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ORIGINAL ARTICLE

Patrick J. O. Miller

Mixed-directionality of killer whale stereotyped calls: a direction of movement cue?

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Abstract The functional and ecological consequences of the directional emission of sounds used for communication remain largely unexplored even though non-uniform radiation patterns have been reported across a wide range of taxa. In this study the spectral structure of stereotyped calls recorded from groups of travelling killer whales (*Orcinus orca*) moving consistently toward or away from a towed hydrophone array was measured by comparing the energy in high-frequency (>5 kHz) with that in low-frequency (1–5 kHz) bands. Relative energy in high-frequency bands was significantly greater when animals were moving toward the hydrophone array, but only in call types that contain a separately modulated high-frequency component. The difference in relative energy as a function of direction of movement was more than 10 dB at the fundamental frequency of the high-frequency component of the two most common types recorded, confirming a strong pattern of mixed-directionality in these calls. Changes in call spectra due to signaler orientation to a receiver may provide an intrinsic cue of a moving signaler's direction of movement. Killer whales have sensitive hearing over the frequency range of this potential cue, and their marked behavioral synchrony suggests its use. The direction of movement cue inherent in the directionality pattern of calls may be an efficient and reliable means for this and possibly other highly mobile species to coordinate behavior and regulate spacing relative to other individuals.

Keywords Directionality · Orientation · Calling · Contact · Killer whales

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P.J.O. Miller (✉)
Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
e-mail: pmiller@whoi.edu
Tel.: +1-508-2893482, Fax: +1-508-4572134

Introduction

Acoustic signals produced by animals commonly radiate in a non-uniform fashion from the signaler (insects: Michelsen and Fonseca 2000; anurans: Gerhardt 1975; Prestwich et al. 1989; fish: Barimo and Fine 1998; birds: Archibald 1974; Witkin 1977; Hunter et al. 1986; Larsen and Dabelsteen 1990; Dantzker et al. 1999; bats: Schnitzler and Grinnell 1977; seals: Schevill and Watkins 1971; odontocetes: Schevill and Watkins 1966; Au et al. 1986, 1987, 1995; Mohl et al. 2000; primates: Dunn and Farnsworth 1939). The directional pattern of sound transmission is thought to arise from directional sound source resonators (Hunter et al. 1986; Au et al. 1987), shadowing by tissues (Schnitzler and Grinnell 1977), and/or gradations in sound speed in fatty structures in the head of delphinids (Aroyan 1990; Au 1993; Aroyan et al. 2000). The echolocation sounds of bats and odontocetes are highly directional, which results in a higher signal-tonoise ratio of returning echoes, a fact which has been exploited by human-designed sonar systems (Urick 1983).

In contrast to our understanding of the function of directionality in echolocation signals, little is known about the functional or ecological significance of the directional emission of sounds used primarily for communication. The lack of research effort in this area may reflect difficulties entailed with measuring the directionality of signals in the field (Larsen and Dabelsteen 1990), a difficulty which new techniques employing arrays of receivers may have the potential to overcome (e.g. Dantzker et al. 1999). In general, directional "beaming" is thought to benefit signalers by increasing signal levels at an intended receiver, while decreasing the risk of signal interception by non-intended receivers such as predators (Witkin 1977; Klump and Shalter 1984; Dantzker et al. 1999). When territorial blackbirds approach a conspecific intruder, they switch from a loud, omni-directional version of their territorial display to a fainter directional display, presumably to reduce detection risk and direct signals at the intruder (Dabelsteen and Pedersen 1988; Larsen and Dabelsteen 1990).

Directionality is predicted to increase with signal frequency because sound source resonators and tissue structures are more effective at absorbing, reflecting, and/or focusing small wavelengths. This effect has been observed in birds as increased directionality in high-frequency portions of the signal (Witkin 1977; Larsen and Dabelsteen 1990), and in the echolocation signals of dolphins (Au 1993; Au et al. 1995). Compound signals containing both directional and non-directional components, coined "mixed-directionality" by Larsen and Dabelsteen (1990), might be used to communicate the location of a predator to flockmates or to direct sounds at a particular, intended receiver by cueing signaler orientation (Hunter et al. 1986).

Here I propose an alternative consequence of signal directionality that may be particularly important for promoting group cohesion and behavioral synchrony in mobile animals: that the production of communication signals with mixed-directionality is a mechanism by which signalers can provide a cue of their direction of movement to intended receivers. Direction of movement would be cued when the received structure of a signal is altered in a predictable fashion depending on the orientation of the signaler, and when direction of movement correlates with animal orientation. Mobile animals that orient in their travel direction would effectively signal their future position to any receiver that is familiar with how directionality alters the signal structure. This study focuses on acoustic signals, but visual signals such as animal markings may also function in this manner (e.g. the white rump region in stotting gazelles; Walther 1969).

Many studies have shown that animals are capable of localizing sound sources by determining the source's azimuth, elevation, and distance (Richards 1981; reviewed in Klump and Shalter 1984; Nelson and Stoddard 1998; Naguib and Wiley 2001). In group-living animals, sound source localization provides a means for receivers to approach or maintain distance from signalers (Marler 1965) or to stay within the acoustic range of other group members (Caine and Stevens 1990). Production of a direction of movement cue would allow signalers to effectively signal their future location to intended receivers with a lower calling duty cycle than that required by tracking source locations. A receiver could use this cue to make corrective turns before its position relative to the signaler changes, resulting in greater efficiency of group coordination and increased synchrony between group members. Finally, tracking may be less reliable for maintaining contact because large changes in distance may be necessary to determine a change in position at long ranges and signalers may move out of acoustic contact between calls.

In this study, I assess whether an acoustic direction of movement cue is generated by the directionality structure of the broadband calls produced by free-ranging killer whales. Several aspects of the ecology of marine mammals support the evolution of an acoustic direction of movement cue, including: short vision ranges relative to acoustic ranges across a wide band of frequencies, relatively low frequency-dependent absorption of sound in seawater, high mobility aided by low locomotion costs (Williams 1999), and high degrees of sociality (Connor et al. 1998).

Fish-eating killer whales produce a group-distinctive repertoire of intense stereotyped calls (Ford 1991; Strager 1995; Miller and Bain 2000). All calls produced by killer whales have a low-frequency (80–2,400 Hz) contour that represents the repetition rate of a click train (Schevill and Watkins 1966; Ford 1987). In addition to the low-frequency contour, many call types also contain a separately modulated high-frequency contour (2–12 kHz; Hoelzel and Osborne 1986; Ford 1987; Strager 1995; Miller and Bain 2000). Both low- and high-frequency contours contain several harmonics. Calling is thought to function to coordinate activities and maintain cohesion among members of highly stable matrilineal social units (Ford 1989). Recent work employing hydrophone arrays demonstrates that separated group members commonly exchange shared calls with each other in tight temporal sequences (Miller et al. 2002). Thus, calling appears to be highly interactive and likely promotes synchrony and social cohesion between members of stable killer whale groups (Ford 1989).

While a transmission beam pattern has never been measured for killer whale calls, Schevill and Watkins (1966) and Bain and Dalheim (1994) anecdotally noted that killer whale clicks and calls appeared to be directional at high frequencies. Calls recorded in the field occasionally lack high-frequency components (HFC), suggesting they were received from animals oriented away from the hydrophone (Miller and Bain 2000). By employing a towed hydrophone array to reliably record calls from free-ranging animals consistently moving toward or away from the array, this study demonstrates that certain killer whale call types are directional at high relative to low frequencies. The potential for signal directionality to generate a functional direction of movement cue is strongly influenced by both social behavior and the ecology of signal transmission, which differ greatly in marine and terrestrial habitats. In the appropriate conditions, the direction of movement cue in acoustic signals may be an important mechanism by which mobile animals synchronize behavior and improve cohesion with preferred associates.

Methods

To measure the effect of signaler orientation and direction of movement on the frequency content of received signals, I approached isolated, compact groups of killer whales which were consistently moving in one direction and vocally active. Using an 11 m research vessel, I towed a 16-element linear hydrophone array (see Miller and Tyack 1998 for details of the array system) roughly 200 m in front of the group, and towed the array parallel to the direction of movement of the animals at minimum speed (~1.5 m/s). At this speed, noise from the engine of the research vessel was negligible, and the vocalizing whales typically passed the array and research vessel over a 15- to 25-min time period (Fig. 1).

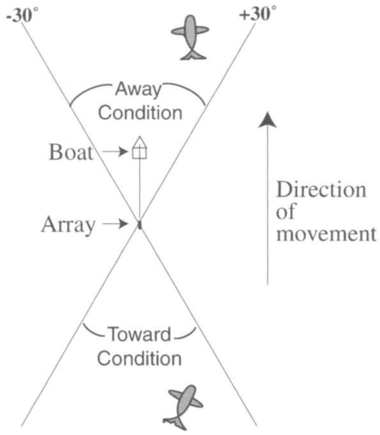

Fig. 1 Technique employed to record sounds from free-ranging killer whales moving toward versus away from a towed hydrophone array. The array was positioned roughly 200 m in front of a group of whales, and whales were allowed to pass the array and boat until sighted 500 m or more ahead. Sounds arriving from within 30° of directly behind, and ahead of the array were grouped as *Toward* and *Away* condition calls, respectively. Visual observers recorded the orientations of surfacing animals in the same locations. The orientation of the whale figures represents the mean surfacing orientation of whales in the Away (158.6° from the array) and Toward (40.4° from the array) conditions

To confirm that animals were consistently oriented in their direction of movement, two teams of observers on the research vessel visually scored the orientations of surfacing whales relative to the array using scan sampling methods (Altmann 1974). One team recorded all surfacing orientations of animals within 30° of directly behind the array, while the other recorded orientations of animals surfacing within 30° of directly in front of the array. Orientations were scored in 30° bins as "o'clocks", with "12" being the value for surfacing orientations directly toward the array and "6" for orientations directly away from the array. Orientation scores were subsequently converted to degrees off the whale-array axis (i.e. 12=0, 3 and 9=90, 6=180, etc.) Pass-by follows were terminated once animals were sighted surfacing 500 m or more ahead of the vessel.

The angle-of-arrival of the sounds recorded during these pass-by sessions was calculated using conventional beamforming techniques (see Miller and Tyack 1998 for details). I grouped calls in the "Toward" condition if they arrived within 30° of directly behind the array, and in the "Away" condition if they arrived within 30° of directly ahead of the array. In addition to the multi-channel array recording system (see Miller and Tyack 1998 for system details), sounds from one hydrophone in the center of the array were recorded on a Pioneer D-9601 recorder (flat ±0.5 dB 20–44 kHz), and re-digitized at a 100 kHz sampling rate using a custom digital processor board.

The hydrophone sensors as well as the combined array were constructed to be symmetric to assure equal frequency-dependent sensitivity to sounds arriving from ahead and behind. The directional response of an individual hydrophone element was calibrated in an anechoic tank, and varied by less than 2.0 dB for any angle within 30° of directly ahead or behind at 12 kHz (USRD no. 8386-32). A hydrophone near the center of the array was used for the analysis so that wires and other array hydrophones were equally present both behind and ahead of the analysis hydrophone. To confirm that the overall system was equally sensitive ahead and behind, the array was towed four times past an omni-directional underwater speaker transmitting a set of tones at 2, 3, 4, 5, 6.2, 7.5, 8.5 and 12.5 kHz. Analysis of the received spectra showed little variation in the relative level of these tones whether the speaker was within 30° of directly in front, or behind, the boat. Over all passes, relative energy in the 1–5 versus 5–14 kHz bands (see below) received from the speaker differed by less than 1.0 dB whether the speaker was in front, versus behind, the array.

All calls recorded during pass-by follows were visualized using spectrograms in Matlab and classified to type according to the naming system devised by Ford (1987, 1991). Call types were grouped as "HFC" or "no-HFC" based on the presence or lack, respectively, of an independently modulated high-frequency component in previous studies (Ford 1987; Miller and Bain 2000). Stereotyped calls N1, N2, N4, N5, and N9 were grouped as "HFC", while N7, N8, and N3 were grouped as "no-HFC". I used custom Matlab software to calculate the power spectral density of each call and a portion of noise immediately prior to the onset of the call. In a few cases, in which loud transient sounds (such as echolocation clicks) overlapped a portion of the calls, I used the longest (never less than 100 ms in duration) continuous non-affected portion of the call. The noise power spectral density was subtracted from that of the call to reduce frequency-dependent effects of external noise sources.

The spectral structure of each call was measured by comparing noise-subtracted signal intensity in different frequency bands. Previous observations suggested that the 1–5 kHz band was considerably less directional than higher frequencies (Miller and Bain 2000), so the intensity of this band was compared to that in higher-frequency bands. The ratio of energy in the low- versus high-frequency bands was obtained by subtracting the energy in the high-frequency (5–14 kHz) band from that in the 1–5 kHz band after conversion to decibels. Although recordings were made to higher frequencies, I limited the quantitative analysis of call spectra to 14 kHz because the array had been carefully calibrated to this frequency. Also, absorption of sound in seawater at 14 kHz is small (0.1–0.2 dB/100 m; Francois and Garrison 1982). Thus, any consistent tendency for whales to be closer or further from the array (within the 500 m maximum range) in the two conditions would have a negligible effect on frequency-dependent sound absorption of call components at and below 14 kHz.

The effect of direction of movement on relative energy in the two bands was assessed using a two-way ANOVA, and simple-main effects analysis of the two-way interaction term (Huck et al. 1974) was used to assess differences in the effect of orientation on call spectra between HFC and no-HFC call type classes (types with and without a high-frequency component, respectively).

Results

I analyzed sounds from a total of six pass-by sessions totaling 124.6 min of recordings on 5 different days in 1999. All sessions were carried out in Johnstone Strait, British Columbia, with animals from pods A5 and W3 present in five sessions and animals from pod A1 present in one session (Ford et al. 1994). As expected, the whales' direction of movement was consistent with surfacing orientations and paralleled that of the research vessel. Animals surfacing behind the array had a mean orientation of 40.4°(±13.8°SD) away from the array, while animals surfacing in front of the array had a mean orientation of 158.6°±14.9° away from the array (Fig. 1). Thus, while not as controlled as captive work in which an animal is trained to vocalize in a fixed position, this method was sufficient to observe the broad directionality effects of animals moving toward versus away from a receiver in the wild.

A total of 666 calls were recorded on the array. Of these 174 arrived within 30° of directly behind the array (–73.4°±5.3°) and were scored as "Toward" condition calls, and 89 calls arrived within 30° of directly in front

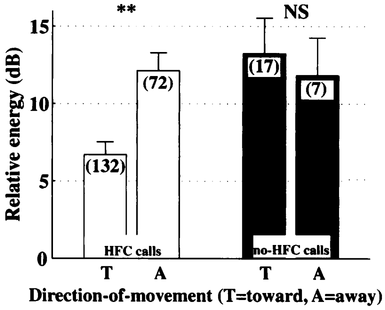

Fig. 2 Mean (+2SE) relative energy in the 5–14 kHz and 1–5 kHz bands of calls recorded from animals moving toward and away from the array for call types that contain high-frequency components (HFC types N1, N2, N4, N5, and N9; *open bars*) and types that do not contain such a component (no-HFC types N3, N7, and N8; *filled bars*). Sample sizes for each condition are given in *parentheses*. Note that direction of movement influenced relative energy in these frequency bands only for the group of call types that contain a high-frequency component. *Double asterisk* indicates $F_{1,224}=1{,}374.8$, $P<0.0001$

of the array (+73.4°±7.2°) and were scored as "Away" condition calls. Of the 174 calls in the Toward condition 132 were of types N2 ($n=9$), N4 ($n=58$), N5 ($n=4$), or N9 ($n=56$) and were classified as "HFC", while 17 were of types N3 ($n=5$), N7 ($n=7$), or N8 ($n=3$) and were labeled "no-HFC". Of the 89 calls in the Away condition, 72 were of types N1 ($n=2$), N2 ($n=10$), N4 ($n=25$), N5 ($n=8$), or N9 ($n=27$) and were classified as "HFC", while seven were of types N3 ($n=1$) or N7 ($n=6$) and were labeled "no-HFC". The remaining rare and variable calls were excluded from the two-way ANOVA analysis of main effects.

The analysis of relative energy in the 1–5 and 5–14 kHz bands revealed significantly more energy in the high-frequency band when animals were moving toward the array, but only for HFC call types (Fig. 2). This finding was confirmed by a statistically significant interaction term in the two-way ANOVA ($F_{1,224}=9.5$, $P<0.01$). Simple main effects analysis revealed that di-

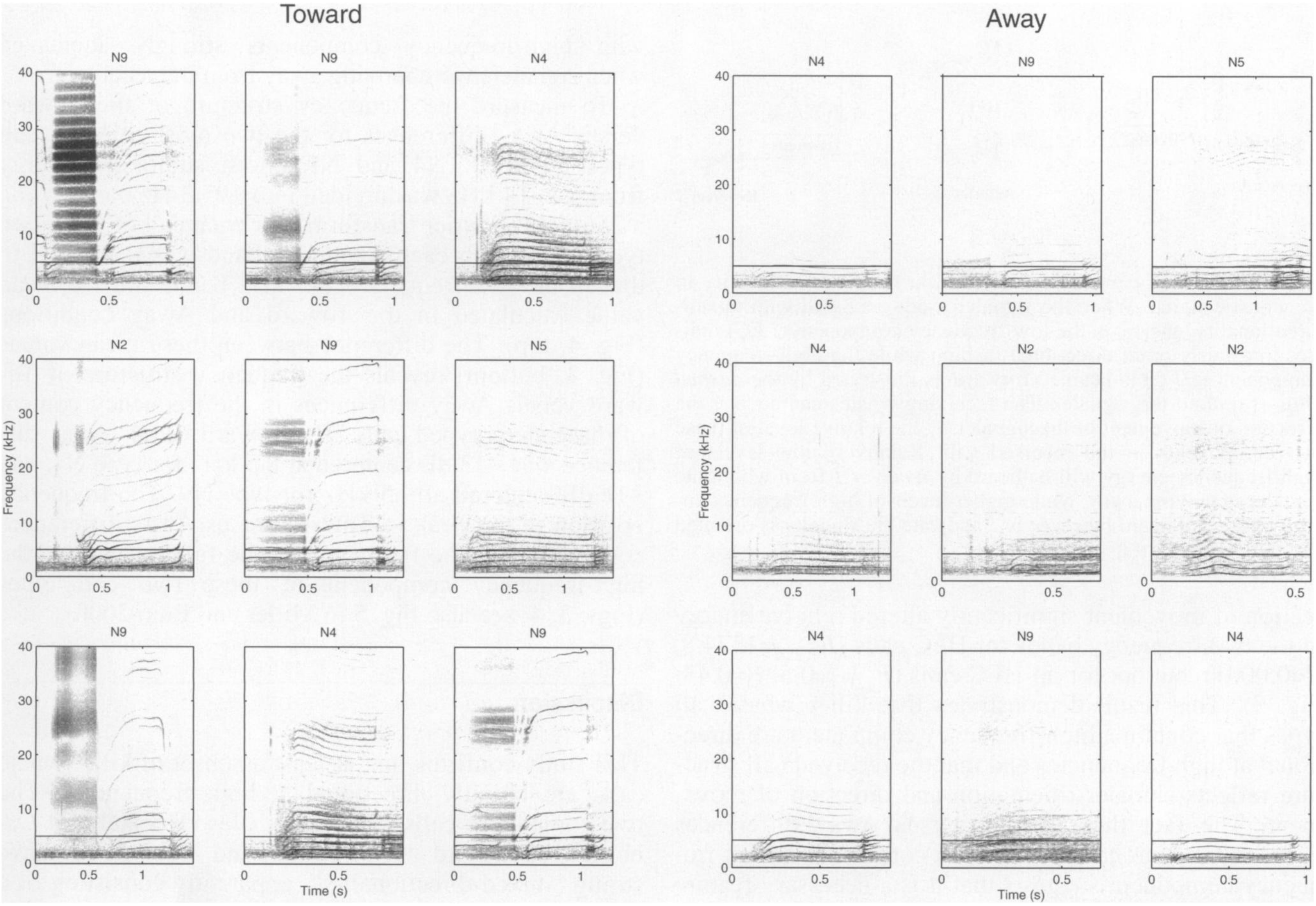

Fig. 3 Spectrograms of a random selection of calls of types that contain high-frequency components from animals moving toward (*left*) and away (*right*) from the array. The type of each call is noted above its spectrogram, and the *line* at 5 kHz marks the frequency below which energy was summed in the 1–5 kHz band. Note the clear differences in the spectral structure of calls depending on the direction of movement of the caller, particularly that the high-frequency component is strongly attenuated when callers were oriented and moving away from the receiver. All spectrograms have an effective filter bandwidth of 48.8 Hz and dynamic range of 55–85 dB re 1 μPa²/Hz

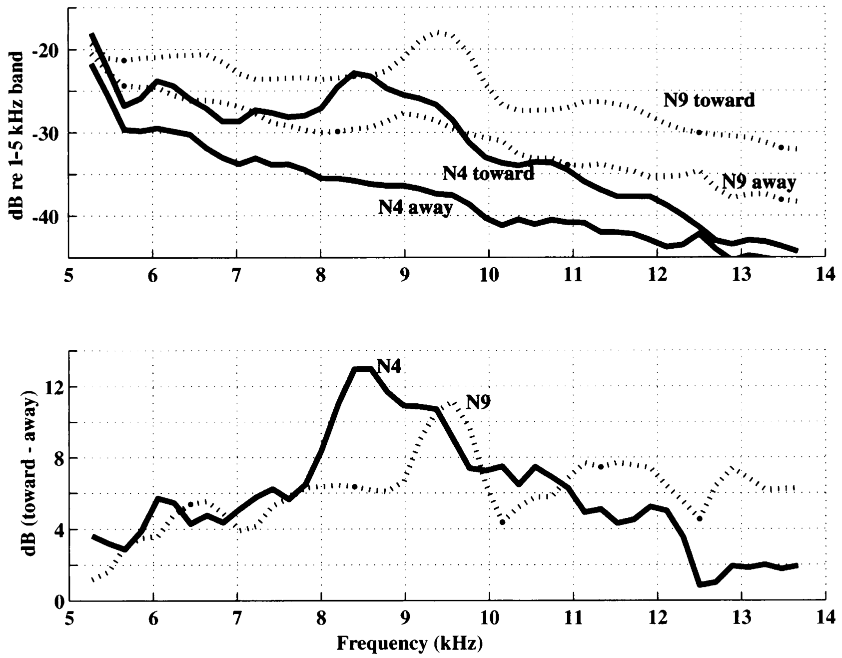

Fig. 4 Frequency structure of the 5–14 kHz band relative to the 1–5 kHz reference band for HFC call types N4 (*solid lines*) and N9 (*dashed lines*) depending on direction of movement. For each call, energy in 195.3 Hz bands from 5 to 14 kHz was compared to that in the 1–5 kHz band. The mean value for each type was calculated in the Toward and Away conditions (*top panel*). The difference between these mean values (*bottom*) represents the frequency structure of Toward versus Away differences in these stereotyped calls. The frequency position of the peaks (8.5 and 9.5 kHz) in the *bottom panel* corresponds with the frequency of the fundamental of the high-frequency component for call types N4 and N9, respectively (see Fig. 3, *panel 1*; see also Fig. 5 in Miller and Bain 2000)

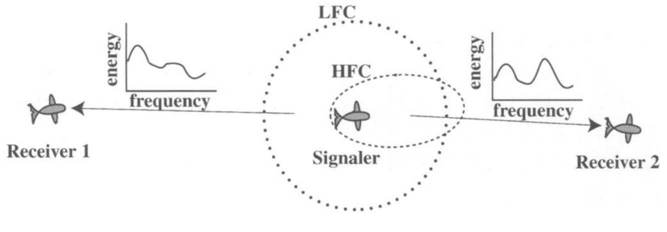

Fig. 5 Direction of movement cueing via mixed-directionality in an acoustic signal. When the signaler produces a call with mixed-directionality, energy in the low-frequency component (*LFC*) radiates in a fairly omni-directional fashion while the high-frequency component (*HFC*) is beamed forward as illustrated by the *dashed ellipses* around the signaler. The receiving whales can deduce the direction of movement of the signaler by the relative level of these two components in the received call. Relatively low levels of high-frequency energy will be heard by *receiver 1* from whom the signaler is moving away, while higher levels of high-frequency energy in the call heard by *receiver 2* indicate the signaler is oriented and moving toward it

rection of movement significantly altered relative energy in the two frequency bands for HFC calls ($F_{1,224}$=1374.8, P<0.0001), but not for no-HFC calls ($F_{1,224}$=0.5, P=0.48; Fig. 2). This result demonstrates that killer whale call types that contain a high-frequency component are directional at high frequencies and that the received call structure reflects signaler orientation and direction of movement. The fact that Toward versus Away differences were only apparent for call types containing a high-frequency component suggests that it is a necessary feature for the generation of a possible direction of movement cue in killer whale calls.

The effect of signaler direction of movement on the spectral structure of HFC calls (types N1, N2, N4, N5, and N9) was readily apparent in spectrographic analysis of a random sample of calls from the two conditions (Fig. 3), with high-frequency components strongly attenuated when signalers were moving away from the receiver.

To measure the frequency structure of the Toward versus Away differences for the two most common call types recorded (N4 and N9), noise-subtracted energy from 5 to 14 kHz was divided into 195.3 Hz bands using a 256-point Fourier transform. For each call of these two types, energy in each frequency band was compared to that in the low-frequency 1–5 kHz band, and the mean value calculated in the Toward and Away conditions (Fig. 4, top). The difference between these mean values (Fig. 4, bottom) reveals the frequency structure of Toward versus Away differences in the frequency content of these stereotyped calls. The Toward versus Away difference was ~13 dB centered at 8.5 kHz for type N4, and ~11 dB centered at 9.5 kHz for type N9. The frequency position of the peak in Toward versus Away differences corresponds to the frequency of the fundamental of the high-frequency component of these two call types (Figs. 3, 4; see also Fig. 5 in Miller and Bain 2000).

Discussion

This study confirms that at least a subset of killer whale calls are broadly directional at high frequencies. The two-component calls of killer whales (Hoelzel and Osborne 1986; Ford 1987; Miller and Bain 2000) have strong "mixed-directionality", apparently consisting of a fairly omni-directional low-frequency component overlaid with a strongly directional high-frequency component. In this study, the spectral structure of these two-component calls correlated with signaler orientation and direction of movement, with high-frequency bands strongly attenuated when animals were moving away from the array. In contrast, no consistent effect of direction of movement was found for call types without a high-frequency component.

The technique used in this study was adequate to demonstrate broad front-to-back directionality in the high-frequency component of stereotyped calls produced by free-ranging killer whales, but does not provide an accurate measure of the radiation beam pattern. The frequency-response of the calibrated analysis-hydrophone was equally sensitive to sounds arriving from a speaker located ahead and behind the array, and low levels of absorption by seawater at and below 14 kHz minimize any effect of differences in range to signalers when ahead and behind the array. The slow movement of the whales relative to the array (<3.0 m/s) relative to the speed of sound in water (~1,500 m/s) rules out any possible influence of Doppler shift on the broadband measures of spectral content in this study. The consistent and strong differences in the spectral content of stereotyped calls in the Toward and Away conditions can only result from forward-directed radiation of high-frequency call components relative to low-frequency components.

Nonetheless, whales behind and ahead of the array were clearly not always oriented directly toward or away from the array when calling (Fig. 1), and whales may have turned underwater when producing some of the calls. Therefore, the measured effect of direction of movement on relative levels of high-frequency energy in calls (Figs. 2, 4) reported here can only be considered a minimum estimate of actual front-to-back differences in the radiation pattern. A complete and accurate transmission beam pattern can best be measured using captive animals trained to vocalize in a fixed position (e.g. Au 1993) within a 360° array of hydrophones.

Toward versus Away differences peaked at frequencies occupied by the high-frequency component (Fig. 4), and were only found for call types known to contain a high-frequency component (Fig. 2). While the mechanism that causes directional radiation of killer whale calls is unknown, these results suggest that the high-frequency component of these calls is particularly directional relative to the low-frequency component. Killer whale calls are pulsed calls, likely produced by the same mechanism as echolocation clicks (Schevill and Watkins 1966), so directionality is likely caused by similar mechanisms thought to cause directionality in dolphin echolocation clicks (Au 1993; Aroyan et al. 2000). Experiments with helium-breathing porpoises found increases in the peak frequency of the low-frequency component of clicks, but no change for the peak of the high-frequency component of clicks, suggesting that the low-frequency component is generated by an air resonance while the high-frequency component in generated by a tissue resonance (Amundin 1991). While research on call production mechanisms in killer whales is lacking, an intriguing possibility is that acoustic energy in the two components propagates along different pathways from the sound resonators to the environment (D. Bain, personal communication). Tissues in the head may be more effective at focusing tissue resonated high-frequency components than air resonated low-frequency components.

Could signalers use mixed-directionality of acoustic signals to cue their direction of movement to intended receivers?

In this study, mixed-directionality caused changes in the received spectral content of calls that correlated with the direction of movement of the signalers. It can be conjectured, therefore, that receivers themselves make use of this information to more efficiently synchronize their movements and maintain contact with signalers (Fig. 5). While playback experiments are necessary to test whether receivers attend to this potential cue, several lines of evidence support the hypothesis that killer whales can and do make use of this feature of their calls. Field observations of killer whales suggest that travel direction is highly synchronized even when individuals are out of visual range with each other, and that calling often occurs immediately before a change in swim-direction (Jacobsen 1986; personal observation). Resident killer whales live in stable, life-long, matrilineal groups with extensive maternal care and evidence for kin-based altruism (Baird 2000), and aspects of their foraging behavior may be cooperative (Barrett-Lennard et al. 1996). By cueing their direction of movement, signalers help receivers make more efficient decisions on how fast, and in which direction (i.e. during turns), to move in order to stay in acoustic contact and coordinate behavior such as foraging. The signaler would benefit from the resulting increase in social synchrony with group members. Type-matching vocal exchanges by killer whales (Miller et al. 2002) may be a means for group members to reciprocally signal their direction of movement to each other.

A signaler must actually be moving for a mixed-directional signal to cue direction of movement to a receiver, with signaler orientation constrained by its direction of movement. In this study, animals were oriented in their direction of movement, but in other less-mobile behavioral contexts, i.e. socializing (Osborne 1986; Ford 1989), direction of movement may not be as closely correlated with orientation as in my sample. In these non-travel contexts, the orientation-cue provided by the directionality structure of calls could serve other functions such as directing displays to an intended receiver as originally suggested by Hunter et al. (1986). A cetacean tag capable of recording audio as well as animal orientation (Johnson and Tyack 2002) may be an ideal tool to systematically explore how free-ranging killer whales orient when calling in different behavioral contexts.

The active space of the proposed direction of movement cue depends on the overall signal source level, the strength of the directionality effect on spectral structure, the sensitivity of receivers to the changes in spectral content of calls, and the degree to which propagation through the environment degrades the cue (Wiley and Richards 1982). In quiet conditions, the intense N9 and

N4 call types are likely to be audible to other killer whales at ranges of 10s of km (Ford and Fisher 1983; Miller 2000). Directionality affects the relative level of the two independently modulated sound contours in a frequency range where killer whales have sensitive hearing (Hall and Johnson 1972; Symanski et al. 1999). The human auditory system can discriminate very small changes in the spectral shape of sound complexes. They are able to detect changes of <1.0 dB in the relative level of simultaneously presented tones (Versfeld and Houtsma 1995). Zebra finches (*Taeniopygia guttata*) and budgerigars (*Melospittacus undulatus*) can detect changes as small as 1.5–2.0 dB in the amplitude of the fifth harmonic of a 570 Hz tone (Lohr and Dooling 1998). While I am aware of no similar work on cetaceans, successive and interaural intensity discrimination in dolphins appears to be similar to that in humans (Ketten 2000), and humans are more sensitive to changes in the level of simultaneously presented than successive sounds (Green et al. 1983). We can therefore predict that dolphins, including killer whales, also have the ability to finely discriminate changes in call spectral content due to signal directionality.

Because both mixed-directionality and frequency-dependent sound attenuation alter the relative levels of different frequency bands, directionality effects will be most reliably discernable over short ranges where frequency-dependent attenuation is minor relative to the directionality effect. While receivers may be able to separate the effect of absorption from that of orientation by judging the range to a signaler using non-absorption cues like reverberation (Naguib and Wiley 2001), this is likely to require complex processing (Hunter et al. 1986).

In the underwater environment, low levels of frequency-dependent attenuation strongly favor the ability of receivers to use the spectral content of signals to deduce signaler orientation. The effect of signaler direction of movement on relative energy from 8–10 kHz versus the 1–5 kHz band in the N4 and N9 call types (Fig. 4) would degrade by less than 0.1 dB over a km of propagation through seawater (underwater absorption at 1 and 10 kHz is <0.001 and 0.01 dB/100 m, respectively; Francois and Garrison 1985). The effect of orientation on signal content should therefore be audible to receiving killer whales over at least several kilometers. Given the low levels of frequency-dependent attenuation of sound underwater, the spectral content of signals will be a less reliable cue for range-assessment than other propagation effects such as overall signal level and reverberation levels (Naguib and Wiley 2001).

In contrast, far greater levels of frequency-dependent attenuation in the terrestrial environment (absorption at 1 and 10 kHz is ~0.6 and 10.0 dB/100 m, respectively; Bass et al. 1990) should strongly limit the range over which receivers can deduce directional effects on signal structure. Hunter et al. (1986) measured a 27 dB directionality effect at 10 kHz from speaker transmissions from a starling (*Sturnus vulgaris*). Frequency-dependent absorption in air will attenuate 10 kHz energy by 27 dB more than 1 kHz energy over 300 m of propagation. Therefore, in terrestrial taxa producing calls from 1–10 kHz, direction of movement cueing through the mixed-directionality of acoustic signals should be effective over ranges of less than a few hundred meters. Visual tracking of movement is likely to be more effective for many terrestrial taxa at such distances, except in cases where vision is blocked due to vegetation or lack of light. This effect supports Witkin's (1977) conclusion that the directionality features of bird sounds should generally be most pronounced in sounds used in close interactions.

A number of other cetacean species including spinner dolphins (*Stenella longirostris*) and humpback whales (*Megaptera novaeangliae*) are likely to produce mixed-directional communication signals and should benefit from increased social synchrony during group foraging and traveling (Lammers and Au 2001; Au et al. 2001). There are also many contexts in which mobile terrestrial animals are predicted to benefit from increased social synchrony with conspecifics. However, an acoustic direction of movement cue may not benefit a signaler if visual inspection by receivers, possibly aided by visual signals, is an effective means of discerning travel direction, particularly if acoustic signaling increases predation risk. One specific context in which an acoustic direction of movement cue might be adaptive in terrestrial systems is the nocturnal flight calling of migrating birds. These calls cover a frequency range shown to have mixed-directionality in birds (Hunter et al. 1986; Larsen and Dabelsteen 1990; Evans 1994), and the benefits of flocking may select for calls that cue the signaler's orientation and travel direction to other birds. Another possible candidate in terrestrial systems are mobile primate groups in forests and savannah habitats where vision is blocked by vegetation (Boinski 1993; Cheney et al. 1996).

While the proposed direction of movement cue is almost certainly audible to killer whales at typical ranges to intended receivers, some degree of familiarity with the sound may be required to decode the directionality effect. Receivers must distinguish calls produced when the signaler is moving away, and thereby lacking high-frequency components, from other call types that are normally produced without a high-frequency component. Familiarity with stereotyped signal structure, and thereby directionality and other propagation effects on the signal (Shy and Morton 1986; Wiley 1998; Naguib and Wiley 2001), may be a significant benefit supporting vocal sharing in this and other species. Further work employing playback experiments are needed to test how receiving killer whales respond to this potential cue, and to assess whether familiarity is necessary for receivers to interpret directionality effects on signal structure.

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