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Research report

Laterality of flipper rubbing behaviour in wild bottlenose dolphins (*Tursiops aduncus*): Caused by asymmetry of eye use?

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Abstract

To determine whether wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) at Mikura Island, Japan, show asymmetry of eye or flipper use during a social behaviour, we investigated the laterality of flipper-to-body (F–B) rubbing, in which one dolphin ("rubber") rubs the body of another ("rubbee") with its flipper. We analysed 382 episodes of video-recorded F–B rubbings performed by identified individuals ($N = 111$ rubbers). F–B rubbing was conducted significantly more frequently with the left flipper than with the right flipper. The duration of F–B rubbings was also significantly longer with the left flipper than with the right flipper. Of 20 dolphins, nine individuals showed significant left-side bias as the rubber in this behaviour, whereas no dolphins showed significant right-side bias. The results indicate a population-level left-side bias of the rubber in F–B rubbing. An analysis of the swimming configurations during this behaviour suggests that the asymmetry in F–B rubbing was caused not only by the laterality of the rubber, but by a preference for use of the left eye in both dolphins during this behaviour. Dolphins used the left eye significantly more frequently than the right eye during the inquisitive behaviour, while they showed no significant bias in flipper use during the object-carrying behaviour. These facts also suggest that the asymmetry of F–B rubbing is caused by the preference for using the left eye. Significant left-side bias was observed only in F–B rubbings initiated by the rubbee, in which the rubbee determined its position during this behaviour. This suggests that this behavioural asymmetry was enhanced by the rubbees choosing the left side of the rubber to ensure better and longer rubs.
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1. Introduction

Studies on behavioural laterality in nonhuman species are important, because laterality suggests functional asymmetry of the brain. In the last two decades, many studies have investigated behavioural laterality and anatomical asymmetry of the brain in various vertebrates [3], suggesting that functional asymmetry of the brain is not limited to humans and can be observed in a wide range of vertebrates. For example, many studies have reported that various vertebrate species show asymmetry of eye use and laterality in the visual hemifield [3]. However, we still have only

few precise studies on behavioural laterality in wild cetaceans. A population-level right-side-down bias in bottom-feeding was suggested based on a right-side bias in the abrasions of the baleen in gray whales (*Echrichtius robustus*) [13] and the jaw in humpback whales (*Megaptera novaeangliae*) [4]. Several reports have also suggested that wild coastal bottlenose dolphins (*Tursiops truncatus*) show a right-side-down bias when they intentionally beach themselves to feed on fish herded ashore [11,23,25]. Some researchers have speculated that these behavioural lateralities are caused by laterality of eye use [4], but this has yet to be determined. For example, humpback whales show a right-side bias in flipper slaps [4], but it is not clear whether the cause of this laterality is flipper use or eye use.

In this study, we focused on the laterality of a social behaviour in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), i.e.,

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flipper rubbing (flipper-to-body [F–B] rubbing), wherein one individual rubs another with its flipper. During F–B rubbing, dolphins cannot perceive the partner by echolocation, because they swim side by side during this behaviour. Therefore, they probably need to monitor the movement of the partner visually to perform this behaviour. Dolphins are also required accurate control of the flippers during this behaviour. We analysed the laterality of this behaviour to determine whether eye use asymmetry was used to recognise conspecifics or whether asymmetry in flipper use regulated this behaviour. Since F–B rubbing is a social behaviour in which two dolphins need to corporate to perform it, we analysed the laterality of both pair partners and possible interaction between the laterality of the rubber and rubbee. We also analysed the laterality of other behaviours using the eyes (inquisitive behaviour) or flippers (carrying an object).

2. Methods

The study was conducted at Mikura Island, a small volcanic island ($19.62\,km^2$) located about 220 km south of Tokyo, Japan. All observations were conducted in an area within 300 m from the coastline, at water depths of 2–45 m during spring to early autumn between June 2000 and July 2004. After sighting dolphins from a research vessel (about 7 m in length with an outboard motor), a researcher entered the water and recorded dolphin behaviour using a digital camcorder (Sony) in waterproof housing (DIV or Sony). The sampling method adopted was an ad lib protocol [1]. In this study, only video-recorded behaviours were analysed. We also used video data recorded by members of Mikura-jima Bandouiruka Kenkyukai (M.B.K, a group for dolphin research at Mikura Island) from 1994 to 2003 for individual identification. M.B.K. has continued underwater video-identification research on this population since 1994 and has estimated that about 160 Indo-Pacific dolphins are resident around this island [16]. The sex of observed dolphins was determined by examining the genital slit. We classified dolphins into four age classes as defined by M.B.K: adult, subadult, juvenile and neonate [16].

We defined "flipper-to-body (F–B) rubbing" (Fig. 1) as a behaviour in which one dolphin (the "rubber") rubbed part of the body of a partner (the "rubbee"), with the exception of the flipper edge ("flipper-to-flipper [F–F] rubbing"). An episode of flipper rubbing was initiated by one dolphin (the "initiator") approaching and physically contacting another dolphin and ended when one of the dolphins departed from the area. We defined "object-carrying" as the behaviour in which a dolphin hooked and carried a piece of plastic bag or seaweed (e.g., *Gelidium elegans*) with its flipper (Fig. 2). For each observation of F–B rubbing and object-carrying, we identified the individuals involved and recorded which flipper was used (right or left). We defined "inquiring" as a behaviour in which a dolphin approached the researcher in a straight line, often emitting clicks, then

Fig. 2. Object-carrying: an adult dolphin carrying a plastic bag with its left flipper.

turned left or right at a point about 1 m from the researcher, looked at the video camera with one eye and began to circle around the researcher (Fig. 3). For each video-documented inquisitive action, we recorded which eye the dolphin used immediately prior to circling. We analysed only episodes in which no other swimmers or dolphins were near the inquiring individual.

3. Results

3.1. Laterality of F–B rubbing

In total, we observed 533 episodes (399 bouts) of F–B rubbing in 2644 min of video records obtained in this study.

In these video-recorded F–B rubbings, the rubber used the left fin in 421 episodes (79%) and the right fin in 112 episodes (21%). We observed 382 episodes of F–B rubbing conducted by 111 identified rubbers. In these F–B rubbings, the rubbers used the left flipper significantly more frequently (292 episodes) than the right flipper (90 episodes, Wilcoxon's signed-ranks test, $R = 625.50$, $N = 111$ individuals, $Z = 6.53$, $P < 0.001$). Of 20 dolphins for which more than five records as the rubber were available, nine individuals showed significant left-side bias, while no dolphins showed significant right-side bias (Fig. 4, binomial test, two-tailed). These results strongly suggest a population-level

Fig. 1. F–B rubbing in Indo-Pacific bottlenose dolphins. (a) No. 318 (subadult male, rubber, above) rubs the ventral side of no. 075 (subadult male, rubbee, below) with its left pectoral fin. (b) Dolphins sometimes switch roles during F–B rubbing bouts. Here, no. 318 changed its posture from horizontal to side up, while no. 075 changed its posture from upside down to horizontal almost concurrently. (c) Following the switch, no. 075 (rubber, right) now rubs the ventral side of no. 318 (rubbee, left) with its left pectoral fin.
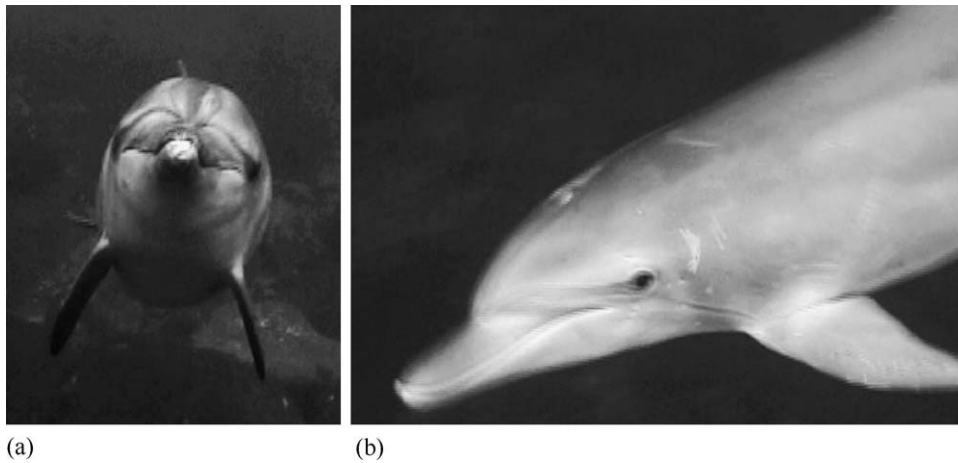
Fig. 3. Inquisitive behaviour: (a) a dolphin approaches the camera directly; (b) it turns left or right to look at the camera with one eye immediately prior to swimming around the camera.

left-side bias of the rubber in F–B rubbing among the studied dolphins. The duration of F–B rubbings was significantly longer when the left flipper was used (mean ± S.D.: 9.3 ± 9.2 s, $N = 120$ episodes, range = 2–53 s) than when the right flipper was used (mean ± S.D.: 6.1 ± 4.8 s, $N = 48$ episodes which we could record from beginning to end, range = 2–29 s; Mann–Whitney U-test, $U = 2196.50$, $Z = 2.41$, $P = 0.015$).

On the other hand, no significant difference was observed in the number of episodes between F–B rubbings to the left side of the rubbee (103 episodes) and those to the right side (128 episodes, Wilcoxon's signed-ranks test, $R = 1729.0$, $N = 108$ identified individual rubbees, $Z = 1.74$, $P = 0.0802$, we excluded cases in which we could not decide which part of the rubbee was rubbed). Of nine dolphins for which more than five records as the rubbee were available, only one individual showed significant asymmetry (left-side bias, left: 8/right: 0 episodes, binomial test, two-tailed, $P = 0.0078$). No significant difference was also observed in the duration between the F–B rubbing to the left

side (mean ± S.D.: 9.5 ± 10.1 s, $N = 47$ episodes, range = 2–51 s) and the right side (mean ± S.D.: 7.4 ± 5.6 s, $N = 55$ episodes which we could record from beginning to end, range = 2–34 s) of the rubbee's body (Mann–Whitney U-test, $U = 1253.0$, $Z = 0.27$, $P = 0.78$). The results suggest that the rubbees showed almost no asymmetry in this behaviour.

Fig. 5 shows the positions of dolphins during F–B rubbing. Most of the configurations observed during F–B rubbing could be categorised into the eight positions illustrated in Fig. 5. In this analysis, we excluded cases in which the dolphins assumed positions other than the eight main types (12 episodes) and cases in which dolphin(s) changed posture during flipper rubbing (26 episodes). We also excluded cases in which we could not decide which part of the rubbee (e.g., ventral side, dorsal side, fluke) was contacted by the rubber (186 episodes). The figure shows that in all four mirror-image pairs of configurations (A–B, C–D, E–F and G–H), the configurations in which the rubber used its left pectoral fin (A, C, E and G) were more frequent than their mirror images, though the difficulty of the configuration should be same between the mirror-image pair. In contrast, the rubbee faced its right side to the rubber more frequently than the left side in some configuration pairs (A–B and E–F), while it faced the left side more frequently in other configurations (C–D and G–H).

The results indicate that the rubbers showed the clear left-side asymmetry while the rubbees showed the inverse asymmetry depending on the configuration. The figure also shows that some configurations were exceptionally rare (D and H, 5 and 0 episodes, respectively).

The table in Fig. 5 shows the combinations of fins used by the rubber and the body side of the rubbee rubbed during F–B rubbing. The eight configurations could be categorised into the following four combinations; left fin–right side (LR combination, A and E), left fin–left side (LL combination, C and G), right fin–right side (RR combination, D and H) and right fin–left side (RL combination, B and F). The table shows that the rubbers used the left fin more frequently than the right fin only when they rubbed the right side of the partner (RR and LR combinations, right: 5/left: 157 episodes). When they rubbed the left
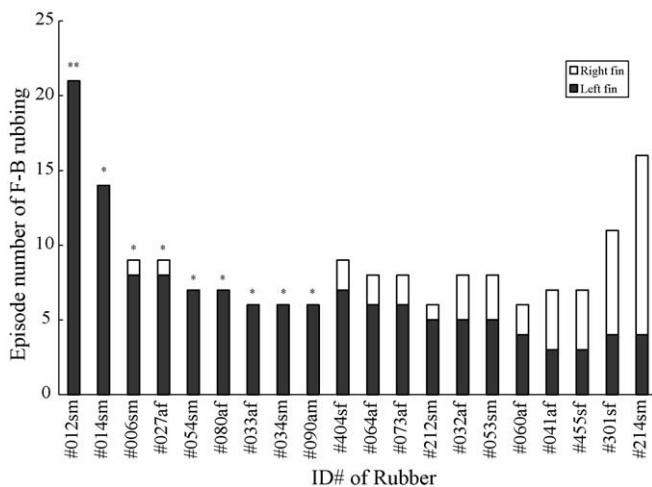

Fig. 4. Observations of flipper use during F–B rubbing. Differences between use of the left and right fin were tested with a binomial test (two-tailed). [**]$P < 0.01$; [*]$P < 0.05$.

A (121)   B (44)   E (36)   F (19)

C (27)   D (5)   G (36)   H (0)

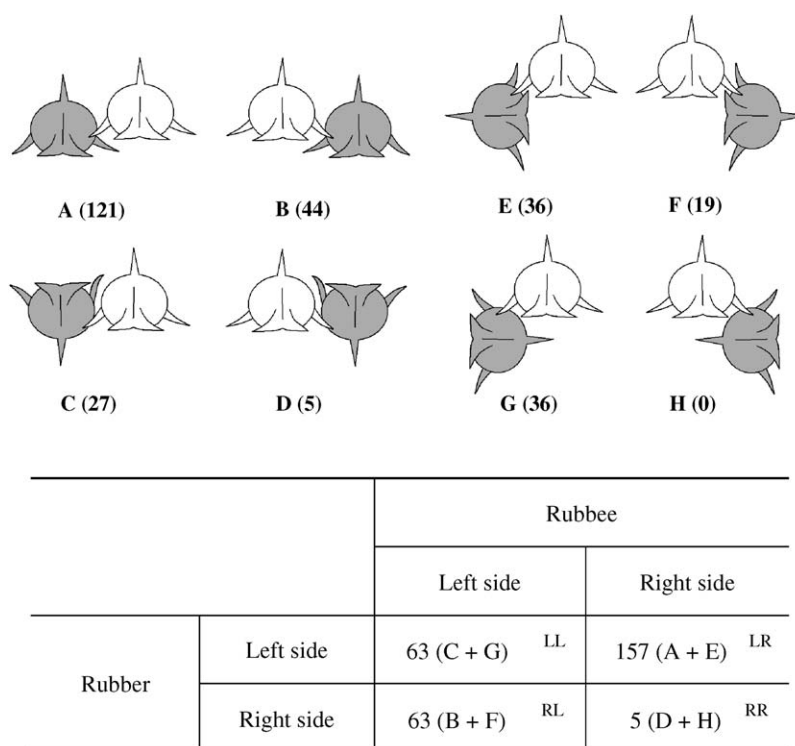|		Rubbee	
		Left side	Right side
Rubber	Left side	63 (C + G) LL	157 (A + E) LR
	Right side	63 (B + F) RL	5 (D + H) RR

Fig. 5. Configuration of rubbers and rubbees during F–B rubbing. White dolphins in the figure indicate the rubber and gray dolphins represent the rubbee. Numbers in parentheses indicate the observed episode number of each configuration. In this analysis, we used only the data in which we could decide the rubber and the rubbee from video-footage and excluded cases in which dolphin(s) changed posture during flipper rubbing.

side of the partner, no asymmetry was observed in their fin use (RL and LL combinations, right: 63/left: 63 episodes). Additionally, the rubbees contacted their right side to the rubber's fin more frequently than the left side when they contacted to the left fin of the rubber (LR and LL combinations, right: 157/left: 63 episodes), while they showed the inverse asymmetry when they contacted to the right fin (RR and RL combinations, right: 5/left: 63 episodes). These results indicate that the laterality observed in this behaviour cannot be explained only by the asymmetry of the rubbers (e.g., that in flipper use and/or eye use) or rubbees (e.g., that in eye use). The result of the table suggests the interaction between the rubber's asymmetry and the rubbee's asymmetry in this behaviour.

The table also shows that the number of the RR combination (D and H) were smallest. The result can be explained only if we assume that both dolphins showed left-side asymmetry in this behaviour. If both dolphins showed right-side asymmetry, the number of LL combination should be smallest. If the rubber and the rubbee showed the inverse asymmetry each other, the number of LR or RL combination should be smallest.

The table shows that both the rubbers and rubbees faced their left side to the partners more frequently than the right side in the configurations in which their partner could not face the left side to the partner (RR and LR combinations for the rubbers; right: 5 (D + H)/left: 157 (A + E) episodes, RR and RL combinations for the rubbees; right: 5 (D + H)/left: 63 (B + F) episodes). This suggests that at least one of the dolphins needed to face the left side of the body to the partner for adequate performance of this behaviour.

3.2. Rubbee's choice of position during F–B rubbing

The position during F–B rubbing seemed to be determined by the dolphin that initiated this behaviour by approaching the partner. In the initiation process of F–B rubbing, some rubbees moved to the far side of the rubber by swimming across the rubber to receive rubs, suggesting that they choused that side of the rubber. In most of these cases (18 of 20 episodes), the rubbees moved to the left side of the rubber from the right side; they moved from left to right in only two episodes. These facts suggest that dolphins tended to select the left side of the rubber when they were the rubbees of rubbing.

F–B rubbing tended to be initiated by the rubbee; in 130 episodes of F–B rubbing recorded from the starting process, 98 episodes were initiated by the rubbee approaching the rubber. In 32 episodes of F–B rubbing initiated by the rubber (performed by 26 identified individuals, mean ± S.D.: 1.23 ± 0.65 episodes per individual), no significant asymmetry of the rubber was observed (Wilcoxon's signed-ranks test: $R = 128.50$, $N = 26$ individual rubbers, $P = 0.38$), though the rubbers faced their left side to the partner slightly more frequently (18 episodes) than the right side (14 episodes). In contrast, in 98 episodes of F–B rubbing initiated by the rubbees (performed by 66 identified rubbees, mean ± S.D.: 1.48 ± 0.88 episodes per individual), the left-side asymmetry in the rubbers was highly significant (left: 75 episodes, right: 23 episodes, Wilcoxon's signed-ranks test: $R = 429.50$, $N = 66$ individual rubbees, $P < 0.001$). These results suggest that the rubber's left-side asymmetry observed in F–B rubbing

was enhanced by the rubbee's choice of position during this behaviour.

3.3. Laterality of object-carrying

We video-recorded 15 episodes of objects being carried with the left flipper and 17 episodes with the right flipper, for a total of 32 episodes of object-carrying. We recorded 24 episodes of object-carrying performed by 19 identified dolphins (mean ± S.D.: 1.26 ± 0.56 episodes per individual). Of these, 15 episodes were performed with the left flipper and nine episodes with the right flipper. No significant asymmetry of fin use was observed in carrying objects (Wilcoxon's signed-ranks test, $R = 60.0$, $N = 19$ individuals, $P = 0.28$).

3.4. Laterality of eye use during inquisitive behaviour

We recorded a total of 543 episodes of inquisitive behaviour in 504 min of video recordings, for a total of 269 episodes of eye use performed by 78 identified individuals (mean ± S.D.: 3.45 ± 3.64 episodes per individual). During this behaviour, the left eye was used significantly more frequently (154 episodes) than the right eye (115 episodes, Wilcoxon's signed-ranks test, $R = 887.0$, $N = 78$ individuals, $Z = 2.24$, $P = 0.025$). This result suggests population-level asymmetry of eye use at the beginning of inquisitive behaviour.

4. Discussion

4.1. Laterality of F–B rubbing

Our results suggest that the dolphins in this population show a left-side bias as the rubber in F–B rubbing at the population level. This is the first report of population-level asymmetry in social behaviour of wild cetaceans. In contrast, they showed no asymmetry in this behaviour as the rubbee.

Our analyses of their configuration during F–B rubbing, however, revealed that the laterality observed during this behaviour was not caused only by the asymmetry of the rubbers, but by the asymmetry of both dolphins that tended to face their left side to the partner.

A possible cause of this laterality is asymmetry of eye use in both dolphins during F–B rubbing. The results shown in Fig. 5 are well explained if we assume that both dolphins tended to use the left eye to see the partner, and at least one of the pair partners needed to monitor the partner with its left eye to perform adequate F–B rubbing. The table shows that in both of the two rare configurations (RR combination, D and H), dolphins turned the right side of their body to the partner, suggesting that the configurations in which both dolphins could not use the left eye to see the partner was rare. The table also shows that both the rubbers and rubbees faced their left eyes to the partners more frequently than the right eyes in the configurations in which their partner could not use the left eye for the monitoring (RR and LR combinations for the rubbers, RR and RL combinations for the rubbees). In contrast, in the configurations in which the partner could use the left eye for the monitoring, the rubber showed no

asymmetry (RL and LL combinations) and the rubbees showed the inverse asymmetry depending on the combination (right-side bias in LL and LR combinations, left-side bias in RR and RL combinations). In configurations in which only one of the dolphins can use the left eye to see the partner, the configurations in which the rubber can uses its left eye (LR combination, 157 episodes) were more frequent than those in which the rubbee can use its left eye (RL combination, 63 episodes), suggesting that the rubber mainly monitor the partner during this behaviour. Significant left-side bias observed in eye use at the onset of inquisitive behaviour also supports this view.

It seems possible that the left-side bias of the rubbers was caused by their preference for use of the left fin or both the left fin and the left eye. However, if it was a case, LL combination (63 episodes) should be larger than RL combination (63 episodes) because the rubbers could use the left fin only in the LL combination, though in both combinations at least one of the dolphin could monitor the partner with the left eye (by the rubbee in RL combination, by the rubber and/or the rubbee in LL combination). In addition, the dolphins showed no asymmetry of flipper use in object-carrying, the behaviour that requires accurate control of the flippers like F–B rubbing. Therefore, the left-side bias of the rubbers in this behaviour was more likely to be caused by the preference for use of the left eye than that of the left fin.

Our results suggest that the asymmetry observed in F–B rubbing was resulted from the preference for left-eye use in both dolphins during this behaviour, in which the rubber mainly monitor the partner to perform it.

Many studies have reported that various vertebrate species tend to use the left eye or left visual hemifield (right hemisphere) to recognise familiar conspecifics [3]. Several fish species show a left-eye preference during sustained fixation on their own mirror image, suggesting a right-hemisphere dominance in viewing conspecifics [26,27]. Chicks show a left eye advantage in individual recognition of familiar conspecifics [29,30]. Sheep show a left visual hemifield advantage when they identify the faces of familiar conspecifics [20]. Hamilton and Vermeire [9] reported that split-brain monkeys (*Macaca mulatta*) showed a significant right hemispheric advantage (left-eye advantage) in discriminating the faces of conspecifics. Morris and Hopkins [19] also reported that chimpanzees showed a left visual hemifield advantage in the perception of human faces.

Such asymmetry of eye use and laterality in the visual hemifield are reported to be especially clear in animals with laterally placed eyes, complete crossover optic chiasmas and relatively small commissural systems, such as birds, fishes and reptiles [3]. Therefore, it is highly possible that bottlenose dolphins, which have laterally placed eyes, complete crossover optic chiasmas [22,28] and a small corpus callosum [18,21], also show a significant preference in eye use.

Several researchers have reported that bottlenose dolphins tend to use the right eye in spontaneous eye use and when they scrutinise objects [22,32], although a quantitative analysis has yet to be conducted. Bottlenose dolphins also show a right-eye advantage in visuospatial discrimination [14], pattern discrimination [31,32] and numerical ability [15]. Such a right-

eye advantage reported in dolphins is exceptional in mammals; most species of mammals and birds show a left eye (or left visual hemifield) advantage in these tasks (humans [10], cats [17], rats [2]). Clapham et al. [4] speculated that the right-side-down bias observed in the beaching behaviour of wild coastal bottlenose dolphins (*T. truncatus*), which intentionally beach themselves to feed on fish herded ashore [11,23,25], was caused by a preference for right-eye use to see fish, although they provided no evidence to support this hypothesis.

In several animals, however, the dominant eye differs depending on the tasks performed. For example, split-brain monkeys showed a left-eye advantage in the recognition of conspecifics, but they showed a right-eye advantage in discriminating the orientation of lines [9]. Rogers et al. [24] reported that small-eared bushbabies (*Otolemur garnettii*) showed a left-eye preference in viewing familiar stimuli but showed a right-eye preference when viewing novel, arousing stimuli. In humans, a right visual half field advantage for lexical decision tasks and figural comparison tasks and a left-visual half-field advantage for face discrimination tasks have generally been reported [10]. Therefore, it is possible that dolphins show a left-eye advantage in the recognition of conspecifics while they show a right-eye advantage during different tasks, although no reports are available on their preference in eye use for the recognition of conspecifics.

In cetaceans, the opposite laterality was reported in the following two behaviours involving flipper use. Most mature Commerson's dolphins (*Cephalorhynchus commersonii*) have sawtooth serrations on the leading edge of the left flipper [8], and two captive mature males used the left flipper predominantly for touching conspecific females [12]. In contrast, humpback whales (*M. novaeangliae*) show a population-level right-side bias in flipper slaps [4]. It is possible that the left-side bias in the touching behaviour of Commerson's dolphins is also caused by asymmetry in eye use, because the dolphins may need to see the partner with the left eye during this social behaviour, as in F–B rubbing. In contrast, humpback whales may not need to see conspecifics during a flipper slap. However, if they need to see underwater conspecifics during this behaviour, they could use the left eye, which faces downward during slaps with the right flipper.

4.2. Effect of the rubbee's choice on the laterality of the F–B rubbing

Our results suggested that the position during F–B rubbing was usually determined by the rubbees which tended to select the left side of the rubbers in the initiation process of this behaviour. Therefore, the left-side asymmetry observed in the rubbers during F–B rubbing was probably affected by the rubbee's choice of the position. The fact that strong left-side bias of the rubbers was observed only in the F–B rubbings initiated by the rubbees supports this view. Our results also suggested that the asymmetry observed in this behaviour was caused by a preference for use of the left eye. However, the left-eye bias observed during inquisitive behaviour seems not so strong enough to explain the prominent left-side bias of the rubbers observed in F–B rubbing. These results suggest that the rubber's left-side asymmetry

observed in F–B rubbing was largely enhanced by the rubbee's choice of the position during this behaviour.

The reason why the rubbees tended to select the left side of the rubbers is still not clear. It is possible, however, that they did so seeking for a longer rubbing episode because F–B rubbings with the left flipper of the rubbers lasted significantly longer than those with the right flipper. Although the precise function of F–B rubbing remains unclear, it has been suggested that F–B rubbing is an affiliative behaviour during which the rubbee receives some benefits (e.g., grooming or receiving a pleasurable sensation) [5–7] from the frictional contact in this behaviour. Therefore, it is possible that the dolphins learned to choose the left side of the partner to ensure better and longer rubbing episodes and to receive more benefits.

Our results suggest an interesting possibility that left-side asymmetry in F–B rubbing is caused not directly by a cerebral functional asymmetry of the subject (the rubber) but by the choice of the other animal (the rubbee), which knows the laterality of the partner.

Acknowledgements

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