24 The Cognitive Dolphin

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Although we may not be able to say definitively what it is like to be a dolphin, there is a good deal that we can know about its perceptual and cognitive system. My work, along with my colleagues and students, has been dedicated to discovering what kinds of representations animals have and how those representations underlie its behavior. The highlight of this research is our work on dolphin biosonar echolocation. Most of this work involves the Atlantic bottlenosed dolphin (*Tursiops truncatus*), although we have on occasion studied other species as well. Like bats, dolphins obtain information about the identity, location, and characteristics of objects in their world by actively interrogating them using their unique biological sonar, which is highly adapted to their aquatic environment.

Although their use of biological sonar is called "echolocation," dolphins use their sonar for far more than just determining how far away objects are. Their biosonar abilities far exceed those of any man-made system. Dolphins can detect and discriminate targets in highly cluttered and noisy environments (Au 1993). One outstanding example of their keen sonar capabilities is their ability to sonically detect, dig out, and feed on fish and small eels buried up to 45 cm beneath the sandy seabed (Rossbach and Herzing 1997). Using echolocation, dolphins can identify many characteristics of submerged objects, including size, structure, shape, and material composition. For example, they can detect the presence of small (7.6 cm diameter) stainless steel spheres at distances of up to 113 m. They can discriminate among aluminum, copper, and brass circular targets, and among circles, squares, and triangular targets covered with neoprene (see Au 1993).

Bottlenosed dolphin biological sonar uses very broadband high-frequency clicks of about 50 µs that emerge from their rounded forehead or melon as a highly directional sound beam with 3 dB (half-power) beam widths of about 10° in both the vertical and horizontal planes (Au et al. 1986). Their echolocation clicks have a peak energy at frequencies ranging from 40 to 130 kHz with source levels of 220 dB re: 1 µPa at 1 m (Au 1993). Dolphin hearing extends to frequencies as high as 150 kHz, which is 8–10 times higher than human hearing limits. They generate their clicks deep within their heads by passing air through a nasal structure called "monkey lips" because of its appearance. The sound travels through the water in a narrow conelike beam and reflects off objects in that beam. The sound is picked up in the dolphin's jaw and conducted to the animal's inner ear, where it is transduced into neural signals for processing by the rest of the brain.

The time between successive clicks depends on the distance between the animal and the target it is scanning. The average time between emitted clicks in a train is typically 15–22 ms longer than the time required for the click to travel through the water to the target and return as an echo (Morozov et al. 1972; Penner 1988).

Although both bats and dolphins use echolocation, the characteristics of the medium in which their signals are emitted, the mechanisms by which the signals are produced, the type of signals, and the neurological apparatus they use to processes those signals differ substantially. Bat biosonar is adapted for use in air, whereas dolphin biosonar is adapted for use underwater. Bat biosonar signals are relatively long in duration (up to several milliseconds), and contain both narrow-band constant-frequency and frequency-modulated components depending on the species (Bellwood 1988; Fenton 1988; Suthers 1988). By contrast, the dolphin echolocation signal is very broadband and, as indicated, extremely short. Echoes typically range in duration from 50 to 200 µs.

Dolphin echolocation is one of the most sophisticated cognitive processes that have been

studied. When a dolphin uses its biological sonar to recognize objects, its brain performs the equivalent of some extraordinarily complex computations. These computations transform one-dimensional sound waves arriving at each of the dolphin's two ears into representations of objects and their features in the dolphin's environment. The process by which this transformation occurs is the focus of our interest.

In the preceding paragraph I asserted, perhaps too boldly, that the dolphin transforms the echo's one-dimensional sound waves into a three-dimensional representation of objects, but that is not the only way that dolphins could use their biosonar to recognize objects. It is conceivable that the dolphin does not solve the object-recognition problem per se, but rather solves a listening problem. Rather than using its sonar to determine the characteristics of objects, it could recognize them by detecting the object's characteristic sonic signature. In this hypothesis, a tuna is recognized, not by its structure, but by the sound signature or profile of its echo. In vision, this would be the equivalent of saying that we recognize an object, not by its perceived structure, but by the characteristic pattern it projects on our retina.

Although such a model is conceivable, it seems unlikely from an ecological perspective. Sensory systems evolved in response to real ecological problems, so it seems reasonable to suppose that they actually do provide ecologically relevant information. Treating echolocation as a listening problem would allow the animal to distinguish one group of objects from another, but it would not provide a very reliable basis for dealing with novel objects. More critically, it would make object permanence into a really difficult problem, for example, because of the strong dependence of the echo characteristics on the angle from which the object is ensonified, called "aspect dependence."

The echo returned by an object depends very strongly on the angle from which it is "viewed." Aspect dependence is also a property of visual perception and in the present context it is prob-
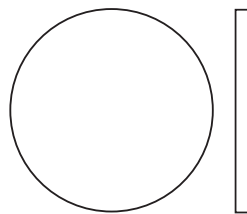

Figure 24.1
A sketch of a coin from the front and from the side.

ably easier to explain in that way. Consider the two objects depicted in figure 24.1, which is a sketch of a coin from the front and from the side. The scene that is projected onto the viewer's retina depends on the angle from which the object is viewed. No features are common between these two views, yet under appropriate circumstances, people can easily tell that it is the same object. We do not get the impression that an object has disappeared, to be replaced by a different one when our viewing angle changes; rather, we tend to perceive the object rather than its projection on the retina—an example of object permanence. Every viewing angle and every viewing distance would project a different pattern on the retina, so it is difficult to imagine how there could be characteristic patterns by which the object could be visually recognized. Visual object constancy over changes in position and angle does not seem to depend on the existence of specific invariant properties in the retinal image per se, but rather seems to be computed from changes in the retinal image.

Sound is also dependent on the angle at which an object is ensonified. Even a small change in angle can have a profound impact on the structure of the echo, especially when there are sharp discontinuities in the object's structure (e.g., corners or edges). Furthermore, unlike vision, sound in the water often penetrates the object so that there are reflections not only from the front surface of the object but also from the back surface. The internal properties of the object also affect the echo. For example, a dolphin can distinguish
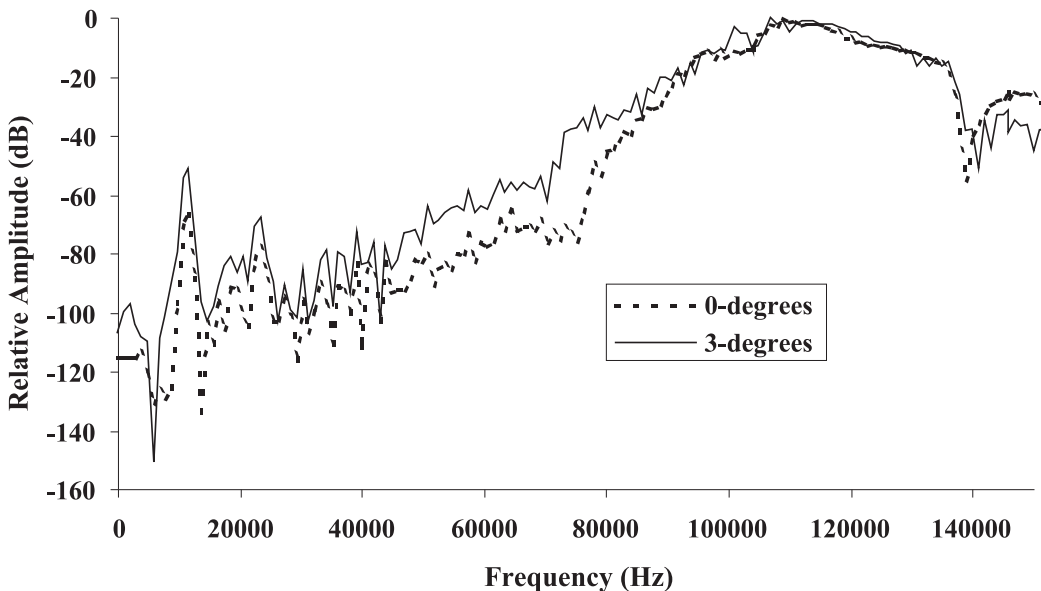
Figure 24.2
Echo spectra from a complex object ensonified at either 0 or 3° relative to the perpendicular.

between identical containers that are filled with different liquids (Roitblat et al. 1993). These physical characteristics all affect the structure of the echo as it is received by the dolphin, but there does not seem to be any simple function that can be used to predict the structure of the echo from one angle given its structure at another angle (the same difficulty exists for vision). The dolphin must use other, presumably cognitive, functions to recognize the constancy in an object viewed at different angles. We can describe some of the characteristics of these cognitive functions.

Figure 24.2 shows example echo spectra from a complex constructed object at two different angles. This object was constructed of a large carriage bolt with several nuts attached. It was ensonified by an artificial dolphin click from a distance of about 1 m. As it rotates, it presents different faces to the sound beam and hence reflects the incident sound in different frequency-

and angle-dependent directions. Notice how even a small rotation of 3° can have a substantial effect on the spectrum of the echo. This is the difference one would expect between the spectrum arriving at the two ears if a dolphin were about 2.7 m away from this complex object, with an interaural distance of about 14 cm. As the dolphin approached the object, the angle between the incident sound beam and the dolphin's two ears would increase and the corresponding differences between the two spectra would also increase. Presumably the dolphin could use these differences as a function of distance and angle to recover many features of the object being echolocated. In vision, Ullman (1979) used similar ideas to show how one could derive shape from motion cues. Each angle and each distance constrains the possible shapes that could be producing the acoustic or visual cues. As a result, one can identify the properties of an object with a high degree of certainty when enough different

samples have been obtained. This sequential sampling method is consistent with what we know of dolphin echolocation. [See Möller and Schnitzler (1999) for a similar analysis in bats.]

Dolphins appear to combine information from multiple echoes when recognizing objects (Roitblat et al. 1990). In the laboratory, they emit on average between five and a hundred echolocation clicks per trial, even when they are recognizing familiar objects. Their performance indicates that they combine information from multiple echoes, rather than simply clicking until they get a particular kind of echo (Roitblat et al. 1991).

The dolphin ear provides an excellent frequency analysis of the echo. Because of the physical properties of the dolphin's cochlea (or any other mammalian ear, for that matter), each point along the basilar membrane resonates at a characteristic frequency. Vibrations received at the oval window of the cochlea excite a traveling wave along the basilar membrane, in which the magnitude of the displacement of each point along the membrane is frequency dependent. Hair cells in contact with the basilar membrane transform this mechanical motion into neural signals, which are relayed by the ganglion cells through the auditory nerve. The cochlea can be described as a bank of bandpass filters, which functions to a rough first approximation, as a mechanical spectrum analyzer, separating the signal into a spectrum of frequencies and their amplitudes. The first neural representation of an echo is (roughly) its spectrum as encoded by the ganglion cells.

Because of the brief duration of the echo and the relatively slow firing rates of neurons (up to about 1 kHz), it is unlikely (though not inconceivable) that the dolphin can detect the temporal properties of the echo directly; rather, it is more likely to derive the temporal properties of the echo from its spectrum. Recall that echoes typically last up to 200 μs, which would be one-fifth of the interspike interval at 1 kHz. Fortunately, according to Fourier theory, it is not difficult in principle to recover temporal information from the spectrum.

Another factor that helps dolphins to recognize objects from multiple angles is the use of two ears. Dolphins' ability to assess the angle to objects depends on using amplitude and time-of-arrival differences in signals arriving at the two ears. This same kind of information also provides cues to the three-dimensional structure of objects returning echoes in that each ear receives the echo at a small angle relative to the dolphin's echolocation beam. This difference between the two ears as well as its head movements help the dolphin to extract structural information. For example, more distant surfaces return echoes slightly later than closer surfaces do. Furthermore, as the dolphin approaches an object on which it is echolocating, the angles between the two ears and the object change, again providing important cues to the three-dimensional structure of the object. Because of differential attenuation of signals of different frequency over distance in the water, the frequency structure of the returning echo also changes as the dolphin approaches. Having two receivers thus not only increases the sensitivity of the system relative to one ear but also provides additional nonredundant information about the structure of the object.

We cannot know what the dolphin's subjective experience of perception is like, but we can know something about what it experiences by identifying the sensory dimensions that are available and assessing how those dimensions might be used by the animal in its day-to-day activities. It seems reasonable to suppose that echolocation, like vision, is used to perceive the properties of objects, but it is unlikely that dolphins use their sonar to "paint" pictures of the objects that they ensonify. There is no evidence to support the hypothesis that dolphins must scan across an object point for point (akin to laser tomography) in order to perceive its structure (cf. Herman et al. 1998). For example, at the rate at which they echolocate (up to about 66 clicks per second), such a scan would result in a very low-density collection of points. At the same time, there is no a priori reason to think that dolphins could not

construct "images" of the objects that they echo-locate, as long as we recognize that images are not limited to just the visual modality (Roitblat et al. 1995).

People, for instance, can image the sound of a symphony, can image a scene from the sound of plates shattering on a floor and can even describe many of the properties of the objects that are breaking and the surface onto which they have fallen, all on the basis of sound. Identifying the properties of objects seems to be the essential characteristic of imagery, not whether it is visual. There is no reason to think that dolphins could not similarly identify the properties of the objects that they echolocate and construct images of the objects in their world. Studies of cross-modal processing in dolphins (Harley et al. 1996), including some ongoing studies, support the notion that dolphins derive corresponding information about the structure of objects from both vision and echolocation.

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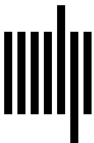**Edited by:** Marc Bekoff, Colin Allen, Gordon M. Burghardt

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