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Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function

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Many animals engage in dyadic vocal exchanges. Studying the patterns of vocal output and spatial arrangement of individuals in these interactions can often reveal information concerning their function. Sperm whales, *Physeter macrocephalus*, frequently exchange short sequences of clicks, termed codas, in social contexts. We analysed the coda vocalizations of sperm whale social units encountered in two different oceans to test hypotheses about how coda exchanges are organized. We also used a dynamic recording array to estimate the spatial scale of these vocal interactions. Coda production was influenced by the timing and types of codas produced by other unit members, resulting in the production of duet-like sequences of coda exchanges between pairs of whales. Codas were more likely to be made within 2 s of another coda than expected by chance, and whales were more likely to match previously produced codas than expected by chance, although matching appeared to be largely a result of the matching of one particular coda type within each social unit. Patterns of overlapping and matching exchanges did not seem to be correlated with relatedness or social affiliation. These exchanges occurred over a range of spatial scales, and are thus likely to be functional both between whales that are near and between those that are comparatively far from one another. The context of these exchanges, reciprocity in coda overlapping, and the sequencing of exchanges into duet-like chains all suggest that coda overlapping and matching function to reinforce social bonds between whales.

Keywords: communication; *Physeter macrocephalus*; sperm whale; vocal interaction; vocalization

Temporally associated vocal exchanges have been observed in a variety of animal species including birds (e.g. Todt & Naguib 2000; Burt et al. 2001; Catchpole & Slater 2008), frogs (e.g. Pallett & Passmore 1988; Jehle & Arak 1998; Gerhardt et al. 2000), primates (e.g. Sugiura 1998) and cetaceans (e.g. Janik 2000; Miller et al. 2004). Animals exchange vocalizations with conspecifics to serve a number of different functions, including kin recognition (Gouzoules & Gouzoules 1990; Collins et al. 2005), mate attraction (Gerhardt et al. 2000), social-bonding (e.g. primates: Snowdon & Cleveland 1984; Masataka & Biben 1987; Geissmann 1999; Lemasson & Hausberger 2004; elephants: Soltis et al. 2005), group cohesion (e.g. Masataka & Symmes 1986; Sugiura 1998; Miller et al. 2004) and territory defence (e.g. McGregor et al. 1992; Burt et al. 2001; Hyman 2003; Mennill & Ratcliffe 2004). Although, within a given species, vocal exchanges in different contexts, and between different individuals, can function in very different ways, studying the patterns of vocal output and spatial arrangement of individuals in these interactions can often reveal information concerning their function (e.g. Burt & Vehrencamp 2005).

For social marine animals, localizing conspecifics and coordinating group movements are particularly dependent on acoustic signals, given the limitations of visual contact in the marine environment (Myrberg 1980). Studies of two social cetaceans, the killer whale, *Orcinus orca*, and bottlenose dolphin, *Tursiops truncatus*, suggest that they use antiphonal calling, and call matching in

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particular, to locate conspecifics when isolated, or maintain contact with group members while travelling and foraging (Tyack 1986; Caldwell et al. 1990; Smolker et al. 1993; Janik & Slater 1998; Miller et al. 2004). Another social cetacean, however, the sperm whale, *Physeter macrocephalus*, engages in vocal exchanges when individuals are in close proximity to one another (Watkins & Schevill 1977; Whitehead & Weilgart 1991). These whales exchange stereotyped patterns of broadband clicks, termed 'codas', which are generally heard during social periods at or near the water surface (Watkins & Schevill 1977). The main social context of coda production is within long-term female social units, within which adults cooperate to care for immature offspring (Whitehead 1996; Whitehead & Weilgart 2000; Marcoux et al. 2006). These units can, although do not always, contain multiple unrelated matrilines (Mesnick 2001).

Codas can be classified into discrete types (Weilgart & Whitehead 1993), which are apparently shared among animals within social units (Rendell & Whitehead 2004). Research in the Eastern Tropical Pacific suggests that social units prefer to associate with other units possessing similar coda dialects. Coda repertoires have therefore been suggested to advertise affiliation to a higher-order social structure, the 'vocal clan' (Rendell & Whitehead 2003). Although it has been observed that sperm whales exchange vocalizations in sequences (Watkins & Schevill 1977; see also Fig. 1), the difficulty of assigning vocalizations to free-ranging cetaceans (Costa 1993) means that rates of overlapping and matching, as well as the spatial scales of coda exchanges, are largely unknown. Such data are important in addressing hypotheses about the function of coda exchange.

In the present study, we analysed the coda vocalizations of two sperm whale units encountered in two different oceans (Eastern Tropical Pacific and Caribbean Sea) to assign codas to individuals, or size classes, and used these data to test several hypotheses about coda exchanges. Overlapping exchanges function in some species to signify dominance or aggressive intentions (e.g. Dabelsteen et al. 1997; Burt et al. 2001), so we looked for directional patterns in overlapping and matching between dyads that would be consistent with this function. In contrast, vocal exchanges can also be affiliative signals (e.g. Geissmann & Orgeldinger 2000; Hall 2004; Lemasson & Hausberger 2004; Mann et al. 2006), and reciprocal patterns of overlapping and matching would be more consistent with an affiliative signal, such as duetting (Hall 2004). Finally, in the Sargasso Sea we localized coda exchanges using a dynamic hydrophone array to estimate the spatial scale of these vocal interactions. These data are important because if exchanges occur only between whales several hundred metres apart (i.e. out of visual contact), then a localization function would be supported (e.g. Janik & Slater 1998), whereas such a function would not be supported if exchanges occur primarily between individuals already in close proximity. This paper provides the first description of coda exchange patterns between individual sperm whales within social units and the first accurate localization data to demonstrate the spatial scale of the exchanges.

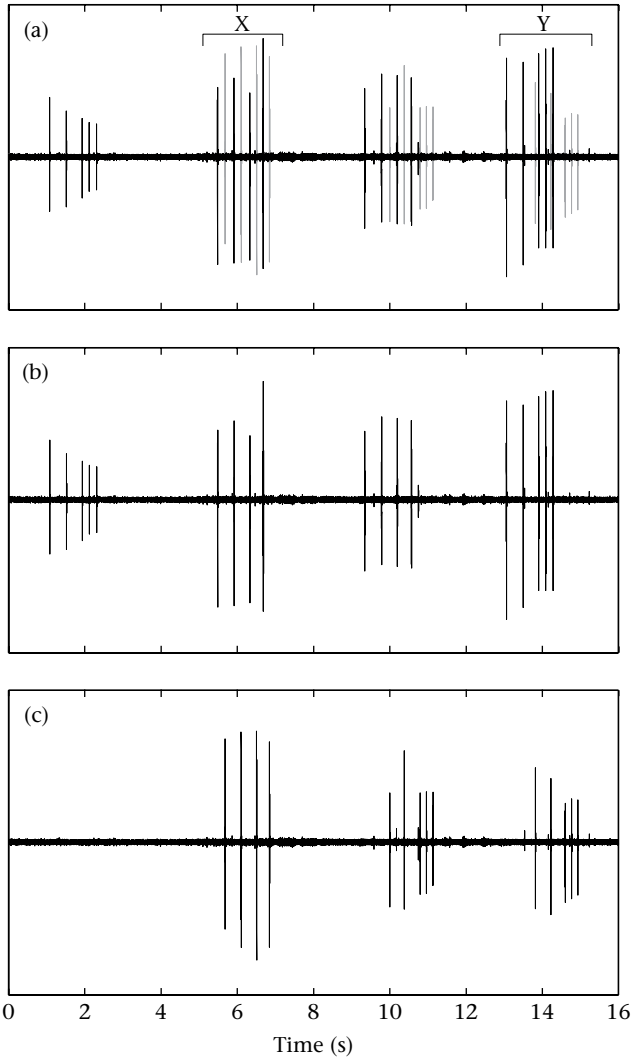

Figure 1. Waveform of a recording segment in which the coda of one whale is followed by three overlapping coda exchanges. The coda clicks in black have calculated interpulse intervals (IPIs) of 3.38–3.42 ms while the coda clicks in grey have IPIs of 3.15–3.17 ms, indicating that there are two individuals of differing sizes producing codas approximately every 3–4 s and that the codas of the first whale (in black) are overlapped by the second whale (in grey). (a) The coda production of both whales. (b, c) The coda production of each whale separately. Two matching overlap exchanges are labelled X and Y.

METHODS

Field Methods: Group of Seven

The Group of Seven is a social unit consisting of five adult females, one juvenile male and one male calf (see Gero 2005), which we followed for a total of 41 days between 16 January and 26 March 2005, off the coast of the Commonwealth of Dominica. Animals were tracked visually during the day, and followed acoustically at night using a directional hydrophone (see Whitehead & Gordon 1986). During daylight hours, individuals at the surface were approached and digital photographs of flukes were taken using a Canon D10 digital SLR for individual identification

purposes (Arnbom 1987). Sloughed skin samples were collected from the slicks of whales (Whitehead et al. 1990), and analysed to reveal the sexes and genetic relationships of these individuals (Gero et al., in press). We made 15 coda recordings of this unit, as well as recordings of their usual clicks (i.e. echolocation clicks) when solitary whales fluked at the start of a foraging dive (Schulz 2007). Recordings were made using a custom-built towed hydrophone with Benthos AQ-4 elements, and recorded on a Fostex VF-160 multitrack recorder sampling at 48 kHz.

Field Methods: Unit T

Unit T is a social unit of nine female and immature sperm whales which we followed for 17 days between 10 March and 12 April 1999, around the Galápagos Islands (see Rendell & Whitehead 2004). As with the Group of Seven, this unit was tracked visually during the day, and acoustically at night, and photographed for individual identification (Canon EOS 50 35 mm SLR). The analysis of sloughed skin samples from five sampled unit members showed that they were largely unrelated (Mesnick 2001; Whitehead 2003b). During social periods, 21 recordings were made using an Offshore Acoustics hydrophone connected to a Sony TC-D5 M cassette recorder, and subsequently digitized at 44.1 kHz onto a standard desktop PC.

Photographic and Genetic Analysis: Group of Seven

Photographic and genetic data from the Group of Seven are presented elsewhere (Gero 2005; Gero et al., in press). Only photographs with a quality rating, $Q \geq 3$ were used in the analyses (Arnbom 1987; Dufault & Whitehead 1993). Individuals were considered to be associated if they were within approximately three adult body lengths (ca. 40 m) from any other surface cluster member (Whitehead 2003a). We used a 2 h sampling period, and the half-weight index (HWI) measure of association, as it accounts best for any observer biases in photoidentification (Cairns & Schwager 1987). Relatedness values were calculated for each pair of Group of Seven whales by analysing sloughed skin samples across 13 microsatellite loci (Gero et al., in press).

Acoustic Analysis: Group of Seven and Unit T

Recordings were analysed using Rainbow Click software (www.ifaw.org/ifaw/general/default.aspx?oid=25653; Gillespie 1997; Leaper et al. 2000). Sperm whale clicks are multipulsed, and the interpulse interval (IPI) is an index of body size (Gordon 1991). We measured the interpulse intervals (IPIs) of clicks using custom routines written in MatLab version 6.1 (MathWorks Inc., Natick, MA, U.S.A.; for description of method see Rendell & Whitehead 2004). The codas recorded from the Group of Seven were assigned to individuals based on the similarity of coda and usual click IPIs (see Appendix; Schulz 2007). Although codas were not assigned to specific individuals for Unit T, codas with IPIs differing by less than 0.05 ms could be assumed to have been produced by the same whale. Codas with IPI differences greater than 0.10 ms were deemed to have been produced by different whales (following Schulz 2007).

The intervals between clicks within a coda (interclick intervals or 'ICIs') were output from Rainbow Click and standardized by coda length. Codas were then classified into types by *k*-means cluster analysis on the Euclidean distances between ICI vectors of codas with the same number of clicks (for details, see Rendell & Whitehead 2004); *k*, the number of types for a given number of clicks, was chosen by calculating the variance ratio criterion (VRC, see Calinski & Harabasz 1974) for clustering solutions at $k = 1,2\ldots 10$. We defined a coda exchange as two in-sequence codas that were produced within 2 s of one another; a 2 s cutoff was chosen based on the distribution of the time differences between codas in our recordings which showed a peak in intervals between codas made by different whales at less than 2 s (Fig. 2). We use the term 'overlapping coda' to describe second-in-sequence codas whose onset occurred after the onset, but before the termination, of the initial coda (see Soltis et al. 2005). In contrast, we use the term 'adjacent coda' to describe second-in-sequence codas whose onset occurred within 2 s, but after the termination, of the initial coda. Accordingly, an 'overlapping coda match' and an 'adjacent coda match' were when overlapping or adjacent codas of the same type were recorded.

Statistical Analyses: Group of Seven and Unit T

We modified the nonparametric randomization techniques described in Miller et al. (2004) to test whether codas occurred within 2 s of each other more often than expected, given the rate and periodicity of coda production within each recording. Within the Group of Seven recordings, we tallied the number of coda exchanges, the number of overlapping codas and the number of adjacent codas by different whales within 2 s, and compared the observed tallies to the probability distribution from 10 000 randomizations that rotated the coda sequences of each whale a random amount of time. This method is similar to that used in Miller et al. (2004) to test for countercalling but, because we were able to distinguish the coda sequences of each whale in the unit, involves the rotating of each whale's coda sequences rather than just the call sequences of a focal animal. For Unit T, however, because the identities and coda sequences of individual whales were not known, within recordings we grouped codas with IPIs within 0.05 ms of each other (Schulz 2007) and within each permutation rotated the coda sequences of these grouped codas a random amount of time. These permutation tests were also used to test for countercalling and overlapping within particular coda types, whether there were tendencies for responding whales to have higher or lower IPIs than the initial whale, and to test for countercalling and overlapping between individual whales in the Group of Seven. The Hemelrijk R_r test (Hemelrijk 1990), a Mantel test variant which ranks values within rows, was used to examine the similarity of elements in a matrix of the proportion of a whale's codas that were overlapped and matched by other individual whales and the elements of its inverse, thereby testing for reciprocity in overlapping and matching between whales.

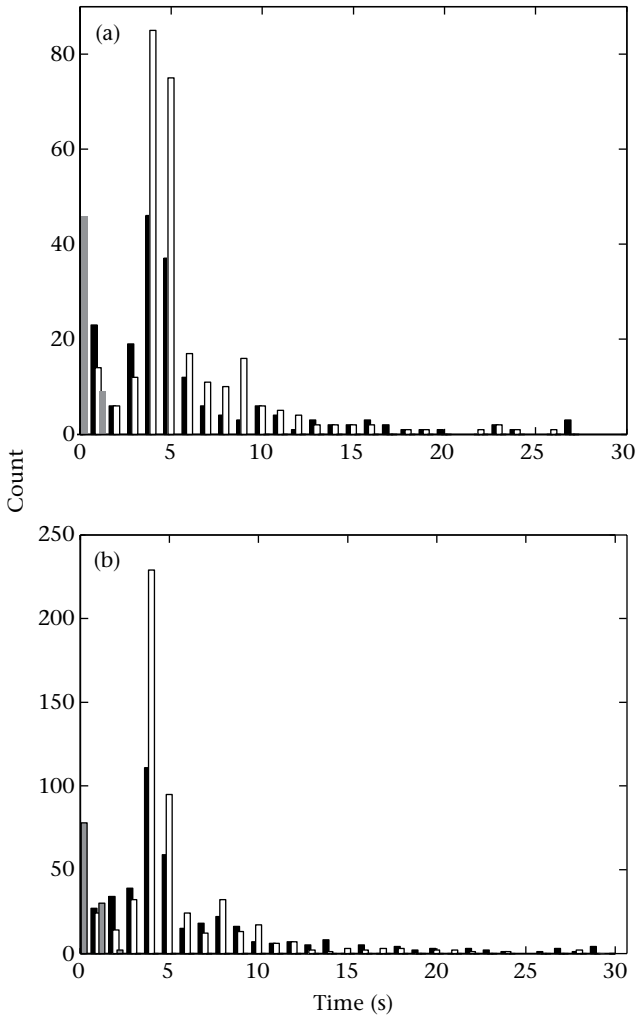

Figure 2. Histogram of the time intervals between contiguous codas made by whales in (a) the Group of Seven and (b) Unit T. In (a) the black bars represent the frequency of time intervals between adjacent but nonoverlapping codas made by different whales and the white bars represent the frequency of time intervals between adjacent codas made by the same whale. The grey bars represent the frequency of time intervals between overlapping codas made by different whales. In (b) the black bars represent the frequency of time intervals between adjacent but nonoverlapping codas with dissimilar interpulse intervals (IPIs) and the white bars represent the frequency of time intervals between adjacent codas with similar IPIs, and thus potentially produced by the same whale. The grey bars represent the frequency of time intervals between overlapping codas with dissimilar interpulse intervals (IPIs) (greater than 0.10 ms difference) and thus probably different whales.

Mantel tests (Mantel 1967; Schnell et al. 1985) and matrix correlation coefficients between the elements of the genetic relatedness matrix and a matrix of the proportion of whale pairs' codas that were in overlapping exchanges were calculated to determine whether highly related whales were more likely to engage in overlapping exchanges than less related whale pairs. Similarly, we calculated Mantel matrix correlation coefficients between the elements of the social association matrix and the overlapping exchange matrix to determine whether social association correlated with patterns of overlapping. In addition, these tests were repeated testing for correlations between matching exchanges and both genetic relatedness and association indices. The calculation of HWI, Mantel tests and Hemelrijk R_r tests were carried out using SOCPROG (2.2, H. Whitehead, available from http://myweb.dal.ca/hwhitehe/social.htm) in MatLab version 6.1.

Field Methods: Exchange Localization

The fieldwork for this part of the study was conducted between 5 May and 20 June 2004 (38 days effort in total) in international waters between Bermuda and the east coast of the United States. We deployed a dynamic acoustic array (Schulz et al. 2006) around groups of whales socializing at the surface. The acoustic array consisted of three small remote-piloted vehicles (RPVs) and one larger research platform, a 12 m sailboat with auxiliary engine, from which the RPVs were deployed. An omnidirectional hydrophone (Vemco VHLF; frequency response: 200 Hz–20 kHz ± 3 dB; midband sensitivity: 147 dB re 1 V/μPa) was suspended approximately 80 cm below the water surface from the side of each RPV. The acoustic signals from each hydrophone were broadcast by FM transmitter (NRG Kits PLL PRO III) to separate radio receivers (SONY ICF-M260) onboard the deployment platform, and digitally recorded on a multitrack recorder (FOSTEX VF-160; sampling rate: 44.1 kHz), allowing simultaneous recording, on separate tracks, of the acoustic data from each hydrophone in the array. On each of the recording platforms, a GPS unit (Garmin GPS25-HVS) logged its position each second and saved the data to a memory card for later retrieval (for more details see Schulz et al. 2006).

Acoustic Analysis: Exchange Localization

We inspected the array recordings for overlapping coda exchanges that were detected on at least three of the four hydrophones in the array. We measured time-of-arrival differences (TOADs) between pairs of hydrophones for each click in these coda exchanges, using cross-correlation methods in MatLab (see Schulz et al. 2006). For each click in each analysed coda, we found the intersections of hyperbolae defined by the TOADs and receiver locations. The average of the calculated intersections was taken as the best estimate of the location of the vocalizing whale (Laurinolli et al. 2003). We estimated location uncertainty from the standard deviation of the hyperbolae intersections in the zonal (ϵ_x) and the meridional (ϵ_y) directions, giving the root-mean-square (RMS) error $\epsilon = (\epsilon_x^2 + \epsilon_y^2)^{1/2}$ (as in Laurinolli et al. 2003). For localizations that yielded more than one solution (e.g. sound sources in end-fire positions), we selected the solution nearest to the least-squared-error fit, that is, the location in the 2-D array grid nearest the highest density of hyperbolae intersections (Hayes et al. 2000); this was necessary for 61% of the localized codas.

For codas in which multiple clicks were successfully localized, the best estimate of the location of coda production was considered to be the mean of the click locations, excluding locations that were unrealistically dissimilar to the others in the coda. The errors for the location of each

produced coda were calculated by taking the mean of each of the errors over the clicks in the coda. The uncertainty in estimating the distance between average locations of codas in overlapping exchanges was calculated as the square root of the sum of the squares of the zonal and meridional errors of the codas' location solutions.

To measure the IPIs of all clicks in codas that were successfully localized with these techniques, we used the methods described above (Rendell & Whitehead 2004; Schulz 2007). Because the clarity of the pulse structure of coda clicks sometimes varied between acoustic channels depending on recording aspect, IPI analysis was repeated using recordings from several hydrophones in the array. These IPI measurements were, when it was possible to check, always consistent between hydrophone receivers. Codas that were in the same recording (i.e. occurring close together in time), localized to similar locations, and had assigned IPIs within 0.05 ms of one another, were assumed to have been made by the same whale. Using these techniques, we were able to examine the range of distances between a given whale and its overlap exchange partners within a recording session. Finally, just as with the data from the social units, we classified the codas recorded in these localized exchanges into types using *k*-means cluster analysis (see Rendell & Whitehead 2004).

Ethical Note

The present study was entirely observational in nature. Fieldwork conducted in national waters took place under appropriate licences from the national governments concerned (the Galápagos Islands, Ecuador for Unit T and the Commonwealth of Dominica for the Group of Seven). Our field protocols were approved by the Dalhousie University Committee on Laboratory Animals (http://animalethics.dal.ca/) and were designed to minimize disturbance by approaching whales slowly from behind whenever possible and using minimum required engine power for manoeuvring. No vessel under power approached whales to within 30 m, although occasionally whales would approach drifting vessels of their own accord, over which we had no control.

RESULTS

Temporal Patterns of Coda Production

The distribution of time differences between adjacent codas made by different whales indicated that the codas of both Group of Seven and Unit T whales were generally responded to by a different whale within 2 s (and often overlapped), or responded to approximately 5 s later (Fig. 2). Similarly, the distribution of time differences between adjacent codas made by the same whale (or whales with similar IPIs) indicated that whales generally produced codas every 3–5 s (Fig. 2). Moreover, whales were consistent in the temporal patterning of coda production even when not engaging in exchanges with other whales. In sequences of codas made by single whales, and not interrupted by codas of other whales, whales still produced codas primarily every 3–5 s. These data illustrate the temporal patterning observed in many Group of Seven and Unit T recordings, in that a coda was often overlapped or quickly followed by the coda of another whale within 2 s, followed by another bout of overlapping or 'exchanged' codas 3–5 s later.

Overlapping and Matching: Group of Seven

We made 15 recordings of the Group of Seven's codas on 14 days over a 45-day period for a total of 42 min; this group was acoustically monitored continuously during the 41 days we spent following them, and recorded whenever they produced codas. Of the 421 codas recorded, 318 (76%) were confidently assigned to a whale in the unit (Schulz 2007). Of these 318 assigned codas, 71 (22%) occurred in the 2 s following a coda produced by a different whale. This value significantly exceeded the expected value generated by 10 000 random rotations of the coda sequences of each whale within each recording (expected: $\overline{X} \pm \mathrm{SD} = 52.4 \pm 7.6$; $P = 0.027$), indicating that coda production by whales in the Group of Seven was temporally synchronized. Moreover, since the number of observed overlapping codas was significantly greater than expected (observed = 50; expected $\overline{X} \pm \mathrm{SD} = 23.9 \pm 5.3$; $P < 0.001$), but the number of observed adjacent codas within 2 s was not (observed = 21; expected $\overline{X} \pm \mathrm{SD} = 28.6 \pm 6.2$; $P = 0.210$), the close production of codas by different whales appeared to be a result of coda overlapping and not adjacent or antiphonal calling.

Overlapping exchanges

Although the Group of Seven produced 16 different coda types, only five types were overlapped in these recordings. The most common coda type of the Group of Seven ('1+1+3') was the most overlapped coda type (27 of 50 overlapped codas) while the second most common Group of Seven coda type ('5R') was the second most overlapped coda type (17 of 50 overlapped codas). No coda type overlapped another coda or was overlapped by another coda more often than expected ($P > 0.172$).

Coda overlapping exchanges in which the overlapped whale had a higher IPI (that is, was larger) than the overlapping whale were no more likely to occur than the reverse ($P = 0.496$). A Hemelrijk R_r test of the rates at which members of a dyad led or followed in overlapping coda exchanges was significant (R_r test matrix correlation = 0.645, $P = 0.003$), indicating that whales tended to overlap individuals that overlapped them.

There was no significant correlation between genetic relatedness and the rates at which individuals were in overlapping exchanges (Mantel test matrix correlation= −0.06, $P = 0.26$). Similarly, there was no significant correlation between the half-weight index of social association and the rates at which individuals were in overlapping exchanges (Mantel test matrix correlation = 0.06, $P = 0.19$). Thus, sperm whale pairs that were closely related or socially associated were not more likely to engage in overlapping exchanges.

Matching exchanges

The number of codas that were matched by different whales within 2 s significantly exceeded the expectation generated by 10 000 random rotations of the coda types of each whale within bouts (observed = 48; expected $\overline{X} \pm \mathrm{SD} = 42.7 \pm 1.7$; $P < 0.008$). The number of coda matches in adjacent (nonoverlapping) pairs was not significantly greater than expected (observed = 7; expected $\overline{X} \pm \mathrm{SD} = 6.6 \pm 0.9$; $P = 0.559$). Only one coda type, '1+1+3', was matched in overlapping pairs more often than expected (observed = 26; expected $\overline{X} \pm \mathrm{SD} = 22.3 \pm 1.6$; $P = 0.013$).

Coda matching exchanges in which the matched whale had a higher IPI than the matching whale, and thus was larger, were no more likely to occur than the reverse ($P = 0.820$). This nonsignificant result was true for both overlapped and adjacent matching exchanges ($P = 0.952$ and $P = 0.203$). The Hemelrijk R_r test on the individual matching rates returned a significant result (R_r test matrix correlation = 0.828, $P = 0.004$), indicating reciprocity in matched overlapping. There were no significant correlations between either the occurrence of matching overlap exchanges between unit members and genetic relatedness (Mantel test matrix correlation = −0.02, $P = 0.25$) or social associations (Mantel test matrix correlation = 0.09, $P = 0.21$).

Overlapping and Matching: Unit T

We made 21 recordings of Unit T on 11 days within a 31-day period for a total recording time of 60 min. Of 621 codas recorded, 575 (93%) were confidently assigned an IPI. Of these 575 codas, 127 (22%) occurred within 2 s of a coda produced by a different whale. This value significantly exceeded the expected value (expected $\overline{X} \pm \mathrm{SD} = 112.9 \pm 7.1$; $P = 0.038$). Moreover, as in the Group of Seven, this appeared to be a result of coda overlapping rather than adjacent calling, because the number of overlapping codas was significantly greater than expected (observed = 87; expected $\overline{X} \pm \mathrm{SD} = 58.3 \pm 7.2$; $P < 0.001$) but the number of adjacent codas within 2 s was significantly less than expected (observed = 40; expected $\overline{X} \pm \mathrm{SD} = 54.5 \pm 7.2$; $P = 0.037$).

Overlapping exchanges

Of the 19 coda types recorded from Unit T, 15 were overlapped. One coda type, '5R', overlapped other codas more often than expected (observed = 12; expected $\overline{X} \pm \mathrm{SD} = 6.1 \pm 1.6$; $P = 0.001$). However, even when overlaps of this coda type were excluded from the analysis, coda overlapping still occurred at a rate higher than expected (observed = 82; expected $\overline{X} \pm \mathrm{SD} = 53.9 \pm 7.3$; $P < 0.0001$). In Unit T, as in the Group of Seven, coda overlapping exchanges in which the overlapped whale had a higher IPI than the overlapping whale were no more likely to occur than exchanges in which the overlapping whale had a higher IPI ($P = 0.182$).

Matching exchanges

The number of codas that were matched within 2 s significantly exceeded expectation (observed = 51; expected $\overline{X} \pm \mathrm{SD} = 33.8 \pm 5.0$; $P = 0.004$). This was true for both overlapped coda matching (observed = 32; expected $\overline{X} \pm \mathrm{SD} = 24.9 \pm 3.6$; $P = 0.024$) and, in contrast to the Group of Seven, for adjacent coda matching (observed = 19; expected $\overline{X} \pm \mathrm{SD} = 13.1 \pm 2.6$; $P = 0.029$). As in the Group of Seven, only one coda type, '2+1', was matched more than expected (observed = 30; expected $\overline{X} \pm \mathrm{SD} = 18.7 \pm 3.0$; $P < 0.001$).

As in the Group of Seven, Unit T coda matching exchanges in which the matched whale had a higher IPI than the matching whale were no more likely to occur than the reverse (all exchanges: $P = 0.756$; overlapping: $P = 0.856$; adjacent: $P = 0.566$).

Temporal Patterns of Overlapping and Matching

Since sperm whales generally tended to produce a coda every 3–5 s (Fig. 2), we further hypothesized that they anticipate and thus coordinate their coda production with other whales so that subsequent codas overlap. To investigate this, we examined the Group of Seven recordings and noticed that 96% of coda overlap exchanges were preceded 3–5 s earlier by a single coda made by one of the two whales in the overlap exchange (excluding cases where the identity of a vocalizing whale in the preceding 3–5 s interval was unknown). These single codas appeared to act as exchange initiators, and the subsequent high rate of overlap exchanges apparently occurred because whale dyads synchronized their coda production. In the case of overlap matching, it would be impossible for a whale to match correctly a coda if it had only heard one or two clicks. In attempting to understand how overlap matching occurs, we found that whales in overlapping exchanges matched a coda type made 3–5 s earlier by their overlapping partner more often than expected, in both the Group of Seven (observed = 53; expected $\overline{X} \pm \mathrm{SD} = 40.6 \pm 5.5$; $P < 0.001$) and Unit T (observed = 45; expected $\overline{X} \pm \mathrm{SD} = 32.2 \pm 4.9$; $P = 0.014$). Furthermore, whales in overlapping exchanges matched codas made by their overlapping partner 3–5 s earlier more often (Group of Seven: 53 coda matches; Unit T: 44 coda matches) than codas that they overlapped (Group of Seven: 41 coda matches; Unit T: 32 coda matches). These results suggest that the similarity in the coda types of overlapping codas is a result of the matching of the recently produced type.

As a result of the apparent synchronization in coda production, 72% of coda overlap exchanges in the Group of Seven recordings occurred in sequences comprising two or more exchanges between two whales, with sequences ranging from two to eight exchanges ($\overline{X} \pm \mathrm{SD} = 2.1 \pm 1.8$ exchanges). These figures changed to 91% ($\overline{X} \pm \mathrm{SD} = 3.1 \pm 2.1$ exchanges) when we excluded exchanges in sequences containing codas that were not confidently assigned to a whale, or codas that did not overlap but still occurred within 2 s. We recorded 13 sequences, of at least two exchanges separated by no more than 10 s, from the Group of Seven. Whales switched between overlapping and overlapped roles in eight of the 13 sequences (that is, the overlapped whale in the first exchange became the overlapping whale in at least one subsequent exchange), and in four of these eight sequences there were

multiple role switches. In three of the 13 sequences the 'responder' (the whale that made the second coda in the first exchange, i.e. the overlapping whale) switched coda types to match the type produced by the 'initiator' (the whale that made the first coda in the first exchange, i.e. the overlapped whale) in a preceding exchange, while in four sequences the 'initiator' was observed to switched coda type to match the 'responder'. In two sequences we observed both 'initiator' and 'responder' switching coda types to match types the other had made in the preceding exchange.

Localized Exchanges

We were able to localize the clicks in 19 paired overlapping coda exchanges (giving 38 codas in total) from three different recording sessions (see Figs. 3 and 4 for examples). The maximum observed RMS error for a localized coda was 51.7 m at a mean range of 364.6 m from the hydrophone receivers. The estimated distance between sperm whales in overlapping coda exchanges ranged from a mean $\pm$ SD of 1.2 ± 6.6 m to 324.2 ± 51.8 m (Table 1), indicating that these vocal interactions occurred at various spatial scales. In one recording session (na. 051403), overlapping coda exchanges that occurred within a few seconds of one another (and thus probably within the same behavioural context) varied greatly in the estimated distance between the localized whales (Table 1), suggesting that coda overlapping serves a function at a range of spatial scales.

DISCUSSION

Our results show that although individual sperm whales regularly produced codas at 3–5 s intervals, the timing of their coda production was affected by that of other social unit members. In the Group of Seven, 22% of codas were followed within 2 s by a coda of another whale and 16% were overlapped by a coda of another whale, over twice as often as expected by chance. Similarly, in Unit T, a social unit in a different ocean, 22% of codas were followed within 2 s by a coda of another whale and 15% were overlapped by a whale's coda with a considerably different IPI, a rate of 1.5 times more often than expected by chance. We do note that others have recorded codas when only a single whale was visually or acoustically observed (Teloni 2005), so such exchanges are clearly not the only context of coda production.

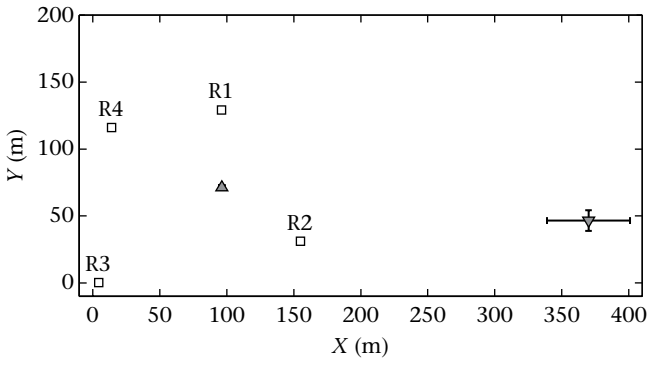

Figure 3. Estimated locations with standard deviation error bars in the zonal and meridional directions for two codas in an overlapping exchange at 23:27:19 UTC in recording no. 051403; one whale (▲) had an interpulse interval (IPI) of 2.95 ms and the other whale (▼) had an IPI of 2.47 ms. The estimated distance between the two whales is 274.8 ± 32.0 m. □: Hydrophone receivers (R1–R4).

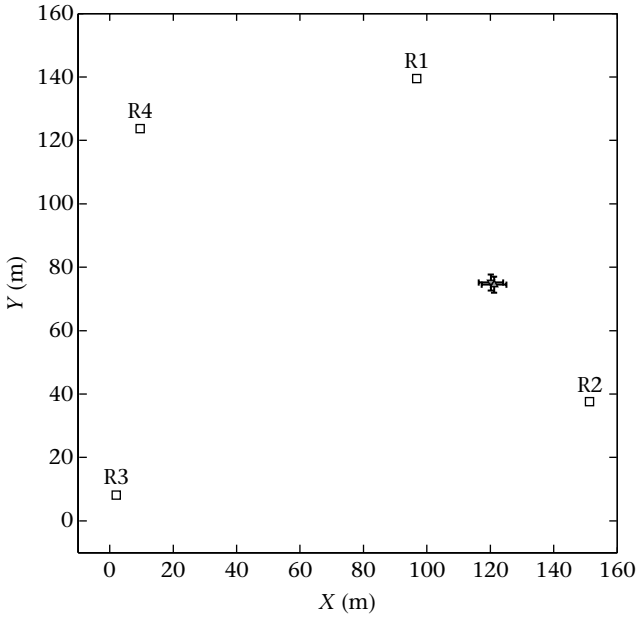

Figure 4. Estimated locations with standard deviation error bars in the zonal and meridional directions for two codas in an overlapping exchange at 23:27:52 UTC in recording no. 051403; one whale (▲) had an interpulse interval (IPI) of 2.95 ms and the other whale (▼) had an IPI of 3.45 ms. This IPI assignment indicates that the first whale (▲) is probably the same as the first whale (▲) localized in Fig. 3. The estimated distance between these two whales is 1.2 ± 6.6 m. □: Hydrophone receivers (R1–R4).

Our study shows that pairs of sperm whales within social units synchronize the timing of their coda production to produce duet-like sequences of temporally associated coda exchanges. It is possible that the apparent synchronizing of coda production could be a result of responses by both animals to the same external stimulus. However, the temporal regularity of coda production both by solitary whales and in overlap exchanges by pairs of whales, and the lack of any obvious acoustic cue in any of our recordings, all favour the hypothesis that sperm whales anticipate and overlap the vocal output of other individuals. Furthermore, our observations of role switching and coda type matching within exchange sequences suggest that these interactions are true exchanges in the sense that each participating animal adjusts its own vocal output in response to the output of the other, although we do not have enough data for statistical analysis of these sequences.

Comparing the form and context of sperm whale coda exchanges to countercalling in other species allows us to form hypotheses about their possible functions. Clearly coda exchanges do not function exclusively, if at all, in mate

Table 1. Estimated distances between whales in overlapping coda exchanges

Record no.	Time	Distance (m)	IPI1 (ms)	1st coda	IPI2 (ms)	2nd coda
051403	23:27:19	274.8±32.0*	2.95	6R	2.47	2+8
051403	23:27:28	324.2±51.8	2.95	2+12	n/a	2+7
051403	23:27:38	290.5±34.1	n/a	2+5	2.49	2+6
051403	23:27:48	290.9±49.9	n/a	2+4	2.47	2+5
051403	23:27:52	1.2±6.6	2.95	2+5	3.45	5A
051403	23:27:55	1.5±6.4	2.95	5R	3.42	2+5
061002	20:28:03	2.4*	3.67	5R	3.24	9R
061002	20:28:11	0.8	3.65	7R	3.24	7R
061002	20:28:15	0.8	n/a	8R	3.24	6R
061002	20:28:19	6.5	3.67	5R	3.24	6R
061002	20:28:31	3.5	n/a	5R	3.24	4R
061002	20:29:36	2.9	3.67	9R	3.24	9R
061002	20:29:42	6	3.65	8R	3.24	7R
061002	20:29:47	0.5	3.67	9R	3.24	8R
061002	20:29:52	3.4	3.67	8R	3.24	11A
061703	13:10:48	10.5±21.0	2.00	11R	2.24	9R
061703	13:10:50	5.4±31.6	2.00	1+8	n/a	1+8
061703	13:10:53	7.9±24.3	1.97	12A	2.54	1+9
061703	13:10:58	31.4±14.8	1.97	11A	2.72	10R

IPI: interpulse interval.
*The standard deviation of the estimated distance is provided only for overlap exchanges in which both the codas were localized using a four-hydrophone receiver array.

attraction because codas were produced and exchanged in both units when no sexually mature males were present. Furthermore, it seems unlikely that coda exchanges function as an acoustic threat, for two reasons. First, coda overlapping and coda matching do not appear to be accompanied by agonistic interactions or an escalation in aggression (cf. Dabelsteen et al. 1997; Beecher et al. 2000; Langemann et al. 2000; Burt et al. 2001; Anderson et al. 2005). Second, sperm whales are cooperative, not territorial, towards other members of their social unit in group defence against killer whales (Whitehead 2003a), allomaternal care of calves (Whitehead 1996), communal knowledge of a large home range (Whitehead 2003b), and perhaps increased feeding success through group foraging (Best 1979).

In the killer whale and bottlenose dolphin, countercalling appears to allow the signaller and responder to locate one another when visually isolated (Janik & Slater 1998; Janik 2000; Miller et al. 2004). Sperm whale coda vocalizations, however, are generally exchanged during social periods at the water surface (Whitehead & Weilgart 1991), although they are also made at the start and end of long (>30 min) foraging dives (Watkins & Schevill 1977). Several of the vocal interactions we localized occurred between whales in close proximity (1–6 m), when the animals must have been in visual contact. Moreover, high rates of overlapping such as we report are not optimal for a localizing function, as it is much easier to locate alternating signals, such as those produced by bottlenose dolphins (Janik 2000). For these reasons, it seems unlikely that coda exchanges function exclusively in helping individuals find each other.

It is also possible that whales engage in vocal exchanges to assert dominance within a social hierarchy. However, in both the Group of Seven and Unit T, whales were just as likely to be overlapped or coda matched by a whale with a higher IPI as by a whale with a lower IPI (i.e. larger or smaller whales, respectively). Furthermore, within dyads whales did not overlap or match each other's codas significantly more than expected in either direction, indicating reciprocity in the overlapping and matching of codas. This suggests that overlapping and matching do not serve to mediate dominance relations.

The temporal arrangement of these coda sequences conforms well with a recent definition of duets as 'overlapping bouts of vocalizations given by paired individuals such that their elements within those bouts have a high level of alternation, or a low coefficient of variation of the intervals between their elements or both' (Hall 2004, page 415). While primate and avian duets generally occur between paired males and females (Geissmann & Orgeldinger 2000; Hall 2004), where precise temporal coordination with a duetting partner may indicate an individual's commitment to a partnership (Wickler 1980), sequences of overlapping codas between female sperm whales may serve a similar bonding function within a group context. The way in which sperm whales synchronize their vocal output such that some vocalizations overlap one another is remarkably similar to the synchronization of vocalizations in gelada monkeys, *Theropithecus gelada* (Richman 1978). In a range of social interactions, a gelada monkey will attempt to produce sounds closely synchronous to the tempo and rhythm of the sequence of sounds already being produced by another monkey (Richman 1978). The temporal regularity with which sperm whales produce codas, and the observation that whales frequently match a coda produced 3–5 s earlier by exchange partners, suggests that sperm whales, like gelada monkeys, respond not directly to the vocalization that they overlap but to the previous vocalization in the vocal sequence of the other animal. Just as long sequences of gelada monkey vocalizations provide a consistent rhythm and permit the synchronization of vocal output between animals, presumably functioning to maintain social relationships (Richman 1978), the

consistent rhythm of sperm whale coda production and consequent synchronization of coda vocalizations into sequences of overlapping exchanges may serve a similar function. Like temporal coordination, coda matching may also serve a social-bonding function. In a social parrot, the orange-fronted conure, *Aratinga canicularis*, individuals increased the similarity between their response calls and playback when they also responded nonaggressively towards the speaker, suggesting that call matching is an affiliative signal in this species (Vehrencamp et al. 2003). In sperm whales, coda matching of a recently produced coda may indicate a shared repertoire, as well as attentiveness on the part of the responder to the vocalization type just produced.

If the production of certain vocalizations in a species or group is specific to particular contexts and/or the context can be induced by particular vocalizations (e.g. alarm calls), then it would not be unexpected for animals to respond to these context-specific calls with similar calls, resulting in apparent but not actual call matching (e.g. right whale, *Eutalaena australis*, 'up calls': Clark 1983). To confirm that the coda matching we observed is not simply an artefact of context-specific calling, we need to consider not only the repertoires of individuals (e.g. Burt & Vehrencamp 2005), but also the vocal repertoires produced by individuals in particular recording contexts (e.g. Miller et al. 2004). Because sperm whales in the social units studied here matched codas more often than expected even when we controlled for the repertoires of individuals within bouts, it appears that sperm whales do engage in true matching. Coda matching appears to be largely restricted to one or two coda types, unlike other species where a variety of call types are matched (e.g. Stoddard et al. 1992; Burt & Vehrencamp 2005). Thus, in sperm whales it appears that coda matching may simply be a result of repeating a 'popular' coda type in the unit repertoire when it is heard. We suggest that such matching probably functions in reaffirming the unit and/or clan membership of the animals involved.

In summary, the results of this study indicate that despite the temporal regularity of coda production by individual whales, sperm whale coda production is influenced by the timing and types of codas produced by other unit members. These influences result in the production of sequences of coda exchanges between pairs of whales. Patterns of overlapping and matching exchanges do not seem to be correlated with relatedness or social affiliation. These exchanges occur over a range of spatial scales, and are thus likely to be functional both between whales that are near and between whales that are comparatively far from one another. The context of these exchanges, the reciprocity in coda overlapping, and the sequencing of exchanges into duet-like chains all suggest the exchanges serve an affiliative function, such as reinforcing group-level social bonds between whales. Future playback studies on sperm whales that broadcast codas at regular 3–5 s intervals are likely to prove highly useful in further examining the structure, syntax and function of the overlap exchange sequences observed in these units, as will further deployments of dynamic localizing arrays around groups of vocalizing whales.

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Appendix

Assigning codas to whales using IPIs

The IPIs of clicks were calculated using a modified version of the custom-written MatLab routines (version 6.1) described in Marcoux et al. (2006) & Rendell & Whitehead (2004). This modified method extracts the maximum cross-correlation peak, rather than the absolute cross-correlation peak (used by Gordon 1991), between pulses for clicks with well-defined pulse structures (see Schulz 2007). The modal IPI was calculated for each recording of usual, echolocation, clicks of solitary, individually identified whales. The usual click IPI for each identified individual whale was calculated by taking the mode of the modal IPIs calculated from each of the recordings in which it was identified.

To determine the IPI criteria with which two codas could be assumed to have been made by similarly sized whales, and so potentially the same whale, we examined the distribution of the differences in IPIs between codas in four recordings in which we were confident from both visual observation and acoustic detection that only two whales were present in the area at the time of recording. Two two-whale recordings were made off Dominica in February 2005, one was made in the Sargasso Sea on 10 June 2005, and another was made in the Mediterranean Sea on 20 July 2005. We only analysed codas that could be clearly identified aurally. Using IPIs calculated using the method described above resulted in a clearly bimodal frequency distribution of IPI differences. The first peak corresponds to the differences in IPIs between codas made by the same whale while the second broader peak corresponds to the differences in IPIs between codas made by different whales. Intrawhale differences in IPIs were less than 0.05 ms, indicating that if two codas have IPIs within 0.05 msec of one another in a recording, it is possible that they were made by the same whale. Furthermore, the intrawhale differences clearly did not exceed 0.10 ms, indicating that recorded codas with IPI differences of 0.10 msec or greater were probably not made by the same whale.

In the 15 recordings of codas, the IPI of each coda was calculated as the mode of the IPIs of the clicks in the coda. We first assigned codas to individuals based on the similarity of coda click IPIs to the usual click IPIs of whales identified as present while the recording was being made. This was done for a subset of eight recordings in which the usual click IPIs of the whales identified as present were at least 0.20 ms different from one another, a conservative criterion given that codas with IPIs differing by more than 0.10 ms are probably not produced by the same whale (see above). Subsequently, we used the IPIs of these assigned codas to calculate the modal coda click IPI for each identified whale. Unassigned codas were then assigned to a whale if its modal IPI was within 0.05 ms of the modal coda click IPI of a whale identified as present at the time of recording and at least 0.10 ms dissimilar to the modal coda click IPI of every other whale identified as present during the recording (see above).

Although whale no. 5561 and whale no. 5560 had modal coda click IPIs within 0.05 ms of one another, in recordings in which only one of these two whales was present (and thus the identity of the vocalizing whale was unambiguous), the modal coda click IPIs of whale no. 5561 were consistently below 3.36 ms ($N = 10$ codas) and the modal coda click IPIs of whale no. 5560 were consistently above 3.36 ms ($N = 43$ codas). Codas in recordings in which both these whales were present were thus assigned to each of these whales using this criterion in addition to the assignment criterion described in the text. The use of these two criteria to discriminate between the codas made by these two whales is corroborated by the fact that, for 35 pairs of recorded overlapping codas, the two codas in each overlapping pair were assigned to

different whales (no. 5560 and no. 5561) whereas for no pairs of overlapping codas were both codas in the pair assigned to the same whale.

Although no modal coda click IPI was initially available for whale no. 5563 (because it was only present during one recording, which did not meet the criteria for the unambiguous assignment of codas to whales), because its modal usual click IPI was very similar to that of another whale (no. 5130), it was assigned the same modal coda click IPI. These two whales were never both identified as present during a coda recording.

Even though the calf is the Group of Seven did not produce usual clicks, because the IPIs of the other whales were all greater than 2.7 ms, codas with clear IPIs of less than 2.0 ms recorded while the calf was present were assumed to have been made by the calf.