



The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*



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The addressing of individuals with learned signals is inherent to human social interactions. It allows individuals to solicit the attention of a particular social companion or to direct information towards an intended recipient. The ability to address individual conspecifics with learned signals is not limited to humans, however. In songbirds, the selective addressing of individuals is facilitated by song type matching but is very much a signal of aggressive intent. The matching of learned signals is also observed in bottlenose dolphins, which will match one another's highly individualized signature whistle. Copying in dolphins occurs between close associates, which suggests that it is an affiliative signal. It could, however, also serve to manage aggression. We investigated the valence of signature whistle matching by performing interactive playback experiments. We waited until an animal produced its signature whistle and then either played back a synthetic version of its own whistle (match) or a different signature whistle (control). A total of 110 playback experiments were conducted with seven different animals from two managed groups of dolphins. The responses to the playback treatments were significantly different. Animals produced a consistent vocal response to being vocally matched, by returning the match, with no associated signal of aggression and did not respond to control playbacks in the same way. There was also an optimum time interval (<1 s) in which a match was most successful in eliciting a vocal response. Our results show that signature whistle matching is an affiliative signal that allows bottlenose dolphins to address social companions. Furthermore, these matching exchanges are driven by temporal associations, which appear to be essential in allowing animals to direct signals to particular individuals in large communication networks.

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Vocal matching with learned signals is a powerful mode of interaction utilized by a select number of animals, namely songbirds (Searcy & Beecher, 2009), parrots (Balsby & Bradbury, 2009; Balsby, Momberg, & Dabelsteen, 2012) and odontocetes (Janik, 2000; King, Sayigh, Wells, Fellner, & Janik, 2013; Miller, Shapiro, Tyack, & Solow, 2004; Schulz, Whitehead, Gero, & Rendell, 2008). Matching can be described as a receiver responding to a signal by changing some features of its own vocal behaviour in order to imitate the preceding signal. The rapid matching of acoustic signals is a way of directing a response towards an intended receiver thus allowing a signaller to address individual conspecifics. Theory predicts that it should be common in complex communication networks in which signals can be directed at a multitude of listeners (McGregor & Dabelsteen, 1996).

The timing of the response is a crucial factor in vocal matching. A rapid response may be perceived as an aggressive act (Beecher, Campbell, Burt, Hill, & Nordby, 2000; Searcy & Beecher, 2009), whereas a long interval between signals may not be seen as a response to the first signal. Studies on a variety of species show that, in general terms, the timing of call production appears to be governed by temporal rules whereby animals reply to a signal within a short time interval (Kureta, 2000; Masataka & Biben, 1987; Nakahara & Miyazaki, 2011; Sugiura, 1993). For example, in nightingales, *Luscinia megarhynchos*, response latencies in vocal matching interactions are much shorter when song types are matched than when they are not (Geberzahn, Hultsch, & Todt, 2013). Geberzahn et al. (2013) suggested that memory of song patterns may influence the response latencies.

The duration of the interval until a matching response is given may also indicate the motivation of the respondent (Todt, 1981; Todt & Naguib, 2000). Todt (1981) considered both overlapping matching and delayed matching (where an animal waits until after

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the signaller has called), with the former hypothesized to be a 'vocal threat' or agonistic in nature as it was associated with high arousal, and the latter as a more affiliative exchange or 'vocal greeting' as it seemed to occur when birds were less aroused (Todt, 1981; Todt & Hultsch, 1996). Overlapping of the same signal type between two individuals occurs in highly escalated vocal contests in some bird species (McGregor, Dabelsteen, Shepherd, & Pedersen, 1992; Vehrencamp, 2001) and may be seen as an extension of rapid matching and therefore agonistic in nature (Naguib & Mennill, 2010). This vocal behaviour does not, however, appear to occur above chance levels and therefore the functional significance of overlapping remains an area of contention (Naguib & Mennill, 2010; Searcy & Beecher, 2009, 2010). Furthermore, overlapping can be found in duetting birds as an affiliative signal (Hall, 2009). In contrast, if a respondent delays a vocal match until after the signaller has called then vocal interference is avoided and more subtle information, encoded in the calls, can be exchanged between the individuals (Todt & Naguib, 2000). As such, the signal value of matching is closely linked to the temporal interval of the response.

To date, vocal matching has been best studied in songbirds; male song sparrows, *Melospiza melodia*, for example, can reply to the song of another male by singing the song type in their repertoire that most resembles it, known as song type matching (Searcy & Beecher, 2009). This matching of vocal signals appears to be an honest signal of aggressive intent (Akçay, Tom, Campbell, & Beecher, 2013; Beecher et al., 2000; Burt, Campbell, & Beecher, 2001; Searcy & Beecher, 2009). Male songbirds may identify one another by becoming familiar with each other's learned song repertoire via location of territories or fine-scale differences between individuals in shared song types (Falls, 1982; Falls & Brooks, 1975; Nordby, Campbell, & Beecher, 2007; Stoddard, Beecher, Horning, & Campbell, 1991). This then allows individuals to choose the song from their repertoire that most closely matches that of the male they wish to address (McGregor & Dabelsteen, 1996; McGregor et al., 1992). This does, however, mean that a male's ability to partake in song type matching may be somewhat limited to the song types it has in its vocal repertoire. Other species, such as orange-fronted conures, *Aratinga canicularis*, and bottlenose dolphins may be less constrained by their repertoire in matching interactions (Balsby et al., 2012; Janik, 2000; King et al., 2013; Tyack, 1991).

The evolution of learned, individually distinctive calls in dolphins is most likely to be linked to their fluid social network and their high mobility coupled with features of the marine environment (i.e. pressure affecting subtle voice features and restricted vision underwater; Janik, 1999; Tibbetts & Dale, 2007). The individual identity of each animal is encoded in the frequency modulation pattern of these whistles independently of general voice features (Janik, Sayigh, & Wells, 2006). Thus, each animal's signature whistle may become a label for that particular individual and conspecifics can then use these learned labels to address one another (King & Janik, 2013). The copying of signature whistles in this way appears to be an affiliative signal that primarily occurs between animals that share strong social bonds (King et al., 2013). Signature whistle copies can also occur in matching interactions (Janik, 2000; King et al., 2013). It is unclear whether this means all such interactions are affiliative or whether they can also serve to manage aggression as seen in songbirds (Searcy & Beecher, 2009).

We investigated how bottlenose dolphins responded to being vocally matched by conducting playback experiments with groups of animals under human care. We waited until an animal produced its signature whistle and then played either a synthetic version of its own whistle (match) or a different signature whistle (control). Following the addressing theory of whistle copying, we hypothesized that signature whistle matching would elicit responsive calling in the target animal but that different signature whistles

would not. To investigate the valence of matching we explored the role of the timing of the match and noted potential signs of aggression such as approaches and threat displays.

METHODS

Study Subjects

Playback experiments were conducted at two facilities: Walt Disney World's Epcot's The Seas in Kissimmee, FL, U.S.A. during May–June 2009 and Dolphin Quest, Bermuda during February–March 2011. The subjects from The Seas were four adult male bottlenose dolphins. Ranier was 28 years old, born in the Gulf of Mexico, and had lived in multiple facilities before coming to The Seas in 2002. The other males were Khyber (18 years), Calvin (15 years) and Malabar (8 years), all born in human care. All four animals had been together for the previous 3.5 years, Ranier and Calvin for 6 years. The dolphins were housed in an indoor facility and usually kept in pairs, with one pair in the main pool (20 318 m³ cylindrical pool with a diameter of 28 m and a depth of 8.2 m) and the second pair in two interconnected back pools that could be separated from the main pool by two watertight gates. The playbacks occurred in the two back pools, which were each approximately 100 m³ (56 m² in area with a 2 m depth). The animals had constant acoustic contact but only had visual contact through one of the gates during playback sessions. Vocalizations at The Seas were recorded with two HTI-96 MIN hydrophones (frequency response: 0.002–30 kHz ± 1 dB) and two CRT hydrophones (C54XRS; frequency response: 0.016–44 kHz, C54XR ± 3 dB; frequency response: 0.016–50 kHz ± 3 dB) onto a Toshiba Satellite Pro laptop using a four-channel Avisoft 416 UltrasoundGate recording device (sampled at 50 kHz, 8 bit; frequency response: 0.02–25 kHz ± 3 dB). Passive acoustic localization was used to identify the caller, by comparing the amplitude of the same sound recorded on four hydrophones placed in different areas of the pools (Janik & Slater, 1998). Video recordings were taken using two digital video cameras mounted above the back pools and from a third analogue VN37CPH underwater camera attached to a Sony Handycam DCR-HC96E and recorded onto mini DV tapes. The Sony Handycam also had an acoustic input from one of the HTI-96 MIN hydrophones.

The subjects from Dolphin Quest Bermuda were four adult females and three calves. Cirrus was 37 years old and was born in the Gulf of Mexico; she was the only female without a calf at the time of study. Both Bailey (22 years old) and Caliban (18 years old) were born in human care and all three of these females had been housed together at Dolphin Quest for the last 15 years. The fourth adult female was Ely (8 years old), and she was born at the facility to Bailey. The three calves were all 11 months old at the time of study. The two female calves were Cavello (calf of Bailey) and Marley (calf of Ely); the male calf was Cooper (calf of Caliban). The animals were kept in outdoor tidal pools with a floating dock, and therefore had both constant acoustic and visual contact. The animals were kept in different group compositions that changed on a daily basis. The playback pool was 120 m² in area with depth dependent on tide and varied across pool area (range 1–7 m). Vocalizations of the animals at Dolphin Quest were recorded with four HTI-96 MIN hydrophones (frequency response: 0.002–30 kHz ± 1 dB) onto a Dell laptop using the same Avisoft 416 UltrasoundGate described above. Whistles were localized to an individual using the TOADY localization program (Quick, Rendell, & Janik, 2008). Video recordings were taken from an analogue VN37CPH underwater camera attached to a Sony Handycam DCR-HC96E and recorded onto mini DV tapes. The Sony Handycam also had an acoustic input from one of the HTI-96 MIN hydrophones.

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