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Sound variation and function in captive Commerson's dolphins (*Cephalorhyncus commersonii*)

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Abstract

Commerson's dolphin (*Cephalorhyncus commersonii*), one of the smallest dolphin species, has been reported to produce only narrow-band high-frequency (NBHF) clicks and no whistles. To clarify their sound repertoire and examine the function of each type, we analysed the sounds and behaviour of captive Commerson's dolphins in Toba Aquarium, Japan. All recorded sounds were NBHF clicks with peak frequency > 110 kHz. The recorded click-trains were categorised into four types based on the changing pattern of their Inter-click intervals (ICI): Decreasing type, with continuously decreasing ICI during the last part of the train; Increasing type, with continuously increasing ICI during the last part; Fluctuating type, with fluctuating ICI; and Burst-pulse type, with very short and constant ICI. The frequency of the Decreasing type increased when approaching an object newly introduced to the tank, suggesting that the sound is used for echolocation on approach. The Burst-pulse type suddenly increased in front of the object and was often oriented toward it, suggesting that it was used for echolocation in close proximity to the object. In contrast, the Increasing type was rarely recorded during approach, but increased when a dolphin approached another dolphin. The Increasing and Burst-pulse types also increased when dolphins began social behaviours. These results suggest that some NBHF clicks have functions other than echolocation, such as communication.

1. Introduction

Commerson's dolphin (family Delphinidae, *Cephalorhyncus commersonii*) is the smallest dolphin inhabiting the inshore waters of Argentina, the Strait of Magellan, and the Falkland and Keruguelen Islands in the Indian Ocean. Like other toothed whales (*Odontoceti*), Commerson's dolphins produce pulse sounds for echolocation (Watkins and Schevill, 1980). However, the species produces only pulse sounds, and no whistle sounds (Dziedzic and De Buffrenil, 1989; Evans et al., 1988; Hatakeyama et al., 1988; Kamminga and Wiersma, 1982, 1981; Shochi et al., 1982; Watkins and Schevill, 1980), while most other delphinids also produce whistles. These species use pulses mainly for echolocation and whistles mainly for intra-specific communication (e.g., *Tursiops truncatus* (Janik and Slater, 1998), *Lagenorhynchus obliquidens* (Caldwell and Caldwell, 1971), and *Sousa chinensis* (Van Parijs and Corkeron, 2001)).

Dolphins in the genus *Cephalorhynchus,* including Commerson's dolphin, two of the genus *Lagenorhynchus* (hourglass dolphin (*L. cruciger*) and Peale's dolphin (*L. australis*)), those of the family Phocoenidae, and the pygmy sperm whale (family Kogiidae, *Kogia breviceps*), all produce short (ca. 130–400 μsec) and narrow-banded (ca. 10–20 kHz) high-frequency (ca. 120–130 kHz) ultrasonic clicks (NBHF clicks) but no whistle sounds (Au, 1993; Au et al., 1999; Dawson, 1988; Kyhn et al., 2010; Madsen et al., 2005; Tougaard and Kyhn, 2010). This may be to avoid predation by killer whales, as the frequency of NBHF clicks exceeds their auditory range (Morisaka and Connor, 2007; Morisaka, 2012).

Although there are no reports of acoustic communication in Commerson's dolphin, acoustic communication using NBHF pulse sounds has been suggested in other NBHF species. Dawson (1991) showed that highly repetitive "click-trains", resulting in a "cry", were often recorded during aggressive behaviour in Hector's dolphin (*C. hectori*). These "cry" sounds were recorded more often in large groups than in small, suggesting a relationship with social interaction. NBHF pulse sounds similar to the cry sound were reported for all *Cephalorhynchus* species, including Commerson's dolphin (*C. commerosonii, C. hectori, C. heavisidii, C. eutropia*)

(Watkins et al., 1977). Harbour porpoise (*Phocoena phocoena*), which has a body size and shape similar to that of *Cephalorhynchus* dolphins, may also use high-repetition NBHF pulse sounds for communication, as these sounds are frequently recorded during social interactions (e.g. aggressive behaviour, and when approaching other individuals) (Clausen et al., 2010; Nakamura et al., 1998). However, more precise analysis of the relationship between the sounds and behaviour is necessary to conclusively demonstrate that acoustic communication using NBHF pulse sounds occurs in these species.

There have been some previous studies on the sounds of Commerson's dolphin in the wild (Dziedzic and De Buffrenil, 1989; Watkins and Schevill, 1980) and in captivity (Hatakeyama et al., 1988; Shochi et al., 1982). Audible sounds similar to the cry sounds of Hector's dolphin were also recorded in some studies (Dziedzic and De Buffrenil, 1989; Hatakeyama et al., 1988; Shochi et al., 1982; Watkins and Schevill, 1980). However, most of these were brief descriptions of the dolphins' behaviours and sounds obtained using a band-limited recording system that recorded only low frequencies < 100 kHz (Dziedzic and De Buffrenil, 1989; Watkins and Schevill, 1980), which does not cover the main frequency of the sound in Commerson's dolphin. Furthermore, most analysed the waveform of a single pulse, though the sounds of Commerson's dolphins consist of click-trains containing from a few dozen to several thousand sequential clicks (Kamminga and Wiersma, 1982). There has been no precise analysis of these click-trains. To examine the possibility of acoustic communication in this species using NBHF clicks, it is necessary to analyse and categorise the click-trains and study the relationships between click-train type and dolphin behaviour.

In this study, we analysed the sounds of captive Commerson's dolphins to categorise their click-trains based on changing inter-click interval (ICI) patterns. We also analysed the relationships between click-train type and dolphin behaviours to infer the function of each type of click-train. Finally, we discuss the possible use of clicks for acoustic communication in this species.

2. Materials and methods

2.1. Study site and subject animals

Video and acoustic recordings of Commerson's dolphins were made at the Toba Aquarium, Mie prefecture, Japan, on July 25 (three animals) and December 27–28 (four animals), 2007. We studied two adult females (Laura: 18 years old, Lala: 16 years old), one adult male (Kai: 10 years old, unrelated to Laura or Lala) and one juvenile male (Peace: 1 year old, son of Laura). All were born in Japanese aquariums: Laura and Lala were born at the Matsushima Aquarium, Miyagi prefecture, Japan in 1989 and 1991, respectively, and have lived in the Toba Aquarium since March 1996. Kai and Peace were born at the Toba Aquarium in 1997 and 2006, respectively. On July 25, 2007, three dolphins, excepting Kai, were housed in the main pool (Fig. 1, 8.4 × 6.8 m and 3.4 m in depth, 194.2 m^3 of water, temperature of 14°C), and Kai was housed in the sub-pool (4.9 × 5.0 m and 1.5 m in depth, 36.75 m^3 of water, temperature of 14°C). On December 27–28, 2007, all four dolphins were housed in the main pool.

2.2. Recording of behaviour and vocalisation

To clarify the vocalisation repertoire and analyse the relationship between sound types and behaviour, we carried out sound recording and video recording of behaviour during the daytime (9:00–17:30) on July 25, 2007, in nine 30-min recording sessions, each starting on the hour. We observed and recorded dolphin behaviour from an underwater observation window (8 × 6 m) in the main pool that enabled observation across almost the entire tank (Fig. 1). Video recordings were made using a Sony (Tokyo, Japan) HDR-HC3 video camera. Sounds were recorded using a hydrophone (Reson, TC4013, Denmark; sensitivity –211 dB re 1V/μPa between 1 Hz to 170 kHz ± 3 dB), an amplifier (Reson, EC6081, Denmark) with 10-kHz high-pass and 250-kHz low-pass filters and 50 dB gain, and one channel of a data recorder (EZ7510, NF corporation, Yokohama, Japan) which consisted of an analogue-to-digital converter (16-bit resolution, 500-kHz sampling rate, 2-V dynamic range) with data stored on a 40-GB hard disk drive (HDD). The hydrophone was placed on a side wall of the main pool at 1-m depth (Fig. 2).

To assess reactions to a newly introduced object, we recorded behaviour and vocalisations on December 27 and 28, 2007, from the same observation window and the pool-side floor of the main pool. The object introduced was a handle with two sucker discs affixed to the pool wall, used by aquarium staff for support while cleaning the pool. The object was attached to the wall of the main pool close to the hydrophone (10 cm above the hydrophone, Fig. 2). Video recordings were made using two video cameras (HDR-HC3, Sony, Tokyo, Japan, and DM-IXYDVM5, Canon, Tokyo, Japan). In three 30-min recording sessions, each starting 5 min after introduction of the object, vocalisations were recorded with the same system and settings used in the previous recording of July 25, 2007. In two sessions, we recorded sounds with a custom click detector (Clicker45, Tachibana Electric Co. LTD., Tokyo, Japan), set between the amplifier (Reson EC6081) and video camera (Canon DM-IXYDVM5), using one channel of the video camera (16 bit, 44000-Hz sampling rate). The click detector converted each click to a 500-μs rectangular signal with a voltage corresponding to the peak level of the click.

To assess the relationship between behaviour and sounds when the dolphins approached the introduced object or began to parallel pair-swim with other individuals, the sounds, position, posture, and swimming speed of the approaching dolphin were recorded for 3–5 s until it reached the object or other individual. Parallel pair-swimming is a behaviour in which two dolphins swim side by side in close (< 0.5 m) proximity without body contact (Sakai et al., 2013).

Sounds produced at the onset of social behaviour (flipper rubbing) were recorded for 5 s before dolphins engaged in parallel pair-swimming initiated flipper rubbing. Flipper rubbing is a behaviour in which one dolphin rubs the other dolphin with its flipper (Sakai et al., 2006).

Although sounds could not be attributed to specific individuals in the July 25 data because the recording was made with a single hydrophone, those recorded December 27–28 were attributed based on the direction and position of all individuals relative to the hydrophone in the video records. In the analysis of sound and behaviour when an object was introduced to the tank, only sounds thought to be produced by the dolphin approaching the object were analysed; i.e. we considered only those recorded when no other dolphins in the tank directed their heads toward the object.

2.3. Sound analysis

All sound records on July 25 and December 27–28 were analysed using the Igor Pro ver.6 software (Wave Metrics Incorporated, Oregon, US) and Adobe Audition 3.0 software (Adobe Systems Incorporated, California, US). Sound spectrograms of all sounds with a good signal-to-noise ratio from July 25 were generated using the fast Fourier transform (FFT) algorithm, with FFT length of 256, 100% frame size, and a rectangular window. The sound frequency with maximum energy (peak frequency) in each click was analysed using Adobe Audition 3.0. Inter-click interval (ICI) is the interval between the envelope peaks of consecutive clicks. We measured ICI using a program that we made in Igor Pro. In this analysis, we eliminated any ICIs < 0.5 ms as they were most likely caused by reflection from the tank walls or water surface. Hatakeyama (1988) reported that the minimum ICI of a captive Commerson's dolphin was 2.9 ms; Kamminga and Wiersma (1981) also reported that the average ICI of a captive Commerson's dolphin was > 2 ms (500 pulses/s) and that the minimum ICI of a captive harbour porpoise was 1.0 ms (Clausen et al., 2010). All statistical analyses in this study were conducted using Igor Pro.

3. Results

All recorded sounds were ultrasonic pulses (clicks). In all, 114,590 pulses were recorded during 270 min from three individuals on July 25, 2007 and 227,910 pulses during 90 min from four individuals on December 27–28, 2007. Two types of pulse sound with different peak frequencies were recorded. The peak frequencies of each type were 129.4 ± 4.9 kHz (mean ± SD, n = 30, 87.1% of recorded pulses) and 113.0 ± 6.0 kHz (n = 30, 11.9% of recorded pulses), respectively.

Figure 3 shows the distribution of ICIs measured for all clicks recorded on July 25, 2007. Ninety-six percent of the measured ICIs were < 100 ms (Fig. 3, mean ICI = 35.16 ± 30.81 ms). Based on this result, we defined a click-train as a group of sequential pulses separated from other pulses by an ICI > 100 ms. Most of the recorded pulses (94.5%) were produced as click-trains, sequences of several clicks (> 5 pulses) with relatively short ICIs, and 5.5% were produced as single pulses or very short click-trains with 2–4 pulses. We removed single pulses or very short click-trains of < 4 pulses from the analysis. A total of 6,449 click-trains were identified on July 25, 2007. The mean values (± SD) of pulse number, ICI and duration of the click-trains were 43.9 ± 32.9, 26.5 ± 20.0 ms and 769.2 ± 700.6 ms, respectively.

3.1. Variation of click-trains

We categorised click-trains by focussing on changes in mean ICI pattern, especially in the last part of the train (including > 5 pulses from the last pulse), because it might reflect changes in target distance if the train was used for echolocation. Click-trains were divided into two groups based on mean ICI: those with very short mean ICIs < 4.0 ms, and others with longer mean ICIs. Those with longer mean ICIs were further divided into three groups based on changing ICI pattern in the last part of the train. Thus, click-trains were categorised into the following four types (Fig. 4): Burst-pulse type, with very short (< 4.0 ms mean) and relatively constant ICI (Fig. 4-A); Decreasing type, with longer mean ICIs, in which ICI continuously decreased by > 2.0 ms in the last part of the train (Fig. 4-B); Increasing type, with longer mean ICI, in which ICI continuously increased by > 2.0 ms in the last part of the train (Fig.4-C); and Fluctuating type, with longer mean ICI, in which ICI fluctuated in the train without a definite continuous increase or decrease in the last part (Fig. 4-D).

The parameters of each type of click-train are shown in Table 1. Only clear click-trains were used for this analysis because the dolphins often emitted sounds simultaneously, confounding assessment. The mean ICI differed significantly among these types (Kruskal-Wallis test: $H = 69.61$, $P < 0.001$). It was highest in the Increasing type (31.6 ms), followed by the Fluctuating type (29.6 ms), the Decreasing type (25.0 ms), and the Burst-pulse type (3.5 ms).

The mean click-train duration was longest in the Fluctuating type (1344.3 ms) and shortest in the Burst-pulse type (458.9 ms), though significant differences were observed only between the Fluctuating type and each of the other types (Kruskal-Wallis test, $H = 61.84$, $P < 0.001$). The range and standard deviation of click-train duration were also largest in the Fluctuating type and smallest in the Increasing type.

The change in click-train ICI (maximum − minimum) was largest in the Fluctuating type (62.7 ± 19.2 ms) and smallest in the Burst-pulse type. The change in ICI and the duration of continuous ICI change observed during the last part of the train were 25.0 ± 14.3 ms and 409.9 ± 240.2 ms in the Decreasing type and 36.0 ± 18.3 ms and 347.6 ± 201.04 ms in the Increasing type, respectively.

Figure 5 shows the frequency (number/min/dolphin) and proportion (percent) of each click-train type in the sounds recorded on July 25, 2007. The Fluctuating (3.7/min/dolphin) and Decreasing (2.7/min/dolphin) types were recorded more frequently than were the other types. The Increasing type was the least common (0.4/min/dolphin, Fig. 5).

3.2. Relationship between behaviour and click-train type

Figure 6 shows the change in the frequencies (number/min/dolphin) of each click-train type observed when a dolphin approached and then left a newly introduced object (n = 165, 90 min in total). The dolphins typically swam in a counter-clockwise routine course near the wall, but after the object was introduced, they often changed course to approach it repeatedly (Fig. 1).

Clicks trains were recorded in 156 of 165 approaching-and-leaving episodes (94.5 %; no or few isolated pulses were recorded in the remaining 5.5%). The frequency of the Decreasing type increased during the approach to the object but decreased suddenly as the dolphin passed (Fig. 6). The Burst-pulse type increased suddenly when the dolphin reached a position immediately in front of the object, and was recorded in 50 of 165 episodes. When the Burst-pulse type was recorded, the dolphin often bent its head toward the object (43 of 50 episodes, 86 %) By contrast, when the focal dolphin was approaching the newly introduced target, the frequency of the Fluctuating and Increasing types did not change markedly, though the Fluctuating type seemed to decrease slightly after the dolphin passed.

The frequency of the Decreasing type during approach (14.7/min/dolphin) was significantly higher than normal (2.6/min/dolphin, the mean value of all recording sessions on 25 July, 2007, Fig. 5) (Wilcoxon test, $P = 6.61E^{-20}$). That of the Burst-pulse type (9.2/min/dolphin) was also significantly higher than the baseline level (1.3/min/dolphin) (Wilcoxon test, $P = 1.25E^{-13}$). The frequency of the Fluctuating type during the approach (10.7/min/dolphin) was significantly higher than the baseline (3.7/min/dolphin) (Wilcoxon test, $P = 4.93E^{-09}$), while that of the Increasing type (0.3/min/dolphin) was slightly lower (vs. 0.4/min/dolphin) but not statistically different (Wilcoxon test, $P = 0.53$).

Figure 7 shows the change in the frequency (number/min/dolphin) of each sound type when approaching another individual, and during parallel pair-swimming (n = 44, 220 s in total) thereafter. The frequencies of the Increasing and Decreasing types increased during the approach to the other dolphin, and decreased before the dolphins took up typical positions for parallel pair-swimming. After starting parallel-pair swimming, the frequency of the Increasing type increased again for about 2 s, and then decreased. By contrast, the Decreasing type gradually decreased after the two dolphins started parallel-pair swimming. The frequency of the Fluctuating type decreased gradually during the approach, and increased again gradually after the dolphin reached its partner and began parallel-pair swimming. The Burst-pulse type increased during the approach until parallel pair-swimming commenced, and decreased again thereafter. However, the change of frequency in Fig. 7 was unclear, probably because the sound-emitting dolphin could not be identified and sounds from other dolphins were included in the analysis for Fig. 7.

The frequencies (number/min/dolphin) of the Increasing and Fluctuating types during the approach were significantly higher than the mean value of the entire recording (Fig. 8, Wilcoxon test, $P = 0.00039$ and $P = 1.10E^{-10}$); the frequencies of the Increasing (2.3/min/dolphin) and Fluctuating (9.7/min/dolphin) types were 5.7- and 2.6-fold higher than the baseline level (0.4/min/dolphin and 3.7/min/dolphin), respectively.

Finally, we compared the frequency (number/min/dolphin) of each sound type between the two approach behaviours: approach to a new object (n = 165) and approach to another individual (n = 44) (Fig. 9).

The frequencies (number/min/dolphin) of the Decreasing (14.7 /min/dolphin) and Burst-pulse (9.2/min/dolphin) types during the approach to the object were significantly higher than those during the approach to the other individual (8.4/min/dolphin and 2.3/min/dolphin; Wilcoxon test, $P = 3.72E^{-21}$ and $P = 9.04E^{-10}$, respectively), while the frequency of the Increasing type (2.3/min/dolphin) was significantly higher when approaching the other individual than when approaching the object (0.3/min/dolphin; Wilcoxon test, $P = 0.00030$). We observed no significant difference in the Fluctuating type (Wilcoxon test, $P = 0.64$).

During parallel-pair swimming before flipper rubbing behaviour (n = 14, 70 s in total), the frequencies (number/min/dolphin) of the Increasing (2.3/min/dolphin) and Fluctuating (8.6/min/dolphin) types were significantly higher than the mean values of the entire recording (0.4/min/dolphin and 3.7/min/dolphin, Wilcoxon test, $P = 0.019$ and $P = 6.86E^{-03}$ respectively). We found no significant difference in the frequency of the Decreasing (2.6/min/dolphin) or Burst-pulse (1.4/min/dolphin) types compared with the mean values of the entire recording (3.2/min/dolphin and 1.8/min/dolphin, respectively; Wilcoxon test, $P = 0.91$ and $P = 0.88$).

4. Discussion

4.1. Variation in recorded sounds

In this study, we recorded only ultrasonic click sounds (ca. 113–130 kHz in peak frequency), with no whistles or audible sounds. In previous studies, low frequency clicks (ca. 1.0–6.0 kHz) were also reported in captive Commerson's dolphins (Dziedzic and De Buffrenil, 1989; Hatakeyama et al., 1988; Shochi et al., 1982; Watkins and Schevill, 1980). Some of these low-frequency clicks were audible to researchers, though not recorded frequently. These click-trains, or cry sounds, include audible low-frequency clicks with very short ICIs, similar to the Burst-pulse type (Shochi et al., 1982). Cry sounds are composed of high (116–133 kHz) and low (1–7 kHz, audible to humans) frequency clicks (Dziedzic and De Buffrenil, 1989; Shochi et al., 1982). Watkins et al (1977) defined the cry sound as a pulse series at a repetition rate rapid enough to produce tonal sounds. Shochi et al. (1982) also reported short clicks in the ultrasonic range superimposed on low-frequency pulses (1–2 kHz) audible to humans only when captive dolphins approached within 20–30 cm of the hydrophone. The two signal components were always synchronous. These reports suggest that the cry sounds were the low-frequency components of clicks caused by high repetition-rate ultrasonic pulses. Therefore, the cry sounds could have been the same sound type as the Burst-pulse type in the present study. The peak frequency of the high-frequency component (116–133 kHz) of the cry sound (Dziedzic and De Buffrenil, 1989; Shochi et al., 1982) was similar to that of the Burst-pulse type (113–130 kHz). Likewise, the peak frequencies of high-frequency clicks recorded in this study (130 kHz) were similar to those reported by previous studies on wild (133 kHz) and captive (116–133 kHz) Commerson's dolphins (Evans et al., 1988; Kamminga and Wiersma, 1981; Kyhn et al., 2010).

4.2. Function of each click-train type

4.2.1 Decreasing type: recognition of a target as it is approached

The ICI pattern of the Decreasing type click-train (Fig. 4), where ICI decreased in the last part of the train, suggests that it is used for echolocation when the dolphin is approaching a target, as the ICI of echolocation clicks may reflect the distance between the dolphin and its target (Au, 1993). Such a rapid decrease in ICI is known as the "approach phase" in the echolocation sounds of harbour porpoise and in bats intercepting a target (Tian and Schnitzler, 1997; Verfuss et al., 2009). The fact that the frequency (number/min/dolphin) of the Decreasing type of click train increased during the approach to an object newly introduced to the tank (a probable target), and when a dolphin approached another individual (Figs. 6, 7), supports this view. However, the change in frequency of the Decreasing type in Fig. 7 was not as clear as that in Fig. 4, probably because the sound-emitting dolphin could not be identified and sounds from other dolphins were included in the analysis for Fig. 7. Shochi et al. (1982) and Watkins and Schevill (1980) also observed that ICI decreased in the click-trains of captive Commerson's dolphins when the dolphins approached a fish or other targets, and suggested that the sounds were used in target echolocation. Similar ICI-decreasing click-trains were reported in wild Hector's dolphins approaching a hydrophone (Dawson, 1991).

In captive harbour porpoises, Clausen et al. (2010) reported similar click-trains in a mother-calf pair when they engaged in aggressive or encounter behaviours ("contact call behaviour") in which the dolphins approached each other. These click-trains were characterised by increasing repetition rate (rapid decrease of ICI), changing from 20 to 800 clicks/s (50 to 1.2 ms ICI). This is similar to the ICI range of our Decreasing type click-trains (89.5 to 1.1 ms ICI). It is possible that the harbour porpoise click-trains were also used for echolocation, though the results of Clausen et al. (2010) suggest that these sounds were used for communication.

4.2.2 Burst-pulse type: short-range target recognition

The fact that most of the Burst-pulse type click-trains were emitted toward the object newly introduced to the tank from a distance of ~0.5 m suggests that they were used for close proximity echolocation. Moreover, we recorded a significant increase in the Burst-pulse type when an object was newly introduced.

However, some "lag time" is thought to be required for the neuronal process of echolocation, and many of the ICIs in the Burst-pulse type (mean

3.5 ± 1.1 ms) may have been shorter than the time required. Lag time is defined as the difference in time between the two-way travel time of the sound to the target and the ICI (Au and Cranford, 2000). Although the lag time of Commerson's dolphin is still not known, the minimum lag time estimated for the Atlantic bottlenose dolphin (family Delphinidae, the same as Commerson's dolphin) was reported as 2.5 ms (Au et al., 1974). However, in the harbour porpoise (family Phocoenidae), a small species such as Commerson's dolphin, the minimum lag time was reported as 1.5 ms (Verfuss et al., 1999). Furthermore, the lag time of bottlenose dolphins decreased from 15.4 to 2.5 ms as the distance to the target decreased from 1.4 to 0.4 m (Evans and Powell 1967). Assuming that the lag time of Commerson's dolphin was similar to those of the bottlenose dolphin or harbour porpoise, most of the Burst-pulse type ICIs were longer than the lag time. Thus, it is possible that the Burst-pulse type could have an echolocation function in Commerson's dolphin.

Kamminga and Wiersma (1981) also recorded a burst of sonar signals (< 2-ms ICI, 500 clicks/s repetition rate, 4-s train duration) similar to the Burst-pulse type when captive Commerson's dolphins approached and inspected newly introduced hydrophones at very short range. The reported mean ICI (< 2 ms) was close to that observed for the Burst-pulse type (3.5 ± 1.8 ms), although the mean train duration (4 s) was not (458.9 ± 304.4 ms). Such bursts of sonar signals emitted toward objects in close proximity were also recorded in other dolphin species (e.g. bottlenose dolphin, white whale), and the possibility of their function in echolocation with ICIs less than the lag time has been discussed (Turl and Penner, 1989).

Burst-pulse sounds have been observed during aggressive social interactions as well as approaching behaviour in NBHF species and other odontocetes, and their function in both communication and echolocation in these species is suspected. Harbour porpoise also emits a cry sound with a mean ICI of 3.7 ms. Harbour porpoises use this cry sound during aggressive behaviour toward other dolphins (Clausen et al., 2010; Nakamura et al., 1998). However, we did not observe such behaviour or any remarkable responses of other dolphins to the Burst-pulse type in Commerson's dolphin, though Watkins and Schevill (1980) reported that cry sounds of captive

Commerson's dolphins seemed to elicit responses from others in the same tank.

The Burst-pulse type was recorded not only when the dolphins faced a newly introduced object in close proximity but also when no obvious echolocation targets were present, other than the tank walls and other dolphins. However, we observed no notable behaviours oriented to those targets (e.g. head bending toward the objects) (Fig. 10). The Burst-pulse type also increased immediately after a dolphin approached another dolphin and initiated parallel-pair swimming, though we could not identify the dolphin emitting the sound. These facts suggest that some of the Burst-pulse type click-trains were used for other functions, such as calls to swim together. However, this increase may also have been due to increased short-range echolocation of the partner when pair swimming. Although Burst-pulse type click-trains aimed at the newly introduced object might also have been alarm calls, we did not observe any obvious reactions in other dolphins when they were emitted. Thus, our results suggest that the Burst-pulse type sounds of Commerson's dolphin in captivity were used as short-range sonar rather than for communication. The fact that the reported cry sounds of Commerson's dolphins were recorded for only a few days after the dolphins were moved to a new tank (a novel environment with many targets for them to inspect) also supports this view, as a prominent increase in the Burst-pulse type was recorded when an object was newly introduced.

4.2.3 Fluctuating type: sensing targets at various ranges

In the Fluctuating type click-trains, ICI fluctuates irregularly over a wide range. If this type of click-train were used for echolocation, the target distance would also change irregularly and widely, because ICI reflects the distance between the dolphin and the target, including the lag time (Au, 1993). Thus, the irregular change of ICI suggests that the Fluctuating type was used for scanning a wide range of space in front of the dolphin rather than for echolocating a particular target. Hatakeyama et al. (1988), who studied captive Commerson's dolphins in a Japanese aquarium, reported that clicks with widely varying ICI (similar to the Fluctuating type) increased when the aquarium lights were turned off, suggesting that they were used for echolocation.

The Fluctuating type was the most frequently recorded sound type, accounting for about half of all recorded click-trains. The Fluctuating type became significantly more frequent than the baseline level when approaching both the introduced object and other dolphins prior to parallel-pair swimming. This suggests that the Fluctuating type increased during active behaviours, though it decreased as other sound types increased just before and after dolphins started parallel-pair swimming (Fig. 7). Shochi et al. (1982), who studied captive Commerson's dolphins, reported that the repetition rate of clicks varied widely (like the Fluctuating type) when the dolphin was resting in the water, motionless, or swimming slowly, though they did not provide precise data. This observation suggests that the dolphins produce Fluctuating-type click-trains even when inactive. The frequent use of this sound type, in both active and inactive states, suggests that it is used for forward scanning; e.g. to avoid collision, to find fish, or to investigate the surroundings (Akamatsu et al., 2010).

Akamatsu et al. (1998) compared the clicks of Baiji, Finless porpoise, and Bottlenose dolphin between captive and wild individuals. They reported that in all studied species, most of the click-trains from the wild dolphins showed irregular ICI change without monotonous increment or decrement, like the Fluctuating type, while those from captive dolphins often showed monotonous ICI decrement, similar to the Decreasing type. Furthermore, these latter sounds were used for echolocation by dolphins approaching targets such as tank walls. Although Akamatsu et al. (1998) did not discuss the function of click-trains with irregular ICIs, their results suggest that the Fluctuating type is not used for echolocating a particular target, as there are fewer target objects in open water than in aquarium tanks. Dolphins in open water may scan their surroundings more frequently than those in aquarium tanks. If so, the frequent use of this sound type in open water also supports our view.

4.2.4 Increasing type: possibly for social communication

The changing pattern of ICI in the Increasing type, in which ICI increased in the last part of the train, suggests that the target distance increased during the train if it was used for echolocating a particular target object. Such an echolocation target (to which the distance from the emitting dolphin increased with time) was largely absent from our study, with the potential exception of other dolphins and the tank walls, because dolphins did not swim backwards. The target distance could increase if the targeted dolphin swam away from the emitting dolphin. It could also increase as the angle between emitted clicks and the targeted tank wall changed as the dolphin changed course at the tank corners.

The frequency (number/min/dolphin) of Increasing-type click-trains increased when a dolphin approached another dolphin and began parallel-pair swimming, while they were rarely emitted when approaching a newly introduced object. They also increased during parallel-pair swimming just before flipper rubbing. These facts suggest that the Increasing type is not used for echolocation. It is difficult to explain these results if we assume that the Increasing-type click-trains were used for echolocating the tank walls, as we observed no obvious change in the emitting dolphin's swimming course. Rather, these facts suggest that the Increasing type was used for initiating social behaviour in which the cooperative movements of two dolphins are required.

There are no previous reports on click trains corresponding to the Increasing type in Commerson's dolphin. In Hector's dolphin, however, Dawson (1991) recorded click trains similar to the Increasing type. He compared the sound types between social and non-social contexts to examine the possibility that the dynamics of the click rate (increasing, constant, and decreasing) carry social meaning, but detected no significant differences. Click-trains similar to the Increasing type were also found in a report on harbour porpoises (Clausen et al., 2010), although it did not describe these click-trains precisely.

We examined the potential functions of each click-train type based on the results of rather preliminary observations in which identification of the sound-emitting dolphin was difficult. More precise studies on the relationship between these click-train types and behaviour are needed to clarify the functions of the various click-train types.

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Figure Titles (Captions) & Legends

Fig. 1

Title: Recording setting.

Legend: Two video cameras and one hydrophone set in the main pool. All dolphins usually swam the course indicated by the grey line. Dotted lines are examples of swimming courses when approaching and leaving the object.

Fig. 2

Title: Example of approaching dolphin to the introduced object, and the hydrophone.

Legend: Frame from video camera A (Fig.1). The sounds of the dolphin were recorded by the hydrophone underneath the object.

Fig. 3

Title: Histogram of all recorded Inter-click-intervals (ICI) on July 25, 2007.

Legend: The right axis shows the ICI value and the left axis the accumulation rate of all recorded ICIs. Ninety-six percent of measured ICIs were < 100 ms (mean ICI ± SD = 35.16 ± 30.81 ms). The grey line indicates the ICI cumulative frequency curve.

Fig. 4

Title: Click-train of each sound type.

Legend: X-axis: time line, Y-axis: ICI; Inter-Click-Interval (ms), SPL: Sound Pressure Level (dB).

Fig. 5

Title: The frequency and percentage of each click-train type.

Legend: The numbers in the upper right are the percentages of all observed trains.

Fig. 6

Title: Change in frequency of each click-train type when the dolphin was approaching and leaving the object.

Legend: The frequency of the Decreasing type increased while approaching the object, and the Burst-pulse type increased suddenly when the dolphin reached a position immediately in front of the object.

Fig. 7

Title: Change in frequency of each click-train type while approaching another individual.

Legend: The right y-axis indicates the number of Fluctuating type sounds. The left y-axis indicates the number of other types.

Fig. 8

Title: Frequency of each sound type while approaching another individual.

Legend: The frequencies of the Increasing (2.3/min/dolphin) and Fluctuating (9.7/min/dolphin) types were 5.7- and 2.6-fold higher than the baseline level (0.4/min/dolphin and 3.7/min/dolphin), respectively.

Fig. 9

Title: Frequency of each click-train type during the approach to two different targets.

Fig. 10

Title: A dolphin bending its head toward the introduced object.

Legend: Frame from video camera B (Fig. 1).

Table 1

Title: Characteristics of each click-train type

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Fig.1

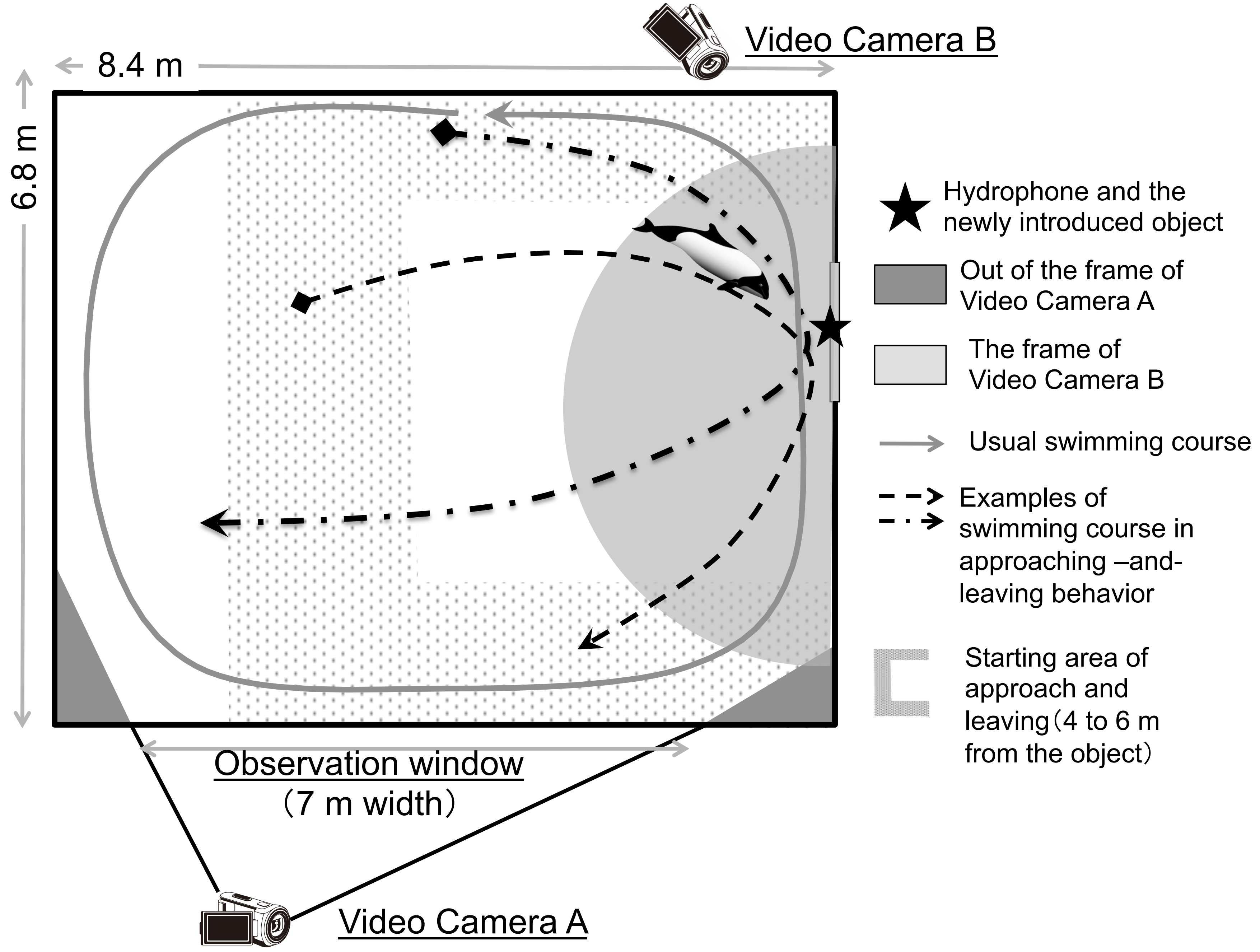

Video Camera B
8.4 m
6.8 m
Hydrophone and the newly introduced object
Out of the frame of Video Camera A
The frame of Video Camera B
Usual swimming course
Examples of swimming course in approaching –and-leaving behavior
Starting area of approach and leaving（4 to 6 m from the object）
Observation window
（7 m width）
Video Camera A

Fig.2

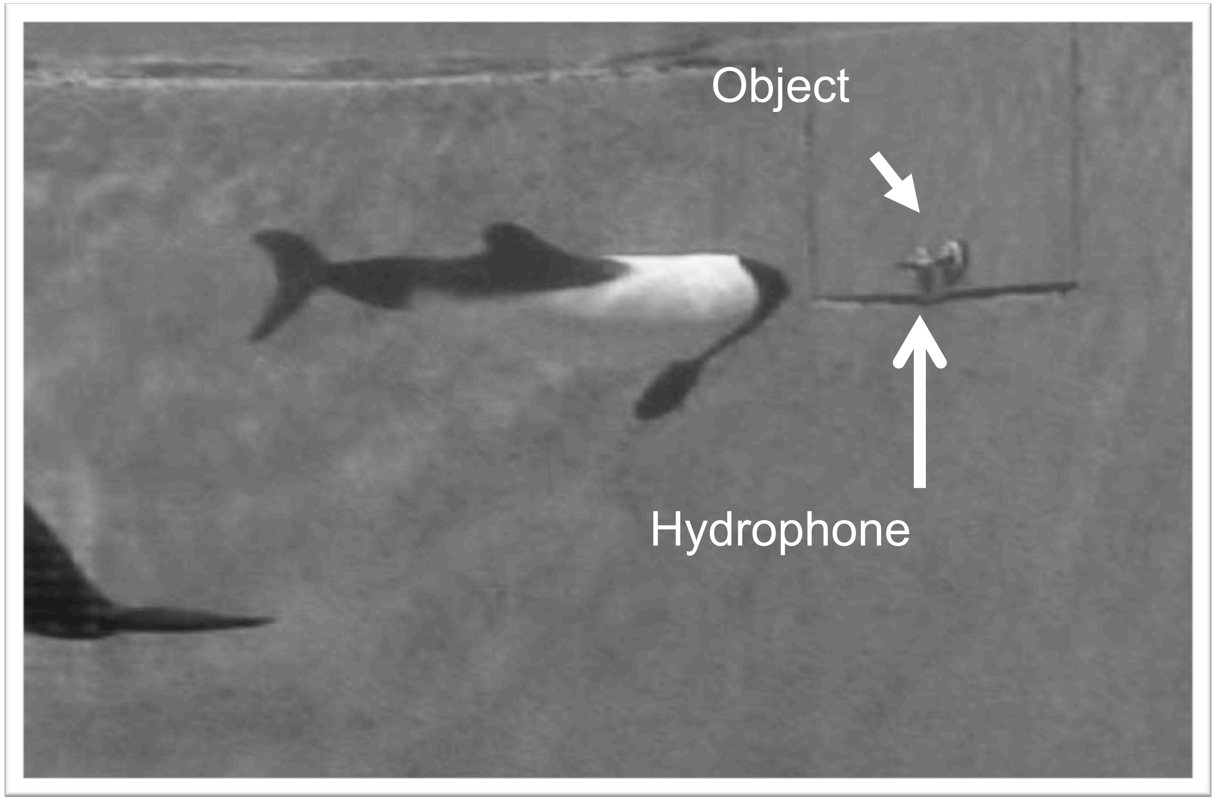


Fig.3

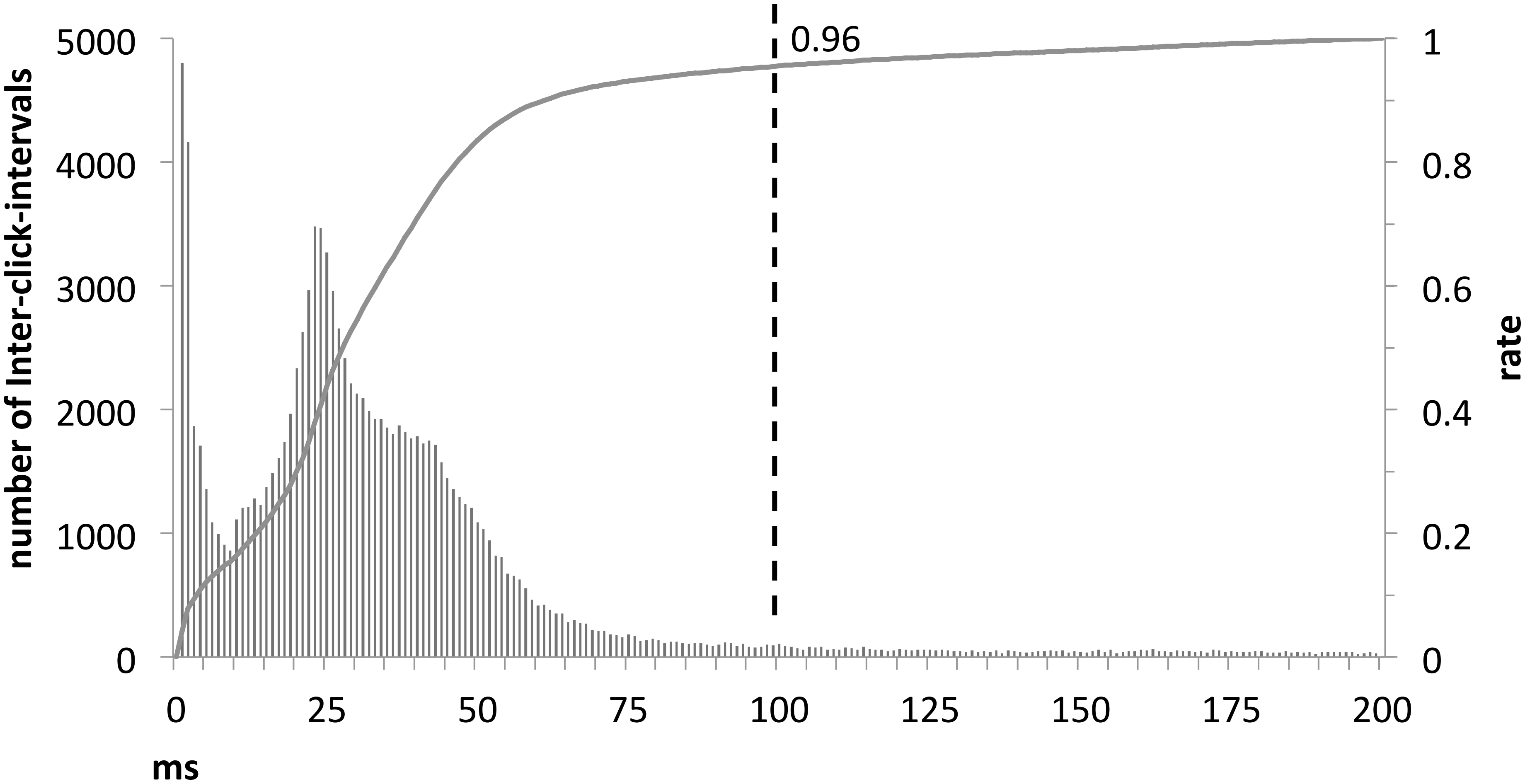

0.96
5000
4000
3000
2000
1000
0
number of Inter-click-intervals
1
0.8
0.6
0.4
0.2
0
rate
0
25
50
75
100
125
150
175
200
ms

Fig.4

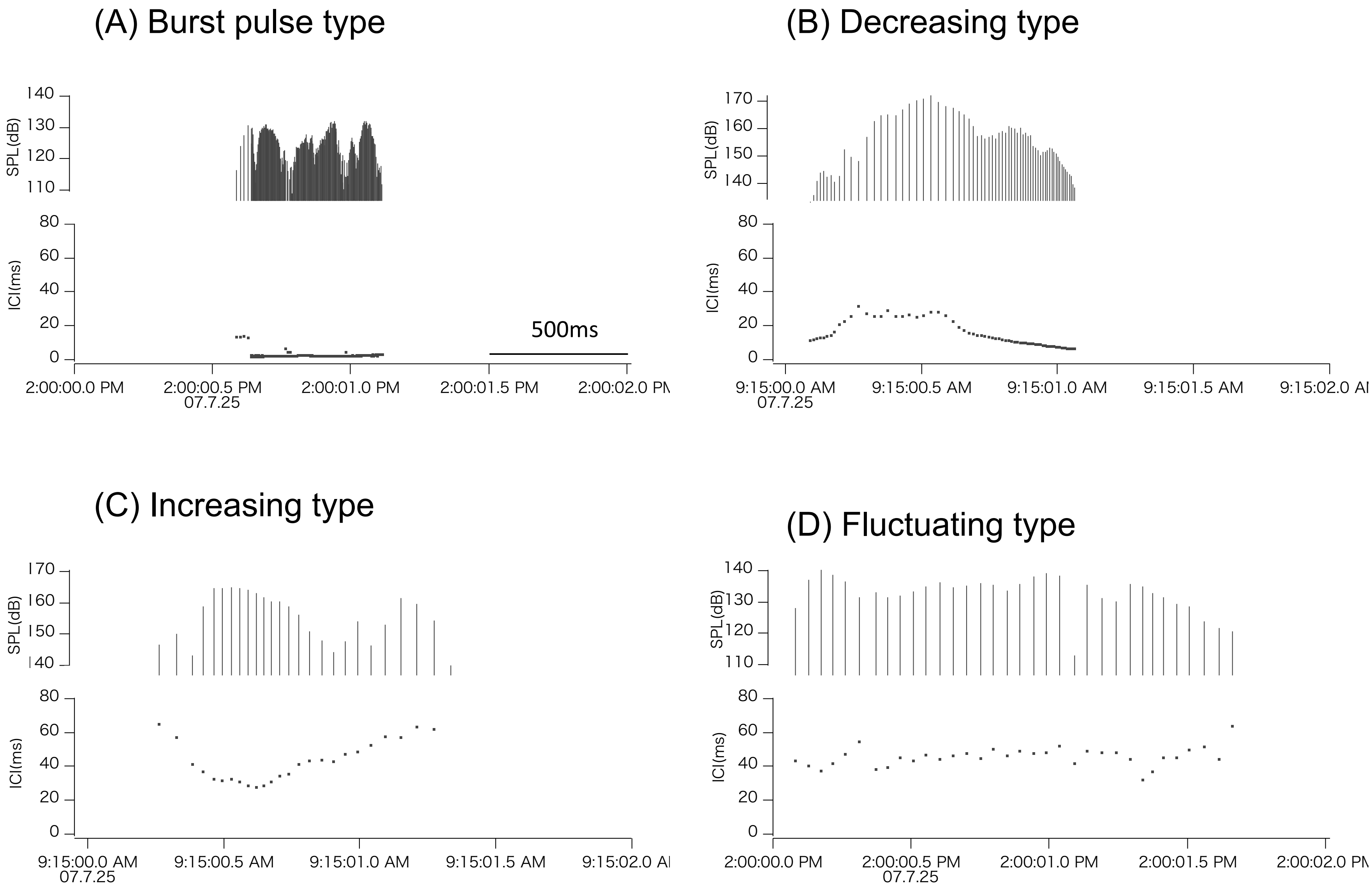
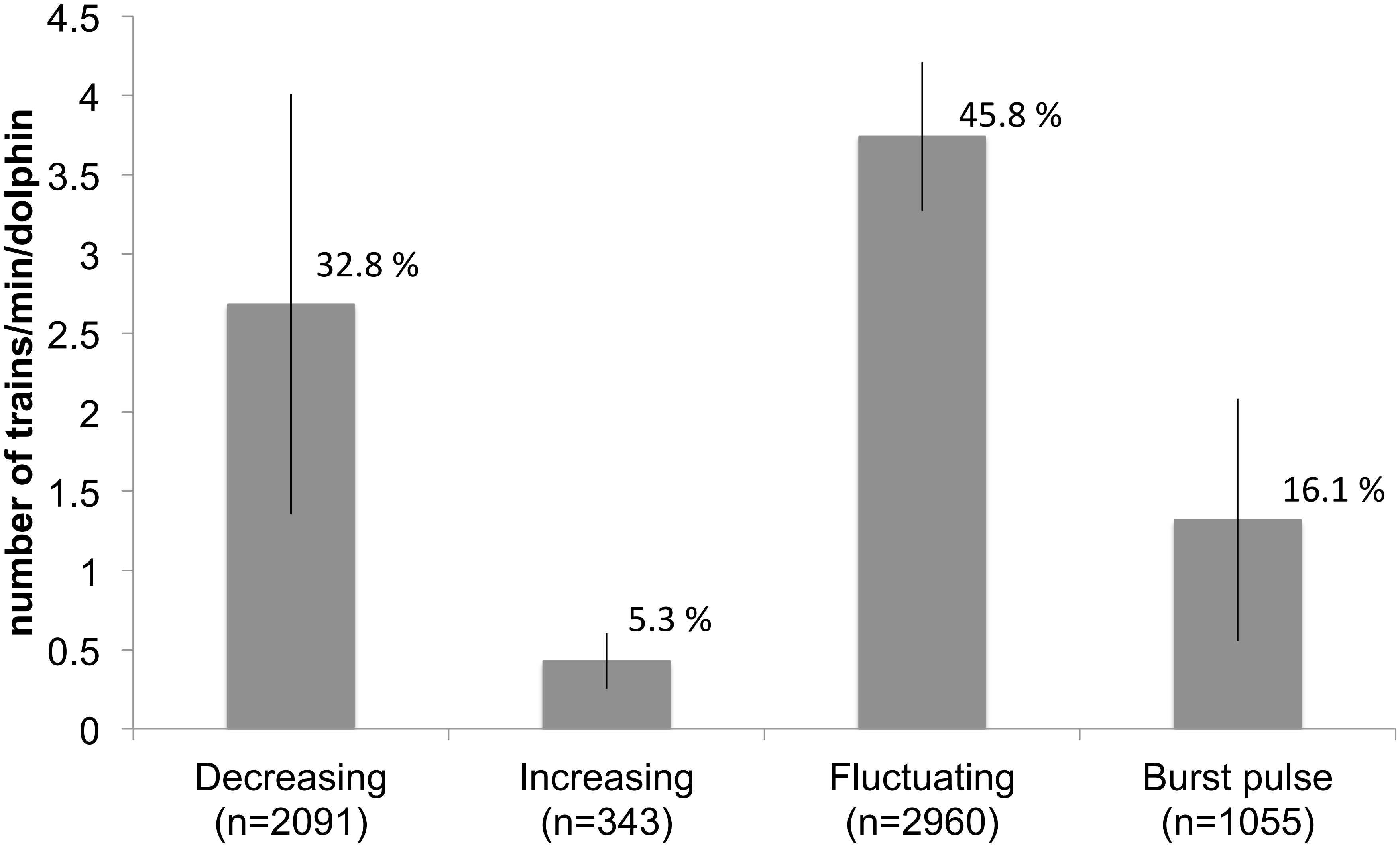
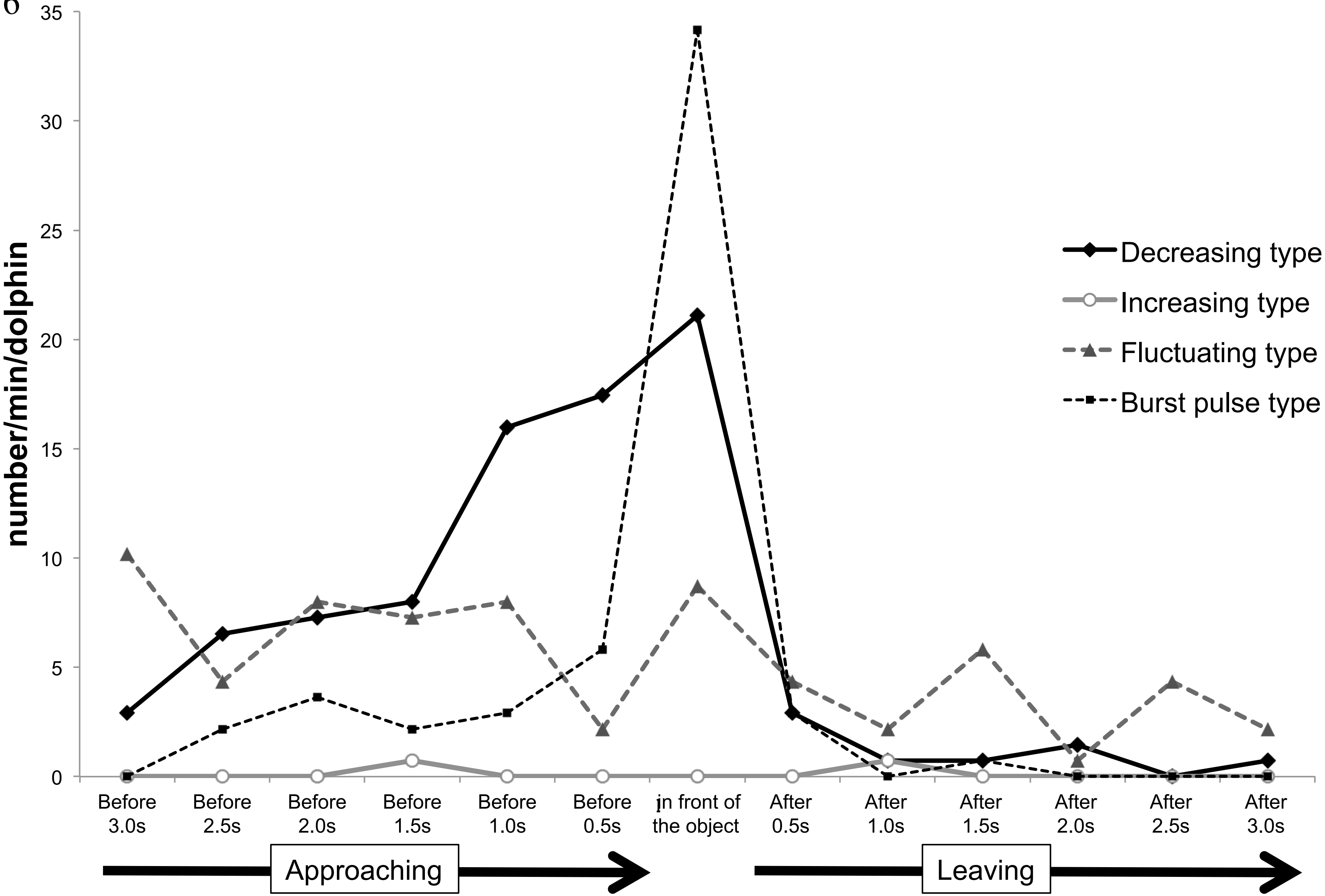

(A) Burst pulse type
(B) Decreasing type
(C) Increasing type
(D) Fluctuating type
SPL(dB)
ICI(ms)
500ms
2:00:00.0 PM
2:00:00.5 PM
07.7.25
2:00:01.0 PM
2:00:01.5 PM
9:15:00.0 AM
07.7.25
9:15:00.5 AM
9:15:01.0 AM
9:15:01.5 AM

Fig.5



number of trains/min/dolphin
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
32.8 %
5.3 %
45.8 %
16.1 %
Decreasing (n=2091)
Increasing (n=343)
Fluctuating (n=2960)
Burst pulse (n=1055)

Fig.6



number/min/dolphin
35
30
25
20
15
10
5
0
Decreasing type
Increasing type
Fluctuating type
Burst pulse type
Before 3.0s
Before 2.5s
Before 2.0s
Before 1.5s
Before 1.0s
Before 0.5s
in front of the object
After 0.5s
After 1.0s
After 1.5s
After 2.0s
After 2.5s
After 3.0s
Approaching
Leaving

Fig.7

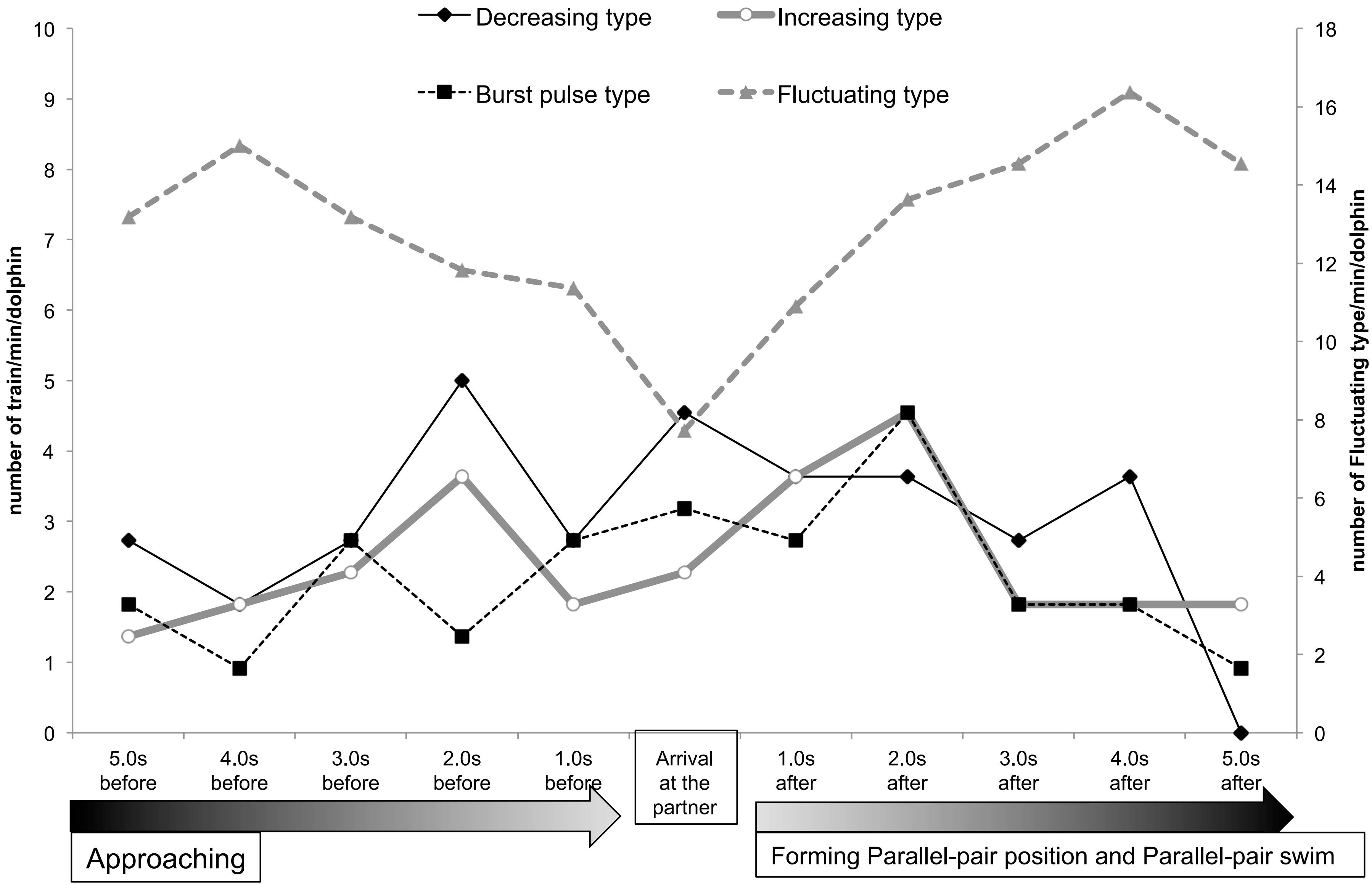
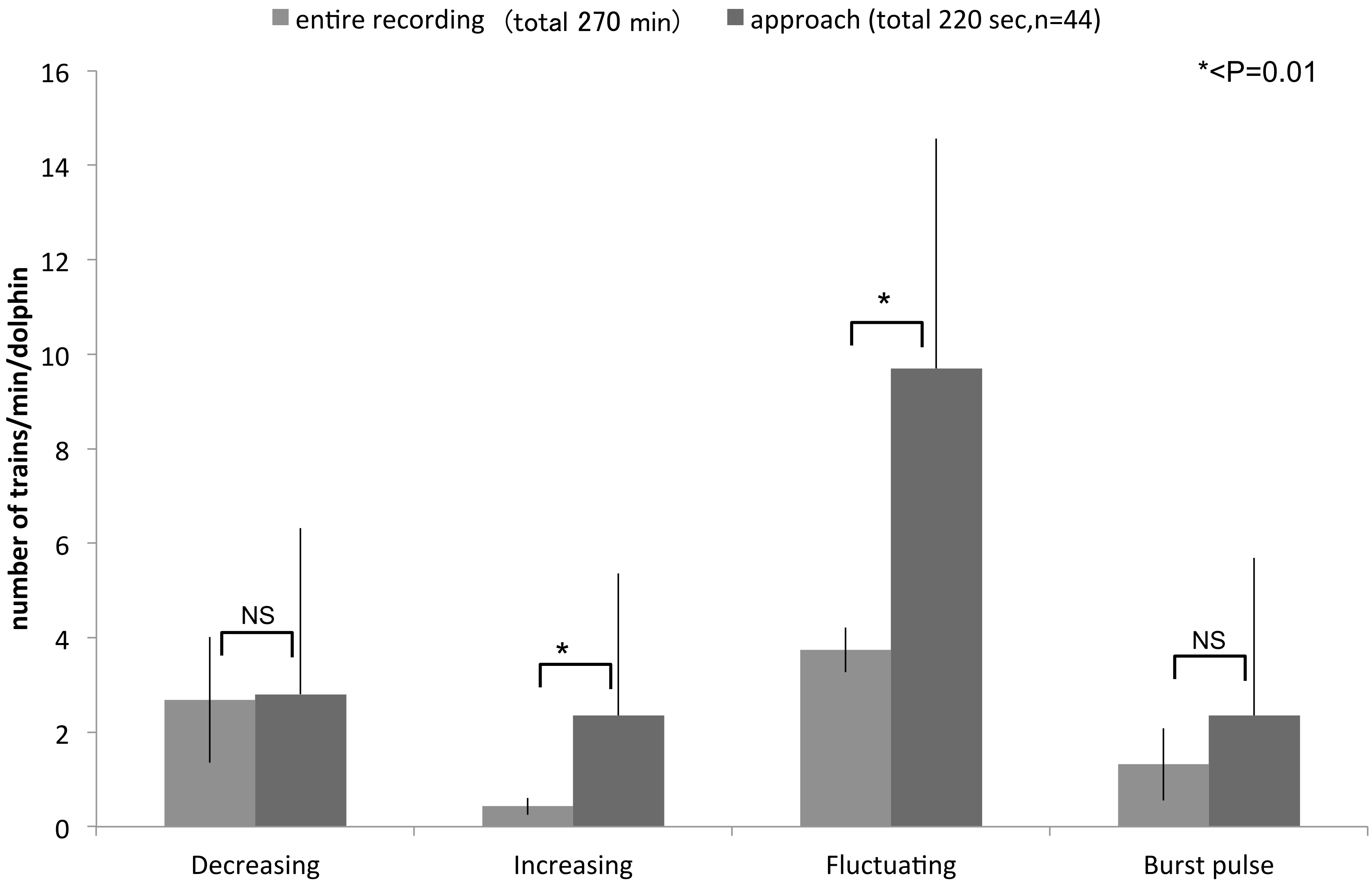
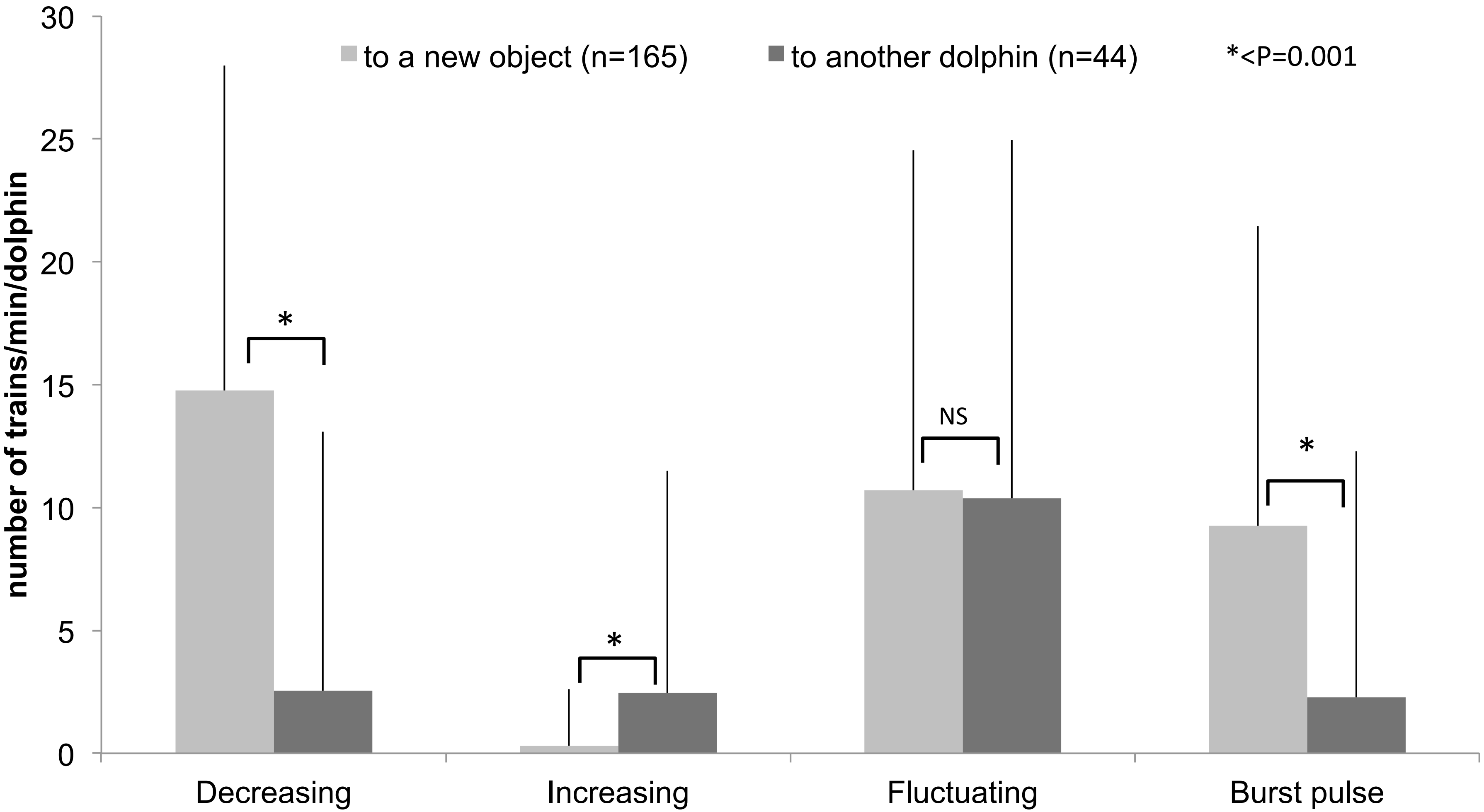

Decreasing type
Increasing type
Burst pulse type
Fluctuating type
number of train/min/dolphin
number of Fluctuating type/min/dolphin
0
1
2
3
4
5
6
7
8
9
10
0
2
4
6
8
10
12
14
16
18
5.0s before
4.0s before
3.0s before
2.0s before
1.0s before
Arrival at the partner
1.0s after
2.0s after
3.0s after
4.0s after
5.0s after
Approaching
Forming Parallel-pair position and Parallel-pair swim

Fig.8



entire recording (total 270 min)
approach (total 220 sec,n=44)
*<P=0.01
number of trains/min/dolphin
16
14
12
10
8
6
4
2
0
NS
*
*
NS
Decreasing
Increasing
Fluctuating
Burst pulse

Fig.9



30
25
20
15
10
5
0
number of trains/min/dolphin
to a new object (n=165)
to another dolphin (n=44)
*<P=0.001
*
*
NS
*
Decreasing
Increasing
Fluctuating
Burst pulse

Fig.10

Table.1

Click-train type (n)	Inter-click interval (ICI) (ms)		Duration of the train (ms)		Change in ICI (ms)	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Decreasing (42)	25.0 ± 12.4	1.1 - 89.5	571.3 ± 324.6	81.2 - 1557.9	25.0 ± 14.3	3.2 - 69.1
Increasing (48)	31.6 ± 13.4	0.5 - 99.5	541.4 ± 264.8	167.9 - 1399.3	36.0 ± 18.4	11.2 - 86.5
Fluctuating (107)	29.6 ± 8.2	10.9 - 99.3	1344.3 ± 751.5	392.1 - 3977.5	62.7 ± 19.2	13.8 - 96.3
Burst Pulse (65)	3.5 ± 1.8	1.8 - 10.7	458.9 ± 304.4	73.1 - 1141.3	19.1 ± 23.2	0.1 - 75.0