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Dolphin Cognition: Representations and Processes in Memory and Perception

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Many people agree that dolphins are sentient beings, but few would claim to know what being a dolphin is like. From a psychological perspective, a dolphin's experiences are a function of its mental capacities, especially those processes that relate to memories, percepts, thoughts, and emotions. This paper reviews what is currently known about dolphins' cognitive abilities, focusing on how they perceive and remember events. Experiments with captive dolphins show that they can flexibly access memories of past events and construct sophisticated representations of the world and themselves. How dolphins act and what they remember about their actions impacts what they perceive, which in turn guides their thoughts and decisions. Many of the actions and events that shape a dolphin's experience are internally generated and monitored. Knowing how dolphins perceive temporal patterns, objects, emotions, actions, agents, scenes, messages, and motivations can help clarify what dolphins' thoughts, memories, and experiences are like. Only by giving dolphins a way to show what they know, or can learn, can we hope to understand what goes on inside their heads.

Why might anyone imagine that a dolphin[1] engages in mental processes that are substantially different from those of a sea star? Stories of wild dolphins interacting with people (Aristotle, 1991; Dudzinski, Frohoff, & Crane, 1995; Frohoff & Packard, 1995; Lockyer, 1990; Lockyer & Morris, 1986; Muller & Bossley, 2002), coordinating their actions with those of humans (Busnel, 1973; Neil, 2002; Perelberg & Schuster, 2009; Pryor, Lindbergh, Lindbergh, & Milano, 1990), and even saving humans in distress (Dudzinski & Frohoff, 2008) certainly provoke some intuitive feeling that dolphins are sentient and intelligent. The size and complexity of the dolphin's central nervous system are also suggestive (Marino et al., 2007, 2008). The strongest indication that something more is going on inside the dolphin's head comes, however, from long-term studies of captive animals (reviewed by Herman, 1980, 1986, 2006; Kuczaj, Gory, & Xitco, 2009; Kuczaj & Walker, 2006; Marino et al., 2007; Reiss, McCowan, & Marino, 1997).

[1]Throughout the paper we use the term "dolphin" to refer to the bottlenose dolphin, *Tursiops truncatus*, unless otherwise noted. This usage should not be misconstrued as suggesting that all delphinid species are comparable to bottlenose dolphins or that bottlenose dolphins are the only delphinids possessing the capacities discussed. It merely reflects the prevalence of experiments with this species relative to others.

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Findings from experimental studies of dolphin cognition have greatly increased public interest in their protection, to the point where some organizations now argue that it is unethical to maintain dolphins in captivity (Rose, Parsons, & Farinato, 2009). Often, these organizations cite the results of dolphin cognition experiments as evidence that dolphins are intellectually advanced relative to many other species of animals, and are therefore entitled to more consideration. The Humane Society of the United States and the World Society for the Protection of Animals, in particular, argue that there is no justification for holding dolphins in captivity, and encourage people to, "start looking at this issue from the marine mammals' point of view instead of our own" (Anonymous, 2010). This raises the question of what the dolphin's point of view might be like. What does a dolphin think or feel or perceive? Is it similar to what a toddler or bonobo might experience? Or, are dolphins' experiences radically different from those of any terrestrial mammal? Is there any sense in which humans can know what it is like to be a dolphin?

The species-dependent nature of an organism's perceptual experiences (or *Umwelt)* can be loosely inferred from variations in behavior and physiology across species (Delfour, 2006; Jerison, 1986; von Uexkull, 1982, 1992), but cannot be directly observed. The kinds of events that are most salient and memorable for dolphins (see Fig. 1) may differ significantly from the ones that are relevant for humans (Jerison, 1986). Although we may never know precisely what being a dolphin is subjectively like (Gould, 1996; Nagel, 1974), we can still gain a clearer view of what dolphins' mental experiences are like through carefully designed experiments. For example, we now know that dolphins can recognize distant objects without being able to see them (Norris, Prescott, Asa-Dorian, & Perkins, 1961). Knowing what dolphins experience is fundamental to making informed decisions about how they should be treated (Lea, 2001).

Here, we consider what is currently known about the mental capacities of dolphins, focusing on what their memories, percepts, and experiences are like. In particular, we review experimental evidence on their capacity to remember past actions, echoically recognize objects, and selectively attend to recurring perceptual patterns (e.g., auditory rhythms). We argue that although past experimental studies provide compelling evidence that dolphins have mental abilities, the findings to date are insufficient for drawing any firm conclusions about what dolphins' psychological lives are like.

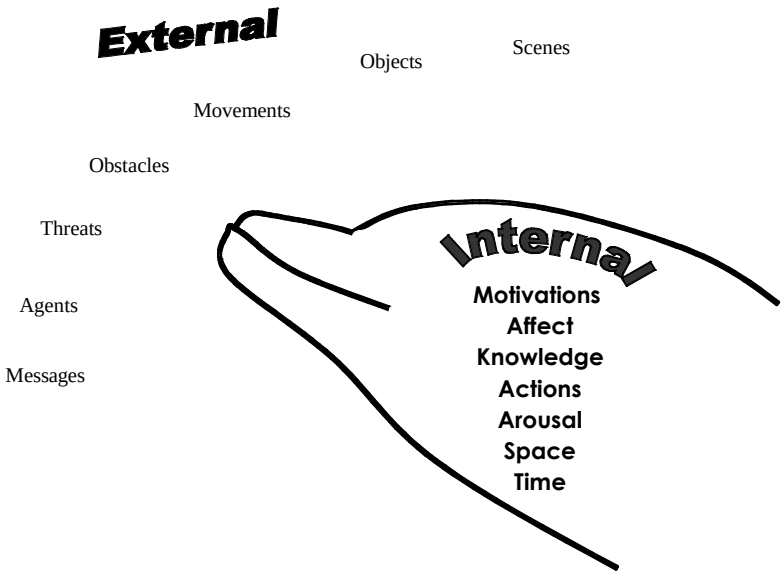

Figure 1. Hypothetical dolphin *Umwelt*. A dolphin's experiences arise from its mental representations of internal and external events. Memories, percepts, and thoughts are essential components of this experience.

Remembering Events

"To know… is to be able to perform, and to remember is to be able to reproduce a performance." - Edelman, 1989, p. 266

A dolphin's experiences depend at least in part on their memories: what they know and remember about the world and themselves. It is clear that dolphins can retain memories of learned skills (called procedural memories) for many years and that they can maintain representations associated with recent events (a process often referred to as working memory) for minutes (Herman, 1980). Less is known about dolphins' long-term memories for information about the world or themselves (called semantic memories), or for events that they have personally experienced (called episodic memory). The extent to which dolphins can voluntarily access memories is also unclear (Mercado & Murray, 1999). What is clear is that memory formation and use are foundational to all cognitive processes of dolphins (Herman, 1980), and that the extent to which human actions can impact the psychological lives of dolphins depends greatly on dolphins' memory abilities (Lea, 2001).

Of particular importance when assessing what dolphins may experience is identifying what they recall of past events and what they can anticipate. Such mental processes are considered to be distinct from the unconscious expression of memories, referred to as implicit memory or conditioned responding (see Nelson, Schreiber, & Mcevoy, 1992; Rugg, Mark, Walla, Schloerscheidt, Birch, & Allan, 1998). Memory recall (which is sometimes called explicit retrieval) generally involves the active re-establishment of mental states that overlap with ones that previously occurred, as well as conscious awareness of those states (Badgaiyan &

Posner, 1997; Reder, Park, & Kieffaber, 2009; Turk-Browne, Yi, & Chun, 2006). In other words, recall is typically associated with voluntary effort followed by a subjective experience of remembering. You, something, or someone provokes you to "think back" and in response you imagine what happened in the past. Essentially, remembering is a particular kind of thinking in which an organism models events that were (or might have been) experienced in the past.

What do dolphins recall?

Experimental studies established early on that dolphins can retain information about past events in ways that are similar to those of many terrestrial species, including humans (Beach & Herman, 1972; Forestell & Herman, 1988; Herman, 1980; Herman & Arbeit, 1973; Herman, Beach, Pepper, & Stalling, 1969; Herman & Gordon, 1974; Herman & Thompson, 1982; Thompson & Herman, 1981). Like other mammals, they show an increased ability to recognize transient events that occurred recently (Herman & Forestell, 1985; Thompson & Herman, 1977), as well as the ability to associate a wide range of sensory stimuli with arbitrary actions and objects (e.g., Delfour & Marten, 2005; Herman, Richards, & Wolz, 1984; Reiss & McCowan, 1993). It is important to note, however, that findings from these experiments do not provide clear evidence that dolphins are remembering events. Neither learning to associate two events (including actions and observations of objects), nor differentiating familiar events from novel ones, requires recall.

For a dolphin to demonstrate that it is recalling items from memory, the dolphin must voluntarily act in some way that makes it possible to compare its memories with its past experiences. For humans, this action would usually involve producing sentences, the contents of which could be compared to records of an individual's experiences. There is nothing magical about sentences, however. A professional mime could probably convey her memories of her experiences almost as effectively, albeit in less detail (Suddendorf & Busby, 2003). The power of reenactments as a window into an individual's memories has been known for some time (Bandura, 1969; Meltzoff, 1995; Piaget, 1952), but only recently have reenactments explicitly been used to explore an individual's capacity to remember (Bauer, 2006; Heimann & Meltzoff, 1996). For example, observations of deferred imitation in infants suggest that they can recall action sequences at least a day after they have observed them (Heimann & Meltzoff, 1996). By reenacting observed sequences, infants provide evidence not only of their memories of observed actions, but also that their visual representations are linked to the motor representations required to recreate them. Dolphins have shown deferred imitation capacities similar to those of infants (Bauer & Harley, 2001; Bauer & Johnson, 1994; Fellner, Bauer, & Harley, 2006; Herman, 2002; Kuczaj & Yeater, 2006; Pryor, 1975; Tayler & Saayman, 1973; Xitco, 1988), although the reliability of recall after days or weeks is not as well established. Deferred imitation might seem to provide clear evidence of recall, but many instances of apparent imitation do not require the imitator to recollect anything (Marler, 1997; Whiten, 1992). One way

that comparative researchers have addressed this limitation is by training individuals to imitate novel "nonsense" actions on command (Custance, Whiten, & Bard, 1995; Hayes & Hayes, 1952; Xitco, 1988). Chimpanzees have learned to imitate actions in response to verbal instructions, whereas dolphins learned to do this when given a gestural instruction (called MIMIC). By instructing dolphins to imitate actions that they would be highly unlikely to spontaneously produce, researchers have established that dolphins can reproduce actions that they have recently observed. The ability of dolphins to follow the MIMIC instruction in various contexts shows that they can convert percepts of observed acts (or heard sounds; Kuczaj, Solangi, Hoffland, & Romagnoli, 2008; Pryor, 1975; Reiss & McCowan, 1993; Richards, Wolz, & Herman, 1984) into action representations sufficiently detailed to enable them to recreate the events that they have observed.

Most experimental work on dolphins' memories for events has examined their memories for external events, especially sounds and sights (including the actions of others). Much less is known about their memories of internal events, such as those associated with feeling emotions or producing actions[2] (see Fig. 1). Dolphins' memories for their own actions typically must be based on representations of internal events, because few external cues reliably discriminate a dolphin's own past actions. The ability of dolphins to avoid repeating certain actions provides some hints that they do remember what they have done in the recent past. This capacity was first documented at Sea Life Park in Hawaii (Pryor, 1975; Pryor, Haag, & O'Reilly, 1969). There, two rough-toothed dolphins (*Steno bredanensis*) learned to sequentially produce novel responses in specific training contexts[3]. Later, several bottlenose dolphins at the Kewalo Basin Marine Mammal Laboratory (KBMML) were trained to self-select arbitrary actions on command (glossed as the CREATE instruction), while avoiding repetition of actions (Braslau-Schneck, 1994). A dolphin could successfully learn to "innovate" actions either by increasing the variety of its actions, or by actively avoiding actions it recently performed (Neuringer, 2004). The latter strategy requires some memory for actions performed in the recent past, whereas the former does not. Unfortunately, past studies of creativity in dolphins were not designed to distinguish between these two possible sources of variability, so it remains unclear to what extent these dolphins used recent memories to select their actions.

Subsequent experiments in which dolphins were taught to respond to a specific gestural instruction (called ANY) by producing one of five possible actions provide stronger evidence that dolphins can keep track of what they have been doing recently (Cutting, 1997; Taylor, 1995). The dolphins were required not to repeat the same action offered the last time they received the ANY instruction.

[2]This bias in emphasis is not specific to studies of dolphin memory. For example, much less is known about motor memory in humans than is known about memories for words.

[3]Undoubtedly, dolphins in the wild often act in ways that are spontaneous and novel, but it is exceedingly difficult to verify that such actions are not simply infrequently expressed species-typical behaviors. Man-made environments, however, give dolphins the opportunity to act in ways that they cannot in the wild. For example, it is fairly certain that coming out of the water and balancing on a tank wall is not an action that dolphins perform in the wild.

Because of this constraint, only four actions were a valid option in any trial other than the first. The four actions that were valid were stable across trials, effectively ruling out increased variability as an account of the dolphins' performance. The dolphins' ability to self-select actions following the ANY command still does not provide strong evidence that the dolphins remembered their recent actions, however. An alternative possibility is that the dolphins used differences in action-dependent physiological states to select their actions. For example, a dolphin that had just jumped might feel more winded than one that had just spit a stream of water. In principle, a dolphin could learn to only spit after receiving the ANY command when it felt winded, and to only jump when it did not. Such contingencies could enable the dolphin to produce variable sequences in response to a single instruction, while avoiding repeating the most recent action, even if the dolphin had no memory of its recent actions. Variability in physiological states could account for variability in the sequence of actions produced as well as errors. In other words, the dolphins could perform correctly in response to the ANY instruction either by discriminating current physical states or by recalling past actions.

How do dolphins represent their own actions?

The strongest evidence that dolphins can remember their recent actions comes from experiments in which they were required to repeat actions on command (Cutting, 1997; Mercado, Murray, Uyeyama, Pack, & Herman, 1998; Mercado, Uyeyama, Pack, & Herman, 1999). Dolphins often repeat actions in the wild; for example, jumping in a similar manner multiple times in a row. Such repetition provides no indication of whether the jumping dolphin remembers that it performed two or three similar jumps in the recent past. By placing the act of repeating under stimulus control (i.e., associating it with a specific gesture, called the REPEAT instruction), however, one can reveal what a dolphin remembers about its recent actions and establish the dolphin's ability to voluntarily access its memories of events.

Four dolphins at KBMML were trained to repeat actions on command[4] (Cutting, 1997; Mercado et al., 1998). Two dolphins, Elele and Hiapo, were the first to be formally tested with the REPEAT instruction. Elele proved to be more proficient at repeating her actions than Hiapo throughout formal testing, correctly repeating most (34 of 40) of the different actions she was tested with more often than would be expected by chance, and rarely repeating an action unless she was instructed to do so (Mercado et al., 1998). Hiapo correctly repeated 27 of the 40

[4]Training progressed over several years. One might conclude from this that the repeating task was difficult for the dolphins to learn. A more likely alternative, however, is that the extensive training reflected the inability of trainers to convey to the dolphins what it was that they wanted them to do. Anecdotally, after more than a year of training, the first dolphin to consistently respond correctly to the REPEAT instruction (named Elele), went from responding inconsistently to repeating confidently within a single training session (E. Mercado III, personal observation). By all indications, once Elele discovered the correct response to the instruction, she had little difficulty implementing it.

different actions, which was many more than expected given his performance prior to testing[5]. The actions that the dolphins successfully repeated included relatively simple actions such as somersaulting and jumping, as well as more complex actions such as jumping belly-up with mouth open and fins waving, or swimming in a circle while spinning with an open mouth. They also were able to successfully repeat novel actions that they learned to perform after testing with the REPEAT instruction began, actions that they produced in response to the REPEAT instruction, and self-selected actions that they produced in response to the CREATE instruction.

In a later study, Elele also showed some ability to repeat actions performed with specified objects. Elele had previously learned that specific gestures were associated with specific classes of objects (Herman, Matus, Herman, Ivancic, & Pack, 2001). This made it possible to instruct her to jump specifically over a ball, or a basket, or a Frisbee, when all of these objects were present in the tank. In each case, the instructed action was the same, but the designated object was different. To repeat correctly in this context, Elele had to not only remember her actions, but also something about where she was performing the act or about the object or instructions she had just seen. In other words, she had to remember a combination of both internal and external events to successfully reenact the most recent episode. During testing, Elele correctly repeated her previous actions to the correct object in 30 of 72 trials (42%) and correctly repeated 10 of the 18 object-action sequences tested, all with accuracy greater than expected by chance (Mercado et al., 1999). Most errors consisted of the correct action being performed to the incorrect object. Interestingly, patterns of errors during Elele's attempts at repeating object-action sequences suggest that her memories of the body part that she used to perform an action may have been even more resilient than her memories of specific actions (see also, Herman et al., 2001). Given that none of her prior training with the REPEAT instruction involved performing actions to specified objects, her rapid generalization of this instruction to object-action sequences indicates that she naturally constructed multimodal representations of ongoing events and had a flexible capacity to remember specific details of those events.

When do dolphins remember actions?

The repeating task can be viewed as a special case of a widely used test of working memory known as delayed matching-to-sample (MTS). In the traditional

[5]During his individual training sessions, Hiapo initially showed little ability to repeat actions on command. However, in a training session conducted after Elele learned the REPEAT instruction, in which both he and Elele were informally tested with this instruction in tandem (i.e., one instruction was given to both dolphins simultaneously), he responded correctly several times to the repeat instruction. It appeared that Hiapo was following Elele's lead in selecting the actions to perform during this joint training session. When Hiapo was later tested alone, however, he continued to respond correctly to the REPEAT instruction for several different actions. This outcome is similar to earlier reports of dolphins learning actions by performing them in unison with an experienced dolphin, or through observation alone (Defran & Pryor, 1980; Herman, 1980; Pryor, 1973), except that in this case, Hiapo could not visually observe how Elele selected the correct action.

MTS task, the organism is first shown a visual stimulus (the sample) and then subsequently shown two or more additional visual stimuli, one of which is the same as the initial stimulus. The correct response is for the subject to choose the alternative that matches the sample. In the delayed MTS task, the sample is removed before the alternatives are presented, requiring the subject to either retain some information about the sample in memory (called retrospective coding) or to anticipate an appropriate response (called prospective coding; Honig & Thompson, 1982; Roitblat, 1993; Wasserman, 1986). For a dolphin given the REPEAT instruction, the "sample" is some subset of the events experienced prior to the REPEAT gesture, and the alternatives are the set of possible actions the dolphins might perform in response to the REPEAT instruction. Put another way, Elele responded to the instruction by selecting an action that in some way matched her representation of her earlier experiences. Elele's immediate use of the REPEAT instruction with novel actions, self-selected actions, and actions performed to specified objects, strongly suggests that she used a multimodal, episodic representation of recent events to direct her actions in response to the REPEAT instruction (see Baddeley, 2000). This episodic representation appeared to contain a combination of retrospective and prospective codes for both internal and external events, with greater emphasis on internal events associated with performing actions (Mercado et al., 1998, 1999).

Currently, there is debate about whether animals other than humans remember anything about their past experiences or can anticipate future events (Roberts, 2002; Schacter, Addis, & Buckner, 2007). In particular, it has been suggested that only humans have the ability to mentally travel through time (Roberts & Feeney, 2009; Suddendorf & Busby, 2003; Tulving, 2002). Describing recall of episodes as a process of mental time travel is a misleading metaphor, because memories that are recalled need not correspond to events that were (or even could be) experienced. For example, it is relatively easy to implant false memories of personal experiences that never occurred (Loftus, 1997; Roediger, Jacoby, & McDermott, 1996). Others have argued that memories must be retained for a sufficient duration to count as memories for episodes (Schwartz, Hoffman, & Evans, 2005). No criteria have been established, however, for determining how long a memory has to persist to qualify as episodic. Although it is not known how long dolphins can remember what they have experienced, or how often they do so, their ability to learn and flexibly apply the REPEAT instruction makes it clear that when they do recall the past, their personal actions are a salient component of those memories.

When dolphins respond to instructions associated with specific motor acts, they may use similar action representations and mental processes to those they use to imitate themselves. Specifically, a dolphin's observations of a particular gestural instruction may act as a cue for recalling the motor representations corresponding to the to-be-performed act. Consistent with this hypothesis, the kinds of actions that an individual dolphin offers in response to essentially identical instructions can vary considerably in location, number, style, and quality. A dolphin that receives an instruction to jump might jump low or high, one time or many times

(or not at all); it might swim around the tank several times before jumping or may make a small leap as it leaves the trainer. Furthermore, dolphins can delay their responses to a given instruction for as long as a minute when instructed to do so (Pryor, 1975). The flexibility and range of dolphins' actions after receiving stereotyped instructions seem more consistent with actions dynamically constructed from a large repertoire than with conditioned responses (analogous to the difference between basketball players shooting during play versus shooting free throws). Just as a dolphin's own actions can generate representations of internal events that enable it to recreate those actions, so too may gestural instructions that it has learned to associate with those actions.

Overall, experimental studies of memory in captive dolphins suggest that it is relatively easy for dolphins to remember their own actions, including movements of particular body parts. This suggests that dolphins may also represent observed actions in terms of the motor acts they themselves would use to reproduce the action (a type of prospective coding). In that case, a dolphin given the MIMIC instruction could correctly follow this instruction using the same mental processes of recall as a dolphin given the REPEAT instruction. The only difference would be that in the imitation task, the dolphin would recall an action she had just envisioned performing, rather than an action she had just performed. The use of common representational mechanisms for both imitation and self-imitation previously has been proposed for human infants (Piaget, 1951; Rochat, 2002) and adult primates (Premack & Premack, 2003; Wilson & Knoblich, 2005). From this perspective, the dolphin's imitation of both self and others is an attempt to simulate the past (i.e., recreate previous mental experiences by remembering and reenacting events) rather than an attempt to copy models (Premack & Premack, 2003). Being able to simulate the past is particularly advantageous when there is a need to anticipate the future (Hesslow, 2002; Schacter et al., 2007). Recent studies of brain function show that many of the mechanisms underlying recall also may contribute to action planning (Clark, 1997; Gallese, 2000; Hopfield, 2010). This suggests that dolphins may remember their recent (and possibly not so recent) actions when those actions are relevant to predicting and controlling what might happen in the future.

Modeling Objects

"Dolphin echolocation is one of the most sophisticated cognitive processes that have been studied." – Roitblat, 2002, p. 183

Dolphins mentally represent not only their own actions and the actions of others, but also the consequences of those actions. Perhaps the best example of this is their use of echolocation. Echolocation is often portrayed as a sophisticated expansion of auditory capacity, but it probably would be more accurate to described echolocation as a kind of self-communication or "autocommunication" (Bradbury & Vehrencamp, 1998; Frazer & Mercado, 2000). Echolocating dolphins provide themselves and others with information about the world around them

(Branstetter & Mercado, 2006; Xitco & Roitblat, 1996). An echolocating dolphin's vocal and motor actions generate a dynamic stream of auditory inputs, from which the dolphin must extract information about objects, scenes, or agents. Laboratory studies examining dolphins' abilities to recognize objects through echolocation suggest that their mental representations of such sound streams are quite sophisticated and flexible.

How do dolphins echolocate?

Dolphins echolocate by emitting very short (40-70 μs), high intensity (170-225 dB re 1 μPa) clicks and listening to the resulting echoes (see Au & Hastings, 2008, for a recent review). An echolocating dolphin sends out approximately 5 – 150 clicks to investigate an object over a period of several seconds (the interclick interval is approximately 15-20 ms plus the round-trip travel time of the sound; Au, 1993). The amplitude and frequency content of clicks produced by an individual dolphin are not fixed. Clicks vary between and within individuals, and dolphins can flexibly modify their clicks based on environmental and task demands. Different dolphins produce clicks that cluster around different peak frequencies (Houser et al., 2005), and will use different click types as well as different strategies depending on the particular task they are performing (Au, 1993; Houser, Helweg, & Moore, 1999).

Dolphins in noisy environments tend to produce high intensity clicks with higher peak frequencies (Au, Floyd, Penner, & Murchison, 1974). When faced with a difficult task, dolphins tend to increase the number of clicks they emit (e.g., when masking noise is increased; Au & Penner, 1981). One dolphin performing an object discrimination task produced more clicks to the object he was most likely to choose incorrectly, suggesting that he made more clicks for objects that were difficult to identify (Roitblat, Penner, & Nachtigall, 1990). In addition, individuals appear to change their clicks over time even when performing the same task. One female dolphin's clicks were recorded as she performed the same echolocation task in two experiments separated by five years (Ibsen, Au, Nachtigall, DeLong, & Breese, 2007). The peak, frequency, source level, and spectrum shape of her clicks significantly changed from the first experiment to the second. Nevertheless, the dolphin performed the task with the same level of success. Possibly, the dolphin suffered from age-related high frequency hearing loss and changed her click content to maximize the useful information she could receive and to minimize frequencies no longer audible to her.

This rich variation in click structure and quantity within and across individuals highlights the fact that dolphin echolocation is an active process. Dolphins control their acts to extract information from the world around them – they shape their echoic percepts by controlling the timing and properties of the clicks they produce, as well as the trajectory and speed of their head and body

movements[6]. For humans, an analogous situation would be using the active sense of touch to explore an object. When you reach out to feel an object, you control the movements of your fingers to gather information about different object features. For example, if you want to know the shape of the object, you may move your fingers along the outside contour of the object to feel its different component parts. If you want to know the texture or hardness of the object, you might press your fingers firmly on the object, or brush your fingers across its surface. Each of your motions provides specific information about certain object properties, enabling you to form a mental representation of the object. Similarly, by continuously varying the features of their click trains, dolphins can more effectively simulate and investigate their surroundings.

Why do dolphins echolocate and why do they generate multiple echoes?

Dolphins echolocate to construct a representation of the world. Echolocation is particularly useful when other sensory systems are not able to provide them with relevant information (e.g., in the dark or turbulent water where visual cues are not available, or to explore far away objects inaccessible to touch), or for supplementing information from other sensory systems (Harley, Roitblat, & Nachtigall, 1996). Since dolphins can perceive very fine changes in echo amplitude, frequency, and duration (Au, Moore, & Pawloski, 1988; Evans, 1973; Thompson & Herman, 1975), echolocation is ideal for revealing subtle details of objects. When information from multiple sensory systems is available (e.g., in bright clear water), dolphins may prefer to use echolocation because it informs them about certain object features (e.g., material, internal structure) that they might not otherwise perceive using vision (Au, 1993).

Dolphins' representations of objects appear to be more informative when they are constructed using multiple echoes. In one study, the amount of noise was varied across trials to control the number of echoes a dolphin could use for detection (Altes, Dankiewicz, Moore, & Helweg, 2003). The dolphin's ability to detect the echoes was directly related to the number of echoes it was permitted to use. Dolphins often encounter noisy environments where relevant echoes may be masked by echoes from other objects in the background (e.g., a fish swimming through coral). In these situations, receiving multiple echoes increases a dolphin's chance of detecting and identifying objects and interpreting auditory scenes.

In MTS tasks in which a dolphin must discriminate among objects, it appears that they integrate information across multiple successive echoes (DeLong, Au, Lemonds, Harley, & Roitblat, 2006; Roitblat, et al., 1990). Dolphins emit clicks in a beam that spans only about ten degrees in the horizontal and vertical planes (Au, 1993). This means that each echo gives the dolphin information about only a portion of its surroundings from a certain orientation. The echoes from an object can vary considerably depending on the angle from which it is acoustically inspected. In fact, echoes from different aspects of a single object can vary more

[6]Some cetaceans, such as belugas, may also be able to control melon shape to affect how clicks are transmitted.

from each other than do echoes from different objects (DeLong et al., 2006). So, if a dolphin wants to mentally represent the shape of an object using echolocation, it must gather multiple echoes from multiple aspects of the object. This is similar to the problem faced by a person attempting to identify the shape of an object using only touch. For example, if a person is blindfolded, asked to feel a coffee cup, and then later asked to draw the cup (with the blindfold removed and the coffee cup now out of sight), a single touch to the bottom of the cup will not enable the person to draw it. Instead, the person must touch the cup multiple times on the smooth sides, on the handle, across the top, and on the bottom in order to accurately represent and draw the cup. Similarly, dolphins must receive echoes from multiple surfaces of an object while emitting a stream of clicks if they want to be able to accurately represent the whole object.

Dolphins may be able to identify some novel objects from inspecting a randomly-selected orientation of the object, even if they have never ensonified the entire object. In a study by Au and Turl (1991), a dolphin learned to discriminate among cylinders made of different materials (e.g., aluminum, coral rock) at three orientations (0°, 45°, 90°). When later tested at novel orientations (15°, 30°, 60°, 75°), the dolphin continued to discriminate among the stimuli with very high accuracy, indicating that for a simple material discrimination there were aspect-independent cues. A dolphin also successfully discriminated familiar objects (a cube, rectangular prism, and pyramid) that were free to rotate, thus varying the aspect of the objects facing the dolphin (Helweg, Roitblat, Nachtigall, & Hautus, 1996). Dolphins need to be tested with a wider variety of objects and contexts to determine when and how they can recognize objects independently of the angle of inspection.

When do dolphins echolocate?

In captivity, dolphins performing echolocation tasks consistently emit streams of clicks towards objects to find the right answer and obtain their fish rewards. However, we do not know when dolphins in the wild choose to echolocate. Echolocation may incur costs like advertising the dolphin's presence to prey and predators. It may be advantageous to remain silent to detect prey that can perceive ultrasonic sounds like the American shad (Mann, Lu, & Popper, 1997), or to avoid predators which can also hear ultrasonic frequencies such as bull sharks (Krizler & Wood, 1961). In cases where other agents in the dolphin's environment can be alerted to their presence if they vocalize, an experienced dolphin would be wise to remain silent and use a different means to find food. Dolphins in Sarasota Bay appear to use passive listening to detect soniferous fish, and then use echolocation to pursue and capture the fish (Gannon, Barros, Nowacek, Read, Waples, & Wells, 2005). Gannon and colleagues found that when dolphins heard calls of prey fish, they turned towards the sound source and began echolocating, whereas when they heard snapping shrimp (not a prey item), they did not. These results imply that dolphins do not always use echolocation to detect prey.

Dolphins may reserve echolocation for certain situations, such as navigating a new environment, capturing rapidly moving prey, investigating a novel object, or discriminating among objects of interest like different fish. It is currently unknown whether dolphins can discriminate between different fish species using only echolocation. Au and colleagues (2007) recorded echoes from live fish, including sea bass (*Dicentrarchus labras)*, pollack (*Pollachius pollachius)*, grey mullet (*Chelon labrosus)*, and Atlantic cod (*Gadus morhua*). Au, Branstetter, Benoit-Bird, and Kastelein (2009) did a qualitative analysis of fish echoes and found that each fish species produced a distinctive pattern of echo amplitude and frequency changes as a function of orientation. They also analyzed echoes using a cochlear model that simulates how a dolphin's ear responds to echoes. The results of these auditory simulations suggested that there should be sufficient acoustic features available to dolphins to distinguish the four species of fish. However, we do not know which specific features a dolphin might actually use to discriminate among the fish. When human listeners were presented with these same fish echoes, they were able to discriminate among the four species using multiple auditory features (DeLong, Benoit-Bird, Au, & Kannyo, 2009). Dolphins in the wild probably use multiple cues (echoic, visual, tactile), as well as prior experience and knowledge to identify objects and agents in their environment. They likely also rely on their memory of similar situations when foraging or navigating. In fact, the contexts and events that provoke dolphins to echolocate may be those in which past experiences and passive stimulation prove to be an insufficient guide for decision making processes or the selection of future actions (Roitblat et al., 1990).

What kinds of representations do dolphins create by echolocating?

How dolphins represent trains of echoes certainly will impact what they remember and how they can think about the objects and agents in their environment. Dolphins could potentially represent and remember only the way echoes from an object sound. In this scenario, a dolphin echolocating a sea bass in the dark might remember the loudness, pitch, duration, and other auditory characteristics of the sea bass echoes, but not the size and shape of the fish. If this were all the information that dolphins' echoic representations provided, then if the sea bass were to swim into the light when the dolphin was not echolocating, the dolphin might not identify the fish as the same one it had earlier heard.

In fact, dolphins' echoic representations do not seem to contain only the auditory characteristics of the echoes. Instead, their representations appear to contain information about object features that allows them to recognize objects across modalities. If a blindfolded dolphin echolocates a sample object (e.g., a cube), and you then remove the blindfold and ask the dolphin to choose the matching object from among several choices using only vision, it will usually succeed (Harley, Putman, & Roitblat, 2003; Harley et al., 1996; Herman, Pack, & Hoffmann-Kuhnt, 1998; Pack & Herman, 1995; Pack, Herman, Hoffmann-Kuhnt, & Branstetter, 2002). This ability implies that echolocating dolphins are able to

recognize object characteristics (e.g., size, shape, material) from the auditory features of the echoes (e.g., amplitude, frequency).

Which object characteristics dolphins typically extract from echoes remains unclear. Some researchers suggest that an echolocating dolphin forms an "echo image" based on perception of the object's shape (Herman et al., 1998; Pack & Herman, 1995; Pack et al., 2002). Others suggest that dolphins can represent certain object features (e.g., material, structure) but perhaps not others, such as shape, when echolocating an object that has not been seen (Harley, Fellner, & Losch, 2009). What is clear is that after a dolphin has both heard echoes from an object and seen it, the dolphin may then blend visual and echoic information into a "rich representation of overall shape and internal structure" (Harley & DeLong, 2008). More long-term studies of well-trained dolphins will be needed to clarify exactly what forms the representation of object features take in the mind of a dolphin.

Another difficult issue is identifying which auditory features (e.g., amplitude, frequency) dolphins use to construct representations of each object characteristic (e.g., size, material). There is no one-to-one correspondence between auditory features and object characteristics. Two objects with different materials can have echoes with different amplitudes, frequencies, and durations. Each object characteristic can impact more than one auditory feature. A dolphin faced with an object discrimination task in which only one object characteristic varies (e.g., size varies but material and structure are held constant) has potentially several auditory features in the echoes that carry information. But which feature is the most important – is one feature ever enough? Or does the dolphin always use multiple features? In one study, a dolphin performed an object discrimination task in which object characteristics varied in size, shape, material, and/or texture (DeLong et al., 2006). The objects used in that task were ensonified with dolphin-like clicks, and then between-object differences in auditory features (e.g, target strength, peak frequency, number of highlights) were examined in conjunction with the specific errors (object confusions) made by the dolphin. This error analysis suggested that the dolphin did not use any one single feature or a simple combination of six features to discriminate among the objects. There were a few auditory features that the dolphin appeared to use frequently (e.g., peak frequency, center frequency, echo spectrum shape), and most likely he relied on multiple auditory features to construct representations of the objects.

Past attempts to explain how dolphins are able to recognize objects across the modalities of vision and echolocation have focused primarily on identifying features of objects that might be available to both modalities either through direct registration or learned associations. An additional possibility, however, is that dolphins might represent the affordances of objects that they inspect (e.g., how they could interact with an object). Gibson (1979) suggested that organisms directly perceive such opportunities for actions when confronted with an object (see Garbarini & Adenzato, 2004, for a more contemporary version of this proposal). In the case of an echolocating dolphin, such affordances might include the motor acts the dolphin could use to grab the object or the vocal acts that would

maximize the acoustic energy reflected from the object. Because the actions an object affords are only weakly dependent on the modality through which the object is sensed, similar affordances would likely register across modalities, providing a possible basis for cross-modal recognition. In principle, the dolphin could recognize similarities and differences in the actions afforded by various objects rather than, or in addition to, physical similarities between the objects. New experiments that control for the manipulability of inspected objects would need to be conducted to further assess this possibility.

Another approach for identifying the salient auditory features of echoes is to present object echoes to human listeners who can typically perform as well as dolphins on object discrimination tasks. The advantage of human listening studies is that the participants can verbalize potential cues and the experiments are much faster to complete (weeks as opposed to years to complete a dolphin study). Human listening studies have in some cases identified cues that dolphins are likely to have used by directly comparing the errors made by the dolphin and the human participants (DeLong, Au, Harley, Roitblat, & Pytka, 2007). One important finding from these studies is that both dolphins and humans attend to the pattern of changes in the echoes across different object orientations, particularly when discriminating among objects that vary in shape.

Interpreting Patterns

"All the properties of objects are actually nothing more than the perceptual cues that are imprinted on them by the subject with whom they enter into a relationship"
– von Uexkull, 1982, p. 74

Dolphins are continuously confronted with many simultaneous internal and external events, some of which are more relevant than others. For example, echolocating dolphins use the outcomes of their past click producing actions (i.e., the resulting echoes), as well as representations of their movements, to dynamically modulate their ongoing vocal and motor acts. In constructing representations of the world, dolphins must necessarily represent only a subset of the available information. A dolphin hearing a sequence of self-generated echoes may represent the absolute acoustic frequencies within the echoes, the relative changes in frequencies across echoes, the durations of echoes, and the intervening silences between them. The dolphin may also represent the actions that generated the sequence, the familiarity of the sequence, the similarity of the sequence to sequences heard before, the events associated with past instances of similar sequences (including actions that might be taken relative to ensonified objects), its confidence in recognition judgments, the nature of likely reflectors, and the location and shape of those reflectors. Knowing something about which elements dolphins include within the representations they construct is critical to understanding what they can do mentally, because these representations provide the scaffolding for all remembering, perceiving, and thinking.

Historically, comparative researchers have viewed representation of relational features (e.g., the spatial configuration of object features) as requiring more sophisticated mental processing than representations of directly sensed features (Hebb, 1949; Herrnstein, 1990; Hulse, 1993; Premack, 1976). When humans hear sound streams, however, relational features typically are more obvious than absolute features such as sound intensity (DeLong et al., 2007; Hulse, Takeuchi, & Braaten, 1992). The ability of dolphins to echoically recognize objects from various angles, and when the objects previously have only been experienced visually, suggests that echolocating dolphins may also find relational features to be more salient than absolute acoustic features. Representations of relational cues are often more stable (perceptually invariant across contexts) than representations of absolute cues, and this "abstractness" makes them particularly relevant for cognitive processes (Herrnstein, 1990; Hulse, 1993; Smith, Redford, Haas, Coutinho, & Couchman, 2008). The following sections describe further experimental evidence showing how dolphins use relational features when they judge similarities and differences between sensory events, and discuss what these findings reveal about how dolphins think about the world and themselves.

How do dolphins perceive melodies?

Perceptual processing is often portrayed as a reflexive reaction to physical events. There is a subtle difference, however, between reacting to events versus responding to event dynamics. Take for example, melodies. A melody is a sequence of tonal sounds that is perceived as belonging together; frequency contours describe the pitch relationship between successive notes that comprise a melody (Page, Hulse, & Cynx, 1989). Humans judge two melodies to be similar if the frequency contours of both melodies are the same, even when the absolute frequencies contained in the melodies are different (Kallman & Massaro, 1979; Morrongiello, Trehub, Thorpe, & Capodilupo, 1985; Trehub, Bull, & Thorpe, 1984). This suggests that when humans hear melodies, the changes across tones are more salient, or at least more memorable, than the absolute frequencies of the tones. In other words, changes in frequencies (acoustic dynamics) are more relevant to most human listeners than the frequencies heard (the acoustic events). Perceived acoustic changes are, however, not external physical events. They are the result of a comparison between memories of past events with ongoing events. Consequently, humans' perception of melodies is as much a reaction to representations of past experiences as it is to ongoing physical events.

Species vary with respect to the attention they give relative features of sound sequences versus absolute features (Braaten, Hulse, & Page, 1990; D'Amato & Salmon, 1982; Kallman & Massaro, 1979; Massaro, Kallman, & Kelly, 1980). Some researchers argue that only humans give greater weight to relative features (Trehub & Hannon, 2006). How an organism codes external events will determine how it recognizes, differentiates, remembers, and predicts such events. Dolphins seem to represent many of the same properties of frequency contours as humans (Ralston & Herman, 1995). In one study of acoustic pattern recognition, the

dolphin Phoenix was presented with two kinds of melodies: tones decreasing in frequency and non-descending patterns, consisting of either constant frequency tones or tones that increased in frequency. Phoenix initially was instructed to press specific paddles whenever she heard certain melodies. When it was discovered that Phoenix whistled exclusively before pressing one of the two paddles, however, the paddles were removed and a listener who could hear Phoenix, but not the patterns, judged her vocal responses.

After learning to distinguish a descending pattern from a constant pattern, Phoenix was tested with 13 novel tonal patterns. In these early tests, she appeared to use the absolute pitch of the tones to determine her response, suggesting that she learned to whistle in response to certain tones. Phoenix was then tested with 15 additional melodies, in which the frequency steps between the tones were more closely spaced. Phoenix classified these sounds in ways that suggested she was attending to absolute frequencies as well as relative changes in frequency. Finally, Phoenix was tested on trials in which she was required to distinguish ascending frequency contours from decreasing frequency contours. Under these conditions, Phoenix appeared to classify melodies based on relative changes rather than on absolute changes in frequency. Phoenix's performance throughout the various generalization tests suggests that she represented both the absolute frequencies of the tones as well as the frequency contours of the melodies (see MacDougall Shackleton & Hulse, 1996, for similar results in birds).

Do dolphins have rhythm?

The ability to recognize patterns in event dynamics is not constrained to detecting patterns of changes in unimodal sensory events. Some changes can be recognized independently of the modality within which they are received. For example, humans can recognize the rhythm of an event sequence (its pattern in time) independently of whether the events are seen or heard. Rhythms are characterized by the duration of tone and intertone intervals within a regular periodic pattern, and are highly salient to humans (Bispham, 2006; Trehub & Hannon, 2006). Rhythm was more salient than pitch for tasks in which human listeners rated similarities of melodies (Carterette, Monahan, Holman, Bell, & Fiske, 1982), and familiar melodies were judged to be unfamiliar when presented with a different rhythmic structure (Jones, 1993).

Dolphins perceive differences between auditory rhythms. One dolphin learned to distinguish six rhythms with high accuracy (94%) by performing a different behavior (e.g., spin, or toss a ball) to each different rhythm (Harley, Odell, Putnam, Goonen, & DeLong, 2002). When the original rhythms were shifted in frequency or tempo, the dolphin still proved able to discriminate them with high accuracy (93%), suggesting that the dolphin's representation of the rhythm did not depend on the absolute pitch of the tones (Harley, Odell, et al., 2003). Large tempo changes initially resulted in poor performance. Performance improved, however, when the dolphin was exposed to a wide variety of tempos before being tested with novel tempo-shifts (Harley, Fellner, Odell, & Putnam,

2005). Such generalization implies that the dolphin represented rhythms based on its experience with variations of the rhythms.

The structure of dolphins' representations of rhythmic sequences is further revealed by their ability to produce rhythms. Spontaneous production of rhythmic actions by dolphins was observed early on (McBride & Hebb, 1948), but researchers have just begun to explore this capability experimentally. One dolphin learned to produce six different rhythms by tapping out specific rhythms to signal its recognition of specific objects (Harley, Crowell, Fellner, Odell, & Larsen-Plott, 2005; Harley, Fellner, et al., 2005). During training, the dolphin spontaneously began producing the rhythms vocally in response to the objects. The dolphin's rendition of each rhythm varied across trials. Specifically, the dolphin varied the absolute duration of the sound and inter-sound intervals as well as the frequencies of the sounds while keeping the distinctive rhythmic patterns intact (Crowell, Harley, Fellner, & Larsen-Plott, 2005). The dolphin's self-produced rhythms imply that it represented the relative durations and frequencies of the sound patterns, consistent with the findings from frequency contour discrimination studies described above. Like humans, dolphins appear to integrate memories of past auditory events with ongoing events. To imitate and transpose heard rhythms, dolphins must merge representations of past and present external events (the sound sequence) with representations of internal events (the vocal motor acts).

When do dolphins recognize repeating patterns?

When a dolphin produces an acoustic rhythm that sounds similar to one it recently experienced, or chooses an alternative object that matches a sample object, it is easy to imagine that the dolphin's initial experience provided a template for its subsequent actions. Put another way, one might say that the dolphin's actions recreate its prior experiences. This raises the question of what dolphins know about recurring events. In humans, events that are re-experienced are often associated with a feeling of familiarity. Similarly, when a person views two or more identical objects, they may describe these objects as being the same. The "sameness" of two events, whether successive or simultaneous, corresponds to the recognition of a repeated experience. Self-reports of familiarity or sameness are thus one objective indicator of whether an individual recognizes that he or she has re-experienced an event.

Several experiments have demonstrated that dolphins can select an object based on its visual or echoic similarity to previously experienced objects (Herman, Pack, & Wood, 1994; Mercado, Killebrew, Pack, Macha, & Herman, 2000; Pack et al., 2002), and that dolphins can identify sounds that they have previously heard (reviewed by Herman, 1980). Dolphins that have learned such classification tasks previously have been described as forming an abstract identity concept or as generalizing a matching rule (Herman et al., 1994). More recently, the ability to classify events based on their sameness has been described as same-different discrimination (Wasserman & Young, 2010), or same-different judgment (Smith et al., 2008). In the comparative literature, judgments about the sameness of

simultaneously presented images are often regarded as more cognitively sophisticated than judgments made when images or objects are presented serially (Premack, 1976). Two dolphins (Akeakamai and Hiapo) trained to classify pairs of simultaneously presented objects as same or different, proved to be able to successfully perform this task when shown novel pairs or triads of objects in novel contexts (Herman et al., 1994; Mercado et al., 2000). Collectively, these studies provide compelling evidence that dolphins can judge when an auditory, echoic, or visual event has been experienced more than once, independently of whether the events are simultaneous or successive, and can use such similarity judgments to control their actions.

Much of the training that dolphins experience involves associating a particular external event (e.g., a gestural instruction or stimulus presentation) with a specific internal event such as the production of a motor act. To learn the REPEAT instruction, however, dolphins had to associate a gestural instruction with a mental act that would provide the cues necessary to select a motor act[7]. In humans, such instructions are relatively common. For example, you might ask someone to think back to what they were just doing, to imagine a tree and describe it, or to add several numbers in their head and tell you the sum. The REPEAT and MIMIC instructions (and possibly the CREATE and ANY instructions) effectively ask the dolphin to think back and select its next action based on its memories. It is important to note, however, that dolphins need not recognize that they are repeating an action (or avoiding repeating an action) to respond correctly to any of these instructions – the ability to maintain and flexibly access representations of recent events is sufficient. Consequently, it remains unclear how dolphins' perceive their performance of the repeating task, or whether they recognize that they are in fact repeating actions.

Are dolphins' thoughts conceptual?

The experiments described above provide compelling evidence that dolphins represent relational features of events, and that they can selectively attend to such relations. Mental processes that involve abstracting general relational properties from specific instances have traditionally been described as conceptual. Concepts are often contrasted with percepts and actions, which are considered to be more primitive mental constructions (see Harlow, 1959; Hebb, 1949; Piaget, 1952). From this perspective, dolphins' conceptual processes link their percepts to their actions in ways that are analogous to how the microprocessor of a computer transforms keystrokes into changes on a display (see Jerison, 1986, for an alternative perspective). This information processing framework has greatly impacted studies of marine mammal cognition, leading researchers to draw sharp distinctions between percepts, concepts, and actions (Herman, 1980; Herman et al., 1994; Reichmuth Kastak, & Schusterman, 2002; Schusterman & Kastak, 2002).

[7]Because a dolphin's mental acts could not be observed, it was not possible to shape their responses to the instruction through successive approximation. Training in this context was more like trying to help someone solve a riddle; the dolphins had to stumble onto the correct solution.

There is an alternative way of framing cognition, however, in which distinctions between concepts, percepts, and actions are not so clear-cut. This framework, referred to as grounded or embodied cognition, suggests that multimodal representations are used to support the selection and production of actions as well as mental simulations of actions and events (Barsalou, 2008; Barsalou, Simmons, Barbey, & Wilson, 2003; Clark, 1997; Garbarini & Adenzato, 2004). From this perspective, much of what has in the past been described as conceptual processing can be reinterpreted as selective attention to representations of internal events. For example, a dolphin that classifies a pair of novel objects as "same" could do so based on the perceived repetitiveness of her visual experiences (an internal event) rather than on the idiosyncratic physical properties of the objects (external events). Distinctions between percepts, concepts, and actions become less important in the grounded cognition framework, because the same mental processes an organism uses to attend to or think about external events might also be used to attend to internal events (e.g., those corresponding to relational features). In this framework, the nature of a dolphin's thoughts and experiences would reflect the organization and contents of its mental representations rather than the complexity of the operations it performed on those representations (see also Mercado, 2008). In contrast, the information processing view of cognition presumes that computational capacity (e.g., the availability of specialized modules for performing particular perceptual or cognitive functions) primarily determines mental abilities.

A few examples may clarify the distinctions between these two explanatory frameworks. From the information processing perspective, the mental outcome of echolocation is the product of a conglomerate of perceptual and conceptual processes. Alternatively, the grounded cognition framework would describe echoic representations of objects as facets of a more global, holistic simulation of ongoing internal and external events related to the act of echolocating and the planning of future actions. Similarly, the production and perception of rhythms and melodies by dolphins could be viewed as a hybrid of perceptual and conceptual processes (the information processing approach), or as the recognition of regularities resulting from internal comparisons of ongoing events to recently experienced events (the grounded cognition perspective). Finally, consider the case of a dolphin that has just observed the instruction to repeat or imitate an action. The visual registration of the gestural instruction is probably similar for all dolphins that observe it, but how this gesture is mentally represented may vary greatly depending on each dolphin's past experiences (Shyan & Herman, 1987). Elele's response to the REPEAT gesture could be viewed as involving a concept[8] about percepts related to actions (the information processing description), or as an externally-triggered pattern recognition process grounded in a capacity to reactivate recently activated, multimodal representations of internal and external events. Ultimately, even processes as seemingly conceptual as

[8]The feature of repeating that makes it conceptual is that a dolphin can respond appropriately to the REPEAT instruction after virtually any novel action without additional training (Herman, 1980; Reichmuth, Kastak, & Schusterman, 2002).

similarity judgments (Herman et al., 1994; Mercado et al., 2000; von Fersen, Manos, Goldowsky, & Roitblat, 1992), numerical judgments (Jaakkola, Fellner, Erb, Rodriguez, & Guarino, 2005; Kilian, von Fersen, & Gunturkun, 2005; Kilian, Yaman, von Fersen, & Gunturkun, 2003), or uncertainty monitoring (Smith, Schull, Strote, Mcgee, Egnor, & Erb, 1995) depend on recognizing patterns in the representations of both external and internal events corresponding to percepts and actions, and do not entail any specialized cognitive processing beyond that involved in echolocation.

Historically, the information processing approach to describing dolphin cognition has been highly productive. Nevertheless, it does not account for some of the more interesting unexpected findings from experimental studies of dolphin cognition. For example, in both the rhythm perception studies (Harley, Crowell, et al., 2005; Harley, Fellner, et al., 2005) and the melody discrimination study (Ralston & Herman, 1995) described above, dolphins spontaneously chose to respond to acoustic events with distinctive vocalizations in addition to the required paddle presses. From an information processing perspective, such unnecessary actions should increase the complexity of the experimental task. Assuming that the dolphins are not intentionally or inadvertently making the tasks harder for themselves, this tendency suggests that dolphins may use memories of their own actions (an internal event) and the outcomes of those actions (an "external" acoustic event) to augment their representations of the arbitrary sound sequences used as experimental stimuli[9]. This interpretation is consistent with findings from studies of dolphins' memories for actions, which showed that dolphins naturally find their own actions to be more memorable than external events (Mercado et al., 1998, 1999). Such representational augmentation is actually predicted by the grounded cognition framework, because making arbitrary external events more "embodied" by linking them to distinctive action-related (i.e., internal) events should increase the ease with which those events can be thought about and remembered.

An interesting question for future study is whether additional external or internal events that are synchronized with features of a sound sequence might further enhance a dolphin's learning capacity and performance. For example, a light might flash in synchrony with a dolphin's sound production, or whenever a sound is broadcast, providing a supplementary visual indicator of rhythm or changes in frequency. This manipulation would be similar to humans' use of mirrors while practicing dance movements. Recent work showing that parrots can synchronize their movements to auditory rhythms suggests that cross-modal

[9]A similar observation of dolphins spontaneously producing particular sounds in association with specific acts is reported by Partan and Xitco, as cited in Fellner et al. (2006). Thompson (1976) notes that dolphins trained to make a spatial response based on an acoustic instruction spontaneously augmented their auditory memories by adopting stereotypical postures after specific sounds. Studies of visual matching-to-sample in a dolphin showed that the availability of acoustic labels facilitated learning of the task (Forestell & Herman, 1988), and spontaneous mimicry of such labels may have similarly enhanced dolphins' performance as they learned to use a keyboard (Reiss & McCowan, 1993).

matching of temporal patterns may be more prevalent in animals such as dolphins that have the ability to imitate sounds and actions (Patel, Iversen, Bregman, & Schuiz, 2009; Schachner, Brady, Pepperberg, & Hauser, 2009). Currently, it is not known whether a dolphin can recognize the rhythmic structure of a tactile or visual event as being similar to a heard event, or even whether a dolphin can distinguish a rhythmic visual sequence from a non-rhythmic one.

Conclusions and Future Prospects

In one of the earliest psychological assessments of dolphin behavior, McBride and Hebb (1948) concluded that, "We have no direct evidence concerning the porpoise's intelligence – the average level, that is, of his problem-solving – and no immediate prospects of obtaining any." Sixty years later, the situation has changed. There is now considerable behavioral evidence regarding bottlenose dolphins' cognitive capacities and numerous techniques available for obtaining more evidence. And yet, the motivation and prospects for obtaining further evidence concerning the mental abilities of dolphins are rapidly diminishing. Groups that believe the costs to dolphins of keeping them in man-made enclosures outweigh any benefits of the knowledge that might be gained from experiments are becoming increasingly organized and influential. Members of these groups argue that we already know the things that are important to know about dolphins. Specifically, because we have already learned that dolphins behave in ways that suggest high intelligence and sociality, this knowledge should compel us to act responsibly toward dolphins and to not constrain their freedom. But, what exactly do we know?

The experimental findings reviewed above show that dolphins perceive and model the world, but they do not reveal what their models are like. They provide evidence that dolphins remember and think, but they provide little insight into what dolphins think about, how much they remember, or when they recollect or think. The results of most cognitive studies to date simply demonstrate that some species of dolphins possess or can acquire some cognitive capacities that resemble those available to other mammals. They reveal that dolphins can represent certain internal and external events, and that they can acquire certain cognitive skills, but they do not reveal how dolphins typically process information. In short, research to date has shown that dolphins can mentally act, but provides an impoverished understanding of what those mental acts entail.

Consider the nature of the events that dolphins represent. Externally, we know that they can sense light and sound in ways that are comparable to most terrestrial mammals. But, they also sense external events in ways that we do not – echolocation being one example. Echolocation is not like hearing or vision because the events are self-generated, and it is not like touch because sound can pass through some solid objects. We can imagine that it is something like a hybrid of touch, hearing, and vision, but it might be substantially different from all of these. Furthermore, dolphins likely sense external events that we have no familiarity with. Magnetoreception (Kirschvink, Dizon, & Westphal, 1986; Zoeger, Dunn, &

Fuller, 1981), electroreception (Wilkens & Hofman, 2008), and pressure/current detection represent just a few possible ways that dolphins may sense physical events that we do not (see also Lende & Welker, 1972). We can see sensory receptors on dolphins, such as vibrissal follicles along the dolphins' jaws (Mauck, Eysel, & Dehnhardt, 2000), and know that dolphins sense something with them, without having any analogous perceptual experiences that might relate to those sensations. Because we have no awareness of the kinds of events these systems sense, we currently have no way to judge whether our actions are negatively or positively impacting dolphins' perceptions of these events. We can avoid deafening dolphins by not introducing loud sounds in their vicinity, but how can we avoid damaging or interfering with other sensory systems when we don't even understand what they sense or how they work[10]?

If our understanding of how dolphins represent external events is incomplete, then our understanding of how they represent internal events is non-existent. An assumption often made by both scientists and animal rights activists is that dolphins' experiences represent a subset of those experienced by humans. As with representations of external events, there is certain to be some overlap. However, whereas overlap in the physiology of sensory systems can provide some indication of the similarities between dolphin and human representations of external events, there are as of yet no such physical markers of modes of representing internal events[11]. If humans express six emotions (e.g., happy, sad, afraid, mad, disgusted, surprised), do dolphins express more or less? Are they experiencing the same emotions, or different ones that we have no familiarity with? How do dolphin express their emotions? (see Kellerman, 1966, for an early attempt at measuring dolphin emotions.) Similar kinds of questions can be asked about dolphins' motivations and interests. In these domains, we are still at the same point where McBride and Hebb (1948) left us. We have no direct evidence concerning how dolphins represent internal events, and no immediate prospects of obtaining any. It seems questionable, given this fundamental ignorance, whether we can adequately evaluate whether any action we take in relation to dolphins will ultimately increase or decrease their quality of life (as well as ours).

Some comparative cognition researchers argue that no animals other than humans experience a temporal stream - that they are stuck in the present (Roberts, 2002) - and suggest that non-humans lack awareness of causality (Penn & Povinelli, 2007). If so, this would seem to preclude any thinking or remembering in dolphins, and would mean that the dolphin's *Umwelt* is so radically different from that of a human that there is no chance of understanding what it is like to be a dolphin. In contrast, we would argue that it is impossible to determine what a dolphin's experience is or is not like without extensive experimentation. Speculations based on introspection, ethological observations, or cross-species

[10]The current plight of beaked whales illustrates the risks of ignorance (Cox et al., 2005).

[11]Jerison (1986) suggests that the structural similarities in the neocortex of dolphins and the paleocortical systems of other mammals may indicate that they represent events along emotional and motivational dimensions to a greater extent than humans do.

comparisons are simply insufficient. Long-term interactions that facilitate inter-species communication and learning opportunities are necessary to develop a full understanding of the dolphin's world (McBride & Hebb, 1948; Norris, 1991; Pryor, 1986; Timberlake, 2002, 2007). Such interactions can effectively increase the similarity of mental processes and representations used by humans and dolphins. Ultimately, one need not know what it is like to be a dolphin to be able to bring the mental worlds of humans and dolphins closer together.

Dolphins involved in laboratory experiments are active, often eager participants (E. Mercado III, C. M. DeLong, personal observations), and the kinds of behavioral tasks that dolphins learn to perform in laboratories might better be thought of as games than as instrumental conditioning (Kuczaj & Xitco, 2002; Pryor, 1981). Nothing forces dolphins to participate in the tasks; they would get fish regardless and sometimes participate when no food is involved (Delfour & Marten, 2005; Kuczaj & Xitco, 2002; Pryor, 1975). McBride and Hebb (1948) noted that captive adult dolphins spontaneously play much more than is typically seen in other mammals. Dolphins in the wild occasionally opt to play these sorts of games, too, although usually not to the same extent as their captive counterparts (Dudzinski & Frohoff, 2008). Different kinds of games make different demands on a dolphin's mental abilities, and the specific kinds of representations and memory skills that a dolphin will bring to bear depends heavily on its past experiences (Herman, 1991; Shyan & Herman, 1987). In particular, the ability of an expert game player to remember events associated with a game is a function of their expertise; masters will recall more than novices (Ericsson & Chase, 1982; Ericsson & Lehmann, 1996). Consequently, a dolphin with extensive training experience likely possesses an enhanced capacity to recall certain events. For example, a dolphin's representations of observed and performed actions, as well as its ability to manipulate and maintain these representations, can become more refined and efficient through practice (Shyan & Wright, 1993). Experiments in which dolphins' abilities to recall events are pushed to their limits may provide a clearer picture of their memory capacities, as well as the features of experienced events that are most relevant to them.

Early laboratory studies of dolphin cognition raised public awareness of their abilities (Sickler, Fraser, Gruber, Boyle, Webler, & Reiss, 2006). In the process, this research inadvertently increased concerns in some individuals about the possible mistreatment of captive dolphins, which consequently decreased future opportunities for dolphin cognition research. It seems unquestionable that a greater understanding of how dolphins perceive, remember, and think would provide more opportunities for improving their lot than would ignorance. The most powerful tools we have for increasing our understanding depend on direct interactions with dolphins over long periods, as evidenced by what researchers have learned about dolphin cognition in the last sixty years compared to what people managed to discover in the previous six thousand. Technological advances may provide new opportunities for interacting with dolphins that avoid many of the complications currently faced by dolphin researchers. For example, touch-screens have given dolphins new ways of interacting with human experimenters

(Marten, Shariff, Psarakos, & White, 1996), and advances in autonomous data recorders can potentially provide new ways of remotely monitoring and training animals (Martin, Phillips, Bauer, Moore, & Houser, 2005). New methods for conducting field experiments may provide further opportunities for examining learning and perception by individuals and groups (see Cheney & Seyfarth, 1990; Thornton & Malapert, 2009). Field experiments could also expand the range of species studied. The mental capacities of bottlenose dolphins are unlikely to be representative of all cetaceans or even all delphinids. For instance, Pryor (1975) reported that rough-toothed dolphins learned more rapidly than bottlenose dolphins (see also Defran & Pryor, 1980). It seems likely that the range of representational capacities across cetacean species is as large or larger than across primate species. Even considering bottlenose dolphins alone, it is unlikely that the small sample of individuals tested so far is representative of the most cognitively capable members of the species. Expanding the phenomenological and methodological scope of future studies of dolphin cognition will provide the best hope for the future progress of both humans and dolphins.

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