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Recognition and Discrimination of Human Actions Across the Senses of Echolocation and Vision in the Bottlenose Dolphin: Evidence for Dolphin Cross-modal Integration of Dynamic Information

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The ability of cetaceans to explore and interpret their world via echolocation has received considerable attention during recent years, and the resulting body of work has revealed a sophisticated cetacean echolocation system. In addition, a number of recent studies suggest that dolphins can relate information that they receive from vision with information that they obtain from echolocation when this information concerns stationary objects. However, the present study is the first test of the cetacean ability to integrate dynamic information about movement across the two senses. Three adult female bottlenose dolphins that had previously learned to interpret visible movements produced by humans stationed on floating docks were asked to interpret a set of these movements produced by an underwater human located behind a visually opaque screen. Although each dolphin had previously demonstrated its ability to reliably interpret movements produced by a human in the air above the surface of the water, none of the dolphins had any previous experience with underwater humans producing movements that the dolphins could see or with underwater humans producing movements behind an opaque screen that prevented the dolphins from using visual information to interpret these signals. The dolphins quickly learned to correctly respond to signals that they could not see but could observe via echolocation. These results demonstrate that dolphins can relate visual and echoic representations of actions, although the amount of experience necessary for such integration has yet to be determined.

The manner in which cetaceans use echolocation to make sense of their world has received considerable attention since the possibility of a cetacean echolocation system was advanced during the 1950s (Kellogg, 1958; Kellogg & Kohler, 1952; McBride, 1956). Subsequent research has revealed a sophisticated echolocation system that enables dolphins to both locate objects and to discriminate objects based on a number of factors, including size, shape, and material composition (Akamatsu, Nakagawa, & Hatakeyama, 1995; Au, 1993; Au & Benoit-Bird, 2003; Au & Hastings, 2008; Harley & DeLong, 2008; Harley, Putman, & Roitblat, 2003; Helweg, Roitblat, Nachtigall, & Hautus, 1996; Pack, Herman, & Hoffmann-Kuhnt, 2004; Roitblat, 2004). These findings are consistent with the notion that wild cetaceans may spontaneously use echolocation to identify and distinguish obstacles, prey, predators and conspecifics, a possibility also supported by the observations that free-ranging harbor porpoises use echolocation to inspect areas before swimming through them (Akamatsu, Wang, Wang, & Naito, 2005).

In addition to their remarkable ability to make sense of their world using echolocation, dolphins possess impressive visual skills (Dawson, 1980; Herman, Hovancik, Gory, & Bradshaw, 1989; Herman, Peacock, Yunker, & Madsen, 1975; Madsen & Herman, 1980). The combination of a sophisticated

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echolocation system and a sophisticated visual system resulted in a number of researchers investigating the possibility that dolphins might be able to integrate information across the senses of vision and echolocation. The extent to which information from multiple perceptual systems is integrated by organisms has intrigued scholars for centuries (see Marks, 1978; Stein & Meredith, 1993), and previous research has found that an ability to relate information from different modalities exists in a variety of species, including bushbabies (Ward, Yehle, & Doerflein, 1970), chimpanzees (Hashiya & Kojima, 2001; Izumi & Kojima, 2004; Parr, 2004; Savage-Rumbaugh, Sevcik, & Hopkins, 1988), humans (Arabzadeh, Clifford, & Harris, 2008; Ernst & Banks, 2002; Giard & Peronnet, 1999; Meltzoff & Borton, 1979; Rose & Ruff, 1987), pigtailed macaque monkeys (Gunderson, Rose, & Grant-Webster, 1990), rats (Delay, 1986), rabbits (Yehle & Ward, 1969), and rhesus monkeys (Cowey & Weiskrantz, 1975).

To date, research with bottlenose dolphins has revealed that dolphins are capable of integrating information from vision and echolocation when the information involves stationary physical objects (Harley & DeLong, 2008; Harley et al., 2003; Harley, Roitblat, & Nachtigall, 1996; Pack & Herman, 1995; Pack, Herman, Hoffmann-Kuhnt, & Branstetter, 2002). Given this ability, one might also expect dolphins to be able to integrate information about actions that they experience visually with information about actions that they obtain via echolocation. However, this ability has yet to be demonstrated empirically. The present experiment tested the ability of one cetacean species, the bottlenose dolphin, to interpret information about the movements of others obtained through echolocation in terms of previous visual experiences with these movements. We did so by taking advantage of the dolphins' previous experience with human movements in the context of human-dolphin training.

Dolphins housed in oceanariums are often trained to respond to movements produced by humans. These movements range from small subtle behaviors (such as a human lightly tapping her foot or slightly nodding her head) to large vigorous behaviors (such as a human quickly moving both arms in a windmill fashion), and are used to request specific behaviors from dolphins. When interpreting these movements, dolphins are typically asked to produce behaviors that serve a variety of functions, including animal husbandry, public education, public entertainment, and human-dolphin interaction (Kuczaj & Xitco, 2002).

The dolphins used in the present study had considerable experience with humans producing movements that the dolphins had learned to discriminate in order to produce the correct responses. However, the dolphins' experience with interpreting human movements was limited to the visual domain. Movements were always produced in the air by a human while the dolphins had their heads above the surface of the water and oriented toward the human. Consequently, the dolphins learned to discriminate these movements visually. Prior to this study, the dolphins had no experience with humans producing movements underwater. This provided a unique opportunity to assess the dolphins' ability to relate information they had learned in the visual modality with information they subsequently obtained from echolocation.

Method

Subjects

Three adult female bottlenose dolphins participated in the present study. These dolphins were housed at MarineLife Oceanarium in Gulfport, Mississippi. Although each dolphin had previously learned to discriminate and correctly respond to many human movements that they perceived visually, none of the dolphins had been asked to respond to human movements produced underwater prior to their participation in this study. Nor had any of the dolphins participated in any research involving echolocation prior to this study.

Apparatus

A portable underwater screen was used to test the dolphins' ability to discriminate movements using echolocation. The screen consisted of an aluminum frame and a lexan panel approximately 6' high, 4' wide, and ½" thick. The screen was positioned below the surface of the water so that a human diver could be stationed on one side of the screen while a dolphin oriented towards the diver from the other side of the screen.

Target movements

Five target movements were selected because they involved relatively large movements, which we believed would increase the possibility that the dolphins would be able to process the movement information using echolocation. Each of the five movements that were selected asked the dolphins to perform distinct behaviors. The *bow* movement informed the dolphin to leap above the water in a particular manner. The *hula* movement informed the dolphin to position itself vertically in the water and spin in a circle. The *bubbles* movement informed the dolphin to produce underwater bubbles by exhaling through its blowhole. The *yes* movement informed the dolphin to nod its head as if it were answering yes to a question. Finally, the *wave* movement informed the dolphin to orient itself vertically in the water and move its pectoral fins back and forth as if it were waving goodbye. Each of these movements was used in dolphin shows, and each dolphin had considerable experience with each of these movements in the above water context.

Procedure

The first step involved desensitizing the dolphins to the portable underwater screen. Desensitization was important because dolphins sometimes avoid novel objects, and we wanted the animals to become comfortable with this aspect of the testing situation. Desensitization was accomplished by placing the screen in the animals' pool for brief periods of time (approximately 5-10 minutes per desensitization session). Ten desensitization sessions proved sufficient to familiarize the dolphins with the screen. By the end of these sessions, the dolphins neither approached nor avoided the screen more often than other changeable aspects of their environment, suggesting that it was no longer a novel stimulus.

After the dolphins had been desensitized to the screen's presence, human divers began to present underwater movements to the dolphins. These movements were ones that the dolphins had already demonstrated that they were able to interpret when the movements were seen in the air. The presentation of underwater movements involved placing the screen in the pool, positioning a diver on one side of the screen, and then sending a dolphin to look at the diver through the screen. In this phase and all subsequent phases, dolphins were tested individually. Initially, the diver produced movements for the dolphin to interpret while the diver was located behind a visually transparent screen. This aspect of the training procedure allowed the dolphins to use the same modality (vision) to interpret movements that they had learned to use in a different context (in air rather than under water). Each dolphin quickly learned to respond correctly to the human's underwater movements, all three dolphins achieving 90 – 100 % correct performance within four sessions. The *bow, hula*, and *bubbles* movements were used during this aspect of the training procedure.

Once a dolphin had demonstrated that she could reliably interpret underwater movements visually, the concept of using echolocation in this context was introduced to the dolphin. In order to familiarize the dolphins with the novel notion of interpreting human movements using echolocation rather than vision, the transparent screen was gradually made darker until it was completely visually opaque. This transitional phase provided the dolphins with the knowledge that the diver was producing movements behind the screen even when the dolphin could not see the diver, and resulted in the dolphins learning to use echolocation rather than vision during this task, as evidenced by the dolphins' increased production of clicks during the transition phase. The *bow, hula*, and *bubbles* movements were used to help the dolphins learn to use echolocation during this process.

The testing phase began once the dolphins were reliably producing echolocation clicks. The opaque screen was used exclusively during testing sessions. Each animal was tested with the five individual human movements described above, each of which the dolphin had consistently responded to correctly when the movements were produced above water and visible. Comparing how the dolphins reacted to individual movements produced in two different domains allowed us to better determine each dolphin's ability to relate information that it had obtained through vision with that it had obtained via echolocation. More specifically, we were able to compare a dolphin's ability to interpret movements it had learned by watching humans above the surface of the water and in air (which required processing visual information) with it's interpretation of movements that were produced underwater and behind an opaque barrier (which required processing information obtained via echolocation). In addition, we were able to compare the dolphins' interpretation of movements that it had never before had to interpret underwater (*yes* and *wave*) with those with which it had previous underwater visual experience and underwater echolocation experience (even though both types of experiences were limited, particularly those involving echolocation in a non-visible condition).

Target movements were presented in a random order constrained only by the fact that each dolphin was to receive a total of fifty target movements (each of the five target movements on ten separate occasions). Each test trial began with the dolphin positioning itself on the side of the screen opposite the human diver. Once the dolphin was orienting on the screen, the diver on the opposite side produced a target movement. The dolphin's response was ascertained by observers, one of who blew a whistle and rewarded the dolphin with a fish if it had correctly interpreted the target movement.

There were approximately six test trials per session, and a maximum of one test session per day. We opted for short sessions for three reasons. First, it proved easier to maintain each dolphin's interest if individual sessions were relatively brief. Second, shorter sessions made it easier to conduct the sessions. Third, the shorter sessions more closely approximated other training and relationship sessions that occurred at MarineLife Oceanarium.

Results

The results were very straightforward. Given their previous experience with the target movements as visual cues provided by humans in the air, we expected the dolphins to perform well when they were asked to respond to target movements that they could see while watching a human stand on a floating dock. This prediction was confirmed. In fact, two of the dolphins were perfect, responding correctly each of the ten times they were asked to do so for each target movement that was presented in the above water and visible condition. The remaining dolphin made two mistakes, one each for the *yes* movement and the *wave* movement. These results are summarized in Figure 1.

But how did the dolphins perform when asked to respond to the same movements produced by an underwater human hiding behind an opaque screen? As shown in Figure 2, this depended on their previous experience with humans producing the movements underwater. For the three movements that had been used in the training phases (*bow, bubbles,* and *hula*), two of the three dolphins were perfect when asked to interpret these movements in the non-visible underwater condition, and the other dolphin made one mistake. Correct responses were less common for the two movements (*wave* and *yes*) that the dolphins had never observed humans performing underwater prior to the underwater non-visible test situation than was the case for the three movements that had been used in the training phase, although this difference was not statistically significant (*t* (2) = 2.29, ns).

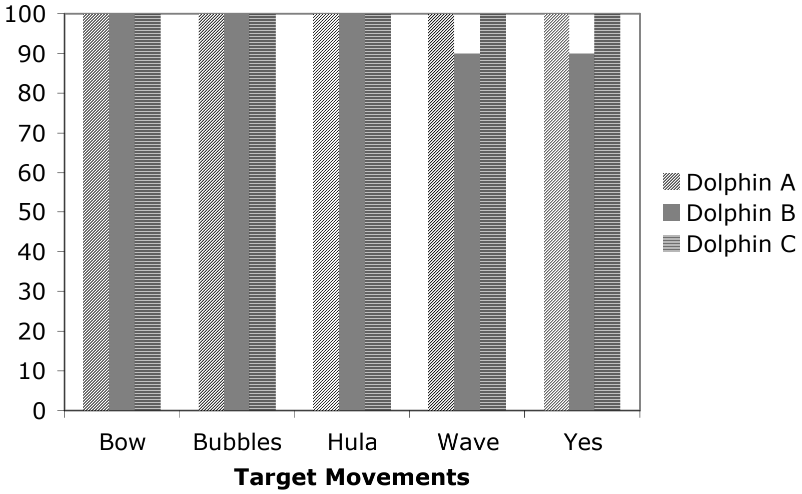

Figure 1. Correct responses to target movements in visible above water condition for each dolphin.

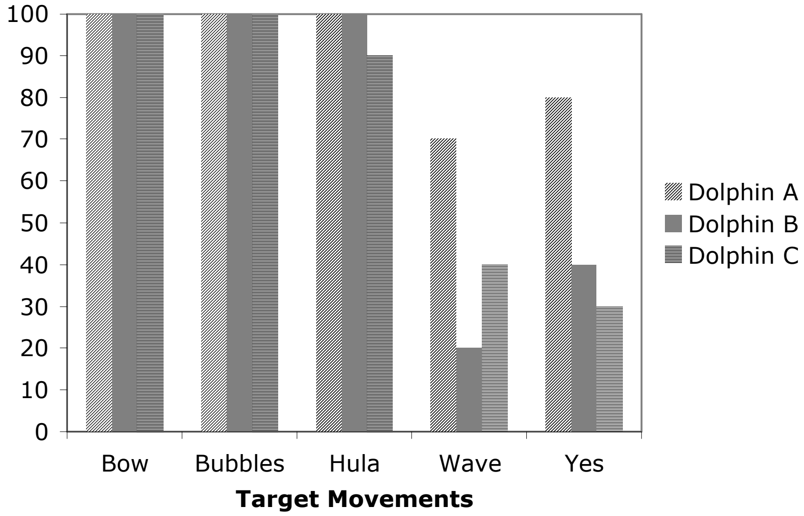

Figure 2. Correct responses to target movements in non-visible underwater condition for each dolphin.

Given the near perfect performances for all target movements in the visible condition, it is not surprising that statistical comparisons yielded no significant differences for either dolphins or target movements in this condition. Similarly, the dolphins' correct responses in the non-visible underwater condition for the three target movements (*bow, bubbles,* and *hula*) that were used in training were also near perfect, and consequently there were no significant differences in the dolphins' correct responses to these three target movements in the visual condition compared to the non-visible condition. Moreover, binomial tests demonstrated that the dolphins performed well above chance for each of these three movements in each condition.

Specifically, each dolphin responded correctly to the *bow* movement significantly more often than she responded incorrectly, both in the visual condition ($p < 0.001$ for each dolphin) and in the echolocation condition ($p < 0.001$ for each dolphin). The same pattern held for the *bubbles* movement. Each dolphin responded correctly to the *bubbles* movement significantly more often than she responded incorrectly, both in the visual condition ($p < 0.001$ for each dolphin) and the echolocation condition ($p < 0.001$ for each dolphin). The *hula* movement yielded similar results. Each dolphin responded correctly to the *hula* movement significantly more often than she responded incorrectly, both in the visual condition ($p < 0.001$ for each dolphin) and the echolocation condition ($p < 0.001$ for dolphins A and B, and $p < 0.01$ for dolphin C).

The dolphins did not fare so well with target movements in the non-visible underwater condition if they had never witnessed a human producing the movements in an underwater environment prior to the test condition. The dolphins were less likely to produce correct responses for the *wave* movement in the non-visible underwater condition than in the visible above-water condition (t (2) = 3.26, $p < 0.05$). They were also were less likely to produce correct responses for the *yes* movement in the non-visible underwater condition than in the visible above-water condition, although this difference did not achieve statistical significance (t (2) = 1.85, ns). Moreover, only dolphin A achieved a success rate of over 50% with either of these movements (and she did so for both target movements). Although binomial tests demonstrated that the dolphins performed well above chance for each of these two movements in the visible condition, such was not the case for the non-visible underwater condition. Specifically, each dolphin responded correctly to the *wave* movement significantly more often than she responded incorrectly in the visual condition ($p < 0.001$ for two dolphins and ($p < 0.01$ for the other dolphin). The same pattern held for the *yes* movement. However, none of the dolphins responded correctly significantly more often than they responded incorrectly to these target movements in the non-visible underwater condition (dolphin A did respond to the *yes* movement correctly eight out of ten times, but this performance did not reach statistical significance, $p < 0.055$).

Discussion

Our results demonstrate that dolphins can respond to underwater movements that they cannot see, at least in the case of movements that they have previously experienced visually. This suggests that dolphins are able to relate dynamic information obtained through echolocation with similar information obtained visually. This ability has been demonstrated for static objects (Harley, 2004; Harley & DeLong, 2008; Harley et al., 2003; Harley et al., 1996; Herman & Pack, 1992; Herman, Pack, & Hoffman-Kuhnt, 1998; Pack & Herman, 1995; Pack et al., 2002), and the present results suggest that the ability to relate visual information and echolocation information exists for dynamic events as well. The ability to relate actions and objects observed visually with those sensed via echolocation suggests that dolphins represent their world in a way that makes cross-modal comparisons possible and meaningful. For example, echolocation and vision are both thought to be important for finding and capturing prey (Au, 1993; Barrett-Lennard, Ford, & Heise, 1996; Purves & Pilleri, 1983; Rossbach & Herzing, 1997), and the ability to integrate information from the two senses most likely maximizes dolphins' predatory efficiency and success. The ability to discriminate and recognize objects echoically and visually facilitates prey detection and selection, and the ability to discriminate, recognize, and anticipate actions in both modalities is a crucial component of successful prey capture and predator avoidance.

Research in recent years has resulted in significant increases in the understanding of the acoustic characteristics of both echolocation clicks and the subsequent returning echoes (Au, 1993; Au & Hastings, 2008; Au et al., 2008; Houser, Helweg & Moore, 1999; Houser et al., 2005; Moore, 1997; Moore, Dankiewicz, & Houser, 2008), as well as an appreciation of the dolphin ability to eavesdrop on the echoes that result from the clicks produced by another dolphin (Götz, Verfaß, & Schnitzler 2005; Gregg, Dudzinski, & Smith, 2007; Xitco & Roitblat, 1996). However, at the present time we know little about the manner in which information is represented and used by dolphins (Harley, Xitco, & Roitblat, 1995; Popper, Hawkins, & Gisiner, 1997; Roitblat, Helweg, & Harley, 1995; Roitblat, 2004). The best available evidence suggests that dolphins recognize equivalences between their visual representations and acoustic representations of objects, although the exact nature of the equivalences is a matter of some dispute (Au & Hastings, 2008; Harley, 2004; Harley & DeLong, 2004; Harley et al., 1996; Herman et al., 1998; Pack & Herman, 1995; Roitblat et al., 1995).

Similarly, the dolphin ability to integrate dynamic information across the two senses of vision and echolocation likely results from the dolphin's recognition of dynamic equivalences between its visual representations and acoustic representations of actions. In their discussion of the role of imagery in dolphin echolocation, Roitblat et al. (1995) suggested that the object-centered representations that result from dolphin echolocation preserve the structural properties of the object, but noted that these representational images need not be vision-like. We also suspect that the representations of actions that result from dolphin echolocation are not visual in nature.

In his theory of perceptual modalities, Gibson (1966) emphasized that the perceptual systems of organisms have evolved to take advantage of the information that exists in the physical world, supposedly because that information is important for the survival of the species. He also suggested that the identification of perceptual stimuli precedes decisions about actions to be taken. Or, in Gibson's words, "what is it?" comes before "what to do about it?" (p. 148). This idea is relevant to our discussion in that dolphins most likely decide what something is before they decide what actions to pursue, regardless of whether the information is obtained via vision or echolocation. Previous experimental work has demonstrated that dolphins can readily identify target objects (Au, 1993; Harley et al., 2003; Houser et al. 2005; Moore et al., 2008), sometimes by eavesdropping on the returning echoes produced by another dolphin (Xitco & Roitblat, 1996), and the present results suggest that dolphins may be able to incorporate an object's movements into decisions about object identity and appropriate reactions to the object, regardless of whether this information comes from information obtained from vision or information obtained from echolocation.

Although our results suggest that dolphins can relate dynamic information obtained via echolocation with that obtained from vision, we recognize that the results are limited. The dolphins in the present study were only tested with human movements that they could readily interpret visually. Consequently, it is possible that the dolphins' ability to relate dynamic information from echolocation and vision depended on prior visual experience, and that dolphins might prove incapable of integrating echoic information about movements with visual information about similar movements if the echoic experiences preceded the visual ones. Although this possibility needs to be tested by training animals to respond to human movements that they perceive echoically before the dolphins are exposed to the movements in the visual domain, we suspect that dolphins will be able to integrate information from the two modalities regardless of which modality provides the initial experience. This has proven to be the case for static object identification (Harley et al., 1996; Harley & DeLong, 2008; Pack & Herman, 1995; Pack et al., 2002), and there is no reason to believe that cross-modal integration of dynamic information should not occur in both directions as well. Of course, data from future studies will determine if our speculations are correct.

The amount of experience that dolphins need to correctly identify dynamic equivalences across the two modalities is also unclear. Dolphins that have visual experience with stationary objects can sometimes recognize one of the objects the first time they are asked to do so using echolocation, and dolphins that have initial echolocation experience with stationary objects can also sometimes recognize one of the objects the first time they are asked to do so visually (Herman et al., 1998; Pack & Herman, 1995). Nonetheless, experience with objects does facilitate dolphins' ability to match the objects across the two modalities. Harley et al. (1996) reported that "dolphins can cross-modally match familiar objects, and when the objects are easily identifiable, the dolphins can cross-modally match in both directions" (p. 172). They suggested that dolphins may find it difficult to cross-modally match unfamiliar objects because their limited experience with the objects has not resulted in the dolphins' encoding sufficient information about the objects to allow cross-modal comparisons.

The results of the present study suggest that dolphins' ability to integrate information about actions across the modalities of vision and echolocation may also depend on the dolphins' experience with the actions. Although each dolphin had considerable visual experience with all five of the target movements, the dolphins had limited experience with three of the movements in an underwater context prior to testing and no experience with the remaining two movements in an underwater context prior to testing. The previous underwater experiences with the *bow, bubbles,* and *hula* movements were sufficient to result in near perfect performances when the dolphins were asked to respond to the movements in the test condition. But the lack of underwater experience with the *wave* and *yes* movements resulted in dramatic decreases in correct responses to these movements for two of the dolphins when they were asked to respond in the test condition. These two dolphins, although near perfect when asked to respond to these movements produced by humans in the visual condition, fared much more poorly in the underwater test condition. Neither of these dolphins produced a correct response the first three times they were exposed to *wave* and the first three times they were exposed to *yes* in the underwater test condition. Evidently, despite their visual experience with these movements, these two dolphins needed echolocation experience with the movements before they were able to relate the information about these movements that they were obtaining via echolocation with the information about the movements that they had previously obtained from their visual experiences. The remaining dolphin proved much better at interpreting the *wave* and *yes* movements in her initial encounters with the movements in the underwater test condition. She responded correctly the first time that she echolocated on the *yes* movement in the test condition. She also responded correctly the second time that she echolocated on the *wave* movement in the test condition. The ability of this dolphin to relate echoic information about movements with previously acquired visual information about these same movements suggests that dolphins can relate dynamic information from the two modalities even with limited experience in one modality. Future studies that systematically examine the role of experience in each modality with dolphins' ability to relate cross-modal information about actions will increase our understanding of the manner in which dolphins represent and make sense of their world.

The finding that dolphins can integrate information about dynamic events obtained via echolocation with that previously obtained from visual experience is not surprising if we assume that dolphins' sensory and perceptual capacities have evolved in order to enhance their ability to make sense of their world, a world in which both vision and echolocation help dolphins detect and avoid obstacles, detect and recognize prey, predators and conspecifics, and determine actions that should be taken to capture prey, meet and interact with conspecifics, and deter or avoid predators. When dolphins are near the surface of the water and the water is clear, vision may suffice to make such decisions. But when dolphins are in deeper or murkier water, the use of vision becomes limited and so dolphins must then rely on their echolocation skills to interpret their world. Although it is possible that dolphins could use two independent representational systems, one for information gathered via vision and the other for information gleaned from echolocation, the results of previous studies with stationary objects and the results of the present study with dynamic events suggest that such is not the case. Dolphins seem predisposed to integrate information from the two perceptual systems, a predisposition that likely facilitates their ability to gather meaningful information about their world.

But what happens when information from one sense conflicts with information from another sense? Sometimes the information is integrated into a perception that is different from what would have occurred if only information from one sense had been involved. For example, when a video of human visual lip movements suggests that one sound will be produced but another sound actually occurs, an audio-visual illusion known as the McGurk effect occurs (McGurk & MacDonald, 1976). Thus, if an adult human sees a video in which the speaker mouths the sound *ga*, but the soundtrack actually produces a *ba* sound instead, the adult will hear the sound *da* (a similar effect has been observed in human infants, which suggests that the integration of auditory and visual information in speech perception requires little experience; Rosenblum, Schmuckler, & Johnson, 1997). The McGurk effect demonstrates that conflicting information from different modalities sometimes results in an integrated perception that does not accurately reflect what actually occurred in either modality. However, this is not always the case when an organism experiences conflicting information from multiple senses. When human adults experience a conflict between visual information and tactile information, the conflict is resolved in favor of the visual information (Rock & Harris, 1967; Power & Graham, 1975). For example, when adults view a square shape through a lens that makes it appear rectangular and also examine the square haptically, subsequent tactual matches are more likely to be based on the visual information (rectangular) than on the haptic information (square). Experiments designed to assess how dolphins respond when visual and acoustic information provide conflicting information about objects and/or actions would be beneficial in terms of increasing our understanding of how dolphins relate information from each sense. Would such information be integrated to create a perception that differs from what would result if the information from either sense was considered independently, as happens in the McGurk effect? Or would one sense "win out" over the other, as happens when vision and touch are put in conflict for human perceivers? Clearly, much remains to be done.

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