitco and Roitblat (1996) in fact showed that an "eavesdropping" dolphin positioned next to an echolocating dolphin could identify the target that the echolocator was interrogating. In further work on pointing, Pack and Herman (2007) showed that the dolphin understands not only the direction in which the human is pointing (*where*)*,* but also *what* is being pointed at.

Herman et al. (1999) showed that Ake understood not only a point to a single object, but also understood a sequence of *two* points, the first toward the object that was a destination and the second toward the object that was to be taken to that destination. For example, if the trainer points at a surfboard, points at a hoop, and then signs the action gesture glossed as "fetch," Ake will transport the hoop to the surfboard. The sequence of two points, first to the surfboard and then to the hoop, is syntactically the same order as the sequence of two object names in Ake's gestural language, where Ake understands that she is to take the second-named object to the first-named object (an *inverse* grammar—Herman et al., 1984). No training on these point sequences was given to Ake. Rather, she

spontaneously understood the significance of the dual points and their relation to the familiar syntactical rule of her gestural language. Such understanding by the dolphin can best be appreciated as a "conceptual leap" in which the dolphin traverses, "in a single bound", the wide gulf separating the familiar and the unfamiliar.

Self-awareness

"Self-awareness" is best regarded as a multi-faceted concept. In animals, it has most frequently been studied through the mirror self-recognition (MSR) task pioneered by Gallup (1970). Early work restricted MSR capability to the great apes, seeming to point to an evolutionary bottleneck in the development of self-awareness and leading some to conclude that only the great apes (including of course humans) were self-aware (e.g., Povinelli & Prince, 1998). Recent work demonstrating MSR in dolphins (Reiss & Marino, 2001), elephants (Plotnick, de Waal, & Reiss, 2006), and even magpies (Prior, Schwarz, & Güntürkün, 2008) have opened that stricture. However, Gallup (1994, p. 48) has recognized that "there is much more to being self-aware than merely recognizing yourself in a mirror." At my lab we investigated two other forms of self-awareness: awareness of one's own behaviors (summarized in Herman, 2002) and awareness of one's own body parts (Herman, Matus, Herman, Ivancic, & Pack, 2001). Herman (2002; also see Cutting, 1997) described a study in which the dolphin, Phoenix, was taught two gestures that required her to self-select a behavior. One gesture, glossed as *repeat,* asked her to do again whatever behavior she had just performed (cf. Mercado, Murray, Uyeyama, Pack, & Herman, 1998; Mercado, Uyeyama, Pack, & Herman, 1999). A second gesture, glossed as *don't repeat,* asked her to choose a different behavior. However, the behaviors allowed were restricted to a set of five, all taken with respect to a single floating object: *leap over, swim under, touch with the tail, touch with the flipper,* and *mouth (bite).* A trial consisted of a sequence of four instructions, beginning with the trainer using a specific gesture to direct Phoenix to do a particular behavior (*B*) of the five, e.g., leap over the object. After completing the leap and returning to the trainer, Phoenix would be given either the *repeat (R)* or the *don't repeat (NR)* gesture. In the latter case, she would have to choose and execute any of the four remaining behaviors. This sequence, a behavior followed by either the *repeat* or *don't repeat* gesture, would occur again twice more, so that a four-item sequence might be, for example, *B—R—NR—R.* All possible three-way permutations of *R* and *NR* were tested multiple times. Phoenix successfully completed approximately 80% of the 160 four-item sequences given her (Cutting, 1997). To complete a sequence successfully, Phoenix had to retain in working memory a representation of the behavior just completed, then process semantically the succeeding gestural instruction to repeat or don't repeat, and finally and conditionally, self-select either the same or a different behavior. Clearly, the process required that she remain consciously aware of her own recent behavior, and update it as each successive behavior was completed. Kinesthetic cues were excluded by the requirement that after each behavior Phoenix must

station herself on a target affixed to the tank wall and remain there until given the next gestural instruction. Gallagher (2000), in a seminal article, referred to two components of conscious awareness of one's own self-directed actions: a sense of *agency* ("I am the author or cause of the movement") and a sense of *ownership* ("I am the one that is moving"). The results of our study suggest that implicit in Phoenix's self-directed actions were these two components of consciousness of one's own actions as explicated by Gallagher.

The concept of a "body image" refers to a conscious representational system that includes both semantic and topographical knowledge of one's own body parts (Gallagher, 1986; Kinsbourne, 1995). For example, we can point to our knee if asked to do so, an example of conscious topographical knowledge of our body parts as well as semantic knowledge of the spoken word "knee". However, with certain lesions of the left parietal lobe, topographical knowledge may be lost, a condition called autotopagnosia. Here, the patient understands "knee" but cannot locate it (Ogden, 1985). The body image is disrupted. We carried out a study to examine Elele's semantic and topographical knowledge of her body parts, as well as her conscious control of them, as a test of another dimension of self-awareness (Herman et al., 2001). We assigned specific gestures to nine of her body parts (rostrum, mouth, melon, pectoral fin, dorsal fin, side, belly, genitals, and tail). We then constructed sentence frames expressed either as *body-part name + action name* (the action is either *shake* or *display; e.g., rostrum + shake,* means shake your rostrum) or as *object name + body-part name +action name* (the action is either *touch* or *toss; e.g., ball + pectoral fin + toss,* means toss the ball using your pectoral fin). Prior to beginning this study, Elele was already familiar with a gestural language similar to that given Ake, but had not been specifically tutored previously in the sentence frame, *object name + body-part name + action name*. This enabled us to construct many sentences (instructions) that were new to her experience. For example, in response to the novel instruction *Frisbee + dorsal fin + touch,* Elele swam to the floating Frisbee, stopped, and then twisting sideways carefully laid her dorsal fin on top of the Frisbee. As another example, in response to the instruction *surfboard + genitals + toss* she swam on her back to the surfboard, continued halfway under it, and then with a vigorous upward thrust of her pelvic region tossed the surfboard aloft. The probability that Elele would successfully carry out three-item sentences like these by chance alone was only 0.11 (Herman et al., 2001, endnote). Her correct performance for 50 different sequences ending in *toss* was 68% and for 60 different sequences ending in *touch,* it was 80%. Elele's responses thus revealed both semantic and topographical knowledge of her "named" body parts and gave evidence of her conscious awareness of those body parts, and of her ability to conceive of them as objects with which she could carry out conscious acts, incorporating both a sense of agency and a sense of ownership (Gallagher, 2000).

Discussion and Conclusions

The suite of laboratory studies summarized here, carried out over a 34-year period, portray the broad scope of dolphin cognitive characteristics and attest to this species' wide-ranging intellectual competencies. Of course it is not human-level intellect, but nevertheless an intellect that meets with some of the hallmarks or offshoots of human intelligence: the mental representation and manipulation of symbol systems and the understanding of symbols as references to tangible objects; the extraction of general rules or concepts from exemplars; an ability to interpret and act on images representing reality as effectively as interpreting and acting on real-world events; innovation of behaviors and strategies in arbitrary situations; social perception (an awareness of the behaviors of others in sufficient detail to closely imitate them); a conceptual understanding of behavioral synchrony through an eliciting symbol requesting synchrony; sensitivity to the referents of the indicating pointing gestures of humans; self perception (conscious awareness of and mental representations of self-initiated behaviors); an understanding of symbolic references to one's own body parts, including an ability to conceive of these body-parts as objects that can be consciously attended to and utilized in novel ways as instructed by symbols. It is significant that the contexts in which these dolphin capabilities were extracted were within laboratory paradigms that access intellectual challenges that are foreign to wild dolphins. That the dolphin is able to operate so well within these paradigms is a measure of a flexible mind, a mind able to understand, adapt, and function effectively in worlds other than that in which it evolved. The studies reviewed should put to rest vigorous denials of intellect (Manger, 2006; cf. Marino et al., 2007) as well as assertions that the large brain is primarily an acoustic (echolocation) processing machine with only marginal capacity for complex cognitive processing (e.g., Wood, 1973).

Although the suite of behavioral studies carried out at my Kewalo Basin laboratory are the most extensive conducted into the mind of the dolphin, there are several excellent studies by others that supplement, or extend, our findings on dolphin intellectual breadth and depth. Included here are the demonstrations of meta-cognition (knowledge of one's own knowledge) by Smith et al. (1995); numeric ability (discriminating lesser and greater among two different ordinal values) (Kilian, Sevgi, von Fersen, & Güntürkün, 2003; Jaakkola, Fellner, Erb, Rodriguez, & Guarino, 2005); the detection of symmetry in displays (von Fersen, Manos, Galdowski, & Roitblat, 1992); and the dolphin's *use* of pointing to gain the attention of another (Xitco, Gory, & Kuczaj, 2001, 2004*)*, in contrast to its *understanding* of human pointing (Herman et al., 1999).

How this intellect is tapped by wild dolphins to meet the challenges of its natural world has just begun to be uncovered, but surely managing the intricacies of a complex social world is a prime area of application that places strong demands on intelligence (Herman, 1980; also see more general discussions of social intelligence in Whiten & Byrne, 1997). In the wild, there are examples that suggest the application of considerable social intelligence, including the learning, using, and mimicking of signature whistles (Janik, 2000; Janik, Sayigh, & Wells, 2006);

organizing synchronous and collaborative feeding (e.g., Duffy-Echevarria, Connor, & St. Aubin, 2007) or reproductive behaviors (Connor, 2007; Connor et al., 2006); teaching of a foraging strategy to offspring (Bender, Herzing, & Bjorklund, 2009; Rendell & Whitehead, 2001); and vertical transmission (from mother to offspring) of tool use (Krützen et al., 2005). It is not difficult to see how such capabilities and behaviors could spring from some of the fundamental laboratory-demonstrated capabilities of dolphins for remembering, learning, concept formation, representation, referential understanding, vocal and behavioral imitation, sensory integration, and conscious awareness of self and others.

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