

Research report

Lateralization of visuospatial processing in the bottlenose dolphin (*Tursiops truncatus*)

Annette Kilian^a, Lorenzo von Fersen^a, Onur Güntürkün^{b,*}

^a *Tiergarten Nürnberg, Am Tiergarten 30, 90480 Nürnberg, Germany*

^b *AE Biopsychologie, Fakultät für Psychologie, Ruhr-Universität Bochum, 44780 Bochum, Germany*

Received 19 April 2000; received in revised form 21 June 2000; accepted 21 June 2000

Abstract

Two adult female bottlenose dolphins were tested for cerebral asymmetries in the visuospatial domain. The animals learned under binocular conditions a three-choice spatial discrimination task with three hoops positioned along a line in the middle of the tank. During a correct trial the dolphins had to swim from a starting position at the tanks wall through one of the hoops, come back to the starting position, choose another hoop, swim back to start and finally swim through the third hoop. For such a trial to be correct, the animals had to swim through all three hoops in a any sequence without omitting or re-using one of them. After reaching criterion binocularly, monocular trials (one eye covered with an adherent suction cup) were introduced where the dolphins carried out the same task alternatingly under left or right eye seeing conditions. For both animals, the right eye performance was clearly superior to that of the left eye. Binocular and right eye performances were similar. As a result of the complete decussation at the optic nerve, this right eye superiority suggests a left-hemispheric dominance for the processing of visuospatial information. This is a remarkable deviation from the usual right hemisphere advantage for these kind of tasks found in different species of mammals and birds. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Cetacea; Cerebral asymmetry; Working memory; Visual system; Evolution

1. Introduction

Once thought to be unique to humans, functional cerebral asymmetries have by now been reported for a large number of animal species [2]. These studies have finally provided the basis for a comparative approach in understanding the biological foundations of lateralizations, and its neuronal organisations. However, only few investigations have focused on possible lateralized brain functions in dolphins. Their remarkable evolution has resulted in enlarged brains of high fissural complexity, with several morphological cortical characteristics being atypical for land mammals [28]. It is yet to be demonstrated whether these anatomical differences also

resulted in functional differences in the brain organisation of cetacea and land mammals. The aim of the present study therefore was to study lateralized functions in the visual domain of the bottlenose dolphin (*Tursiops truncatus*) under behaviourally controlled conditions.

Neuroanatomical findings — the asymmetrical cranium in toothed whales [37], and a larger surface area of the right hemisphere cortex in *Tursiops* [36] — together with a number of behavioural lateralities, point to the existence of cerebral asymmetries in marine mammals. Coastal bottlenose dolphins show a clear preference for beaching right-side-down when feeding on fish herded ashore [15,30,38]. A right side bias is also found during bottom feeding in gray and humpback whales [6]. Several studies on dolphins in confinement report a strong tendency to favour a swimming direction, which is mostly counterclockwise ([5,35,39]; but see Refs [25,26]). This direction of swimming places

* Corresponding author. Tel.: +49-234-3226213; fax: +49-234-3214377.

E-mail address: onur.guentuerkuen@ruhr-uni-bochum.de (O. Güntürkün).

the right eye towards the enclosure wall and thus towards any events outside the pool which could be of importance for the dolphins. This finding is accompanied by the observation that captive dolphins favour the right eye when approaching or scrutinising objects [34]. In a single-subject study, Fersen et al. [10] presented experimental evidence that bottlenose dolphins learn faster and achieve higher discrimination scores in pattern distinction tasks when using the right eye. Due to the complete crossing of the optic nerve fibers at the chiasm [12,17,40], a right eye superiority is probably due to a left hemisphere advantage for pattern discrimination. This is different from several species of land mammals studied up to now, which usually reveal a right hemisphere dominance in these kind of experiments (humans: [13], cats: [22], rats: [4]).

Thus, there is evidence for laterality in dolphins and this evidence makes it likely that at least visual cerebral asymmetries for object recognition are organized differently from land mammals. Up to now visuospatial tasks have not been employed in a lateralized setting in dolphins. Spatial orientation is right hemisphere based in land mammals including humans [16,18,20,43]. Therefore, the present study examines whether the processing of visuospatial information is lateralized in two bottlenose dolphins and tests if this asymmetry follows the pattern found in land mammals. As human cortical specialisations do not fully mature until puberty [29], and as Ridgway [34] estimates that Atlantic coastal Tursiops only reach full brain development in 9 or 10 years, mature bottlenose dolphins were chosen for our investigation to ensure a full display of cerebral asymmetries.

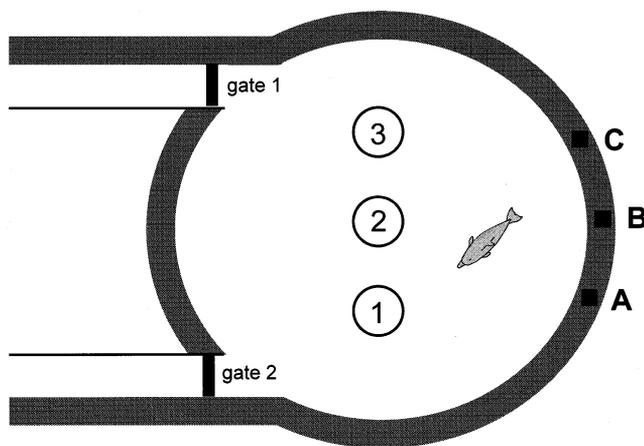


Fig. 1. Schematic overview of the testing conditions. Trials started with positioning the animal at one of the three starting positions (A, B, C). After a signal the dolphin had swim through one of the hoops (1, 2, 3). It then came back to the starting position where it had started and was sent again to choose another hoop. In a correct trial the dolphin swam through all three hoops without omitting or re-using one hoop. In this picture the hoops are shown as if floating on the water. In fact, they were positioned vertically just underneath the water surface.

2. Method

Subjects were two adult female bottlenose dolphins, Anke and Emy (approximate ages 16 and 17 years) housed at the Dolphinarium of the Zoo Nürnberg (Germany). Both animals underwent regular medical examinations including a check-up of the eyes by a veterinary surgeon, which revealed that they were in good health. Before the experiment, the two dolphins had training sessions where their eyes were alternately covered by an eyecup. Their behavioural reactions to subtle familiar hand signals showed no differences according to the viewing conditions. Therefore, any acuity differences of the eyes are unlikely.

In daily sessions, the two bottlenose dolphins were trained separately in a three-choice spatial discrimination task. During experimental sessions the subject was on its own in a 14 m diameter circular indoor tank (depth 4.7 m). Three hoops (diameter 1.5 m) were positioned vertically in a line just underneath the water surface in the middle of the tank, with a constant distance of 1.2 m between the hoops. Three starting positions (A, B, C) were marked at the tank walls (Fig. 1). Each trial started with positioning the animal at one of the starting positions. A slight touch on the forehead was the signal for the dolphin to swim through one of the hoops. It then came back to the starting position from where it was sent again to choose another hoop. In a correct trial the dolphin swam through all three hoops without omitting or re-using one hoop. Each correct choice of a hoop was followed by a secondary reinforcer (continuous whistle blow), and primary reinforcement by fish was provided at the end of such a correct trial. A trial also ended when the dolphin used one hoop twice (false response). Incorrect choices were followed by a specific non-continuous whistle blow without providing fish. The sequence of visiting the hoops was up for the animal to choose. Thus, performance in this task was dependent on visuospatial working memory since the order of visits had to be maintained during a single trial but had no relevance for the next. The starting positions changed in a random sequence for each session, but did not change within one trial.

Learning was considered successful after reaching at least 75% correct responses in four consecutive sessions (each consisting of 10 trials), with chance level at 22.2%. Thereafter monocular trials were introduced, in which one of the dolphins' eyes was covered with an eyecup made of a special gelatine mixture [19]. These cups were removed directly after each monocular trial. Each dolphin completed four session blocks with monocular and binocular trials. Each block consisted of 48 trials equally distributed over six sessions. Monocular trials alternated with binocular trials, which resulted in one session block comprising of 24 monocular (12

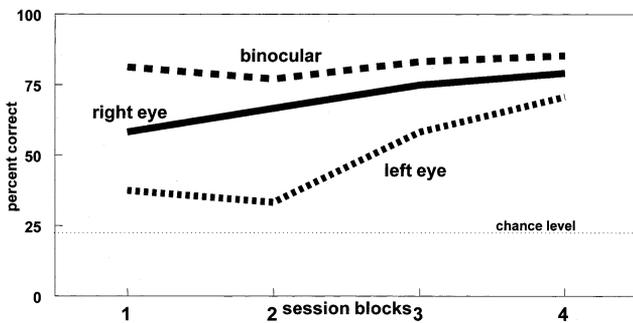


Fig. 2. Average percent correct performances of the dolphins in the three viewing conditions in the visuospatial working memory task over four testing blocks. The dotted horizontal line depicts the chance level of 22.2%.

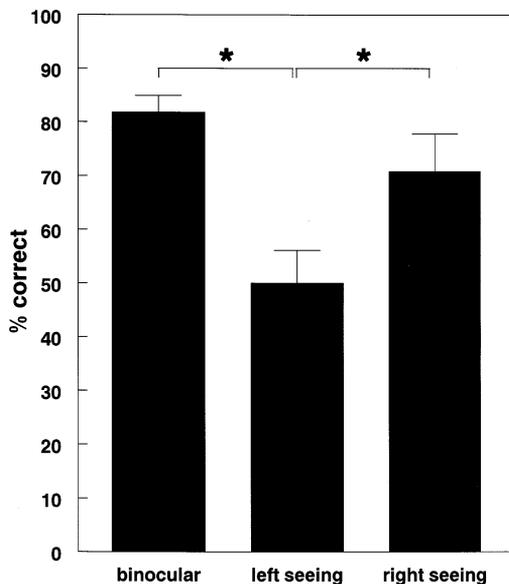


Fig. 3. Overall performance of the dolphins in the three viewing conditions. Asterisks indicate significant differences at the 5% level.

right-eye seeing, 12 left-eye seeing) and 24 binocular trials. Thus, a typical sequence consisted of R-B-L-B-R-B-L-B, etc. The starting positions were equally distributed among the two monocular situations, as well as for the binocular trials. The daily sessions always started with a monocular condition, with left and right eye sequences being balanced as starting conditions for this 1st trial.

3. Results

During acquisition of the task, both dolphins demonstrated a clear preference for certain sequences of visiting the hoops. These sequences clearly depended on the starting position. From 1st trial to criterion, the following sequences occurred most frequently:

Pos A: Anke: 1-2-3 (100%); Emy: 1-2-3 (80.4%)
 Pos B: Anke: 2-3-1 (52%), 1-2-3 (40%); Emy: 2-3-1 (72.5%)
 Pos C: Anke: 2-3-1 (76.5%); Emy: 3-2-1 (53.1%), 2-3-1 (31.3%)

Thus, the animals had a tendency to start with the nearest hoop and then to proceed to the more distant ones.

After switching to monocular conditions a clear difference between the eyes emerged. Overall, performance with the right eye was higher than with the left (Fig. 2). For Emy this difference vanished after the second block, possibly at least to some extent due to a ceiling effect. For Anke it was valid throughout the whole study. These differences between the three viewing conditions were found to be significant (Friedmann-test, $k = 3$, $n = 8$, $\chi^2 = 12.3$, $P < 0.05$). Significant differences existed between binocular and left (Wilcoxon-test, $Z = 2.5$, $T = 0$, $P < 0.02$) as well as between left and right viewing conditions (Wilcoxon-test, $Z = 2.2$, $T = 0$, $P < 0.03$), while there was only a tendency for the animals to achieve higher performance scores in the binocular compared with the right viewing condition (Wilcoxon-test, $Z = 1.9$, $T = 1.5$, $P < 0.06$) (Fig. 3). While the generally higher performance under binocular conditions could be due to the binocular acquisition and the higher number of binocular trials during the four blocks, the left-right difference is unlikely to be due to the training conditions in use.

During monocular trials the animals were handicapped to overlook the hoops when seeing with the left eye and starting from C, as well as when seeing with right and starting from A. In both cases they had to start swimming towards the hoops with their blind side. Under these conditions the performance of the animals was on average at 37.5% when seeing with their left eye but at 65.6% when seeing with their right (Wilcoxon-test, $Z = 1.89$, $T = 1.5$, $P < 0.06$). However, despite the problem that they were in these cases initially heading blindly towards the hoops, both animals stuck largely to their usual sequence:

Position A, right eye seeing: Anke 1-2-3 (100%); Emy 1-2-3 (50%), 2-1-3 (38%)
 Position C, left eye seeing: Anke 2-3-1 (50%), 3-2-1 (50%); Emy 3-2-1 (57%), 2-3-1 (43%)

4. Discussion

The present study clearly demonstrates that in the two female bottlenose dolphins the accomplishment of a complex visuospatial task is higher when using the

right eye. It is unlikely that this lateralized effect is due to acuity differences between the eyes. The hoops were quite large and clearly visible under water. Additionally, the animals had no problems to see and follow even subtle gestural commands. Therefore, the right eye superiority is probably related to a dominance of the left hemisphere for the processing of visuospatial information [12,17,40].

It is conceivable that the animals also had used echolocation to distinguish between absolute and relative positions of the hoops. However, the differences between the viewing condition clearly show that they were not relying on auditory cues entirely but were also using visual perception to guide their behaviour.

The majority of investigations in this field support a right hemisphere advantage for spatial orientation in mammals, including humans, and birds (humans: [8,31]; cats: [22]; rats: [3,27], but see Ref. [1]; baboons: [43]; chicks: [33]; marsh tits: [7]). This is supported by recent imaging studies showing a right hippocampal activation if subjects had to make use of real world topographical information to find their way through a large city [23,24]. However, spatial orientation is a multi-component feature in which several cognitive processes with diverse cerebral asymmetries interact [14]. Is it therefore conceivable that our dolphins had used a cognitive strategy which is more left-hemisphere based? Two such possible left-hemisphere based strategies are feature tracking and novel configuration learning. In the following we will argue that it is unlikely that any of these strategies were used to an important extent by our animals.

Ulrich et al. [41] showed that pigeons were more efficient in homing along a 32 km path when seeing with their left hemisphere. As discussed by Ulrich et al. [41] it is likely that this was due to a strategy in which the birds utilized visual memory snapshot tracking to pursue visual features along their pre-learned route. Pigeons are known to be left-hemisphere dominant for memorizing [9] and discriminating visual features [11]. Thus, in the homing experiment, it is indeed likely that the task was in part performed by a succession of visual feature discriminations. If pigeons are tested in a maze where they can't utilize this strategy, the left hemisphere advantage vanishes [32]. Contrary to the homing example, in the present study the visual features (hoops) were all visible at a glance and were visited in changing successions depending on the starting point in use. Thus, it is unlikely that our dolphins solved the task mainly by visual feature tracking.

A second possible left hemisphere strategy could be novel configuration learning. LaMendola and Bever [21] showed that rats learn a novel foraging pattern better with their right-side whiskers (left hemisphere) than with their left-side whiskers. Rotating an already learned maze relative to the external environment most

strongly reduced right-whisker performance, while starting an already learned maze at a different location reduced left-whisker performance. If a similar mechanism would have taken place in the present study, the left hemisphere superiority of the dolphins should be due to the novelty of the task. However, this was not the case since the animals had learned the task under binocular conditions and were well accustomed to it. It is also unlikely that the dolphins perceived any kind of configurational change after the introduction of the eyecups. If this would have been the case, changes in the swimming sequences would be likely. However, as outlined in the results section, this was not the case.

We are therefore inclined to believe that the dolphins of the present study were faced with a task which would be right hemisphere based in land mammals. However, our data reveal a clear left hemisphere dominance. If the two dolphins studied here are representative for their species, their left hemispheric dominance in the processing of visuospatial information would be a remarkable deviation from the usual pattern found in other mammals. Meanwhile there is an abundance of evidence that spatial orientation in a known environment is mainly dominated by right hemisphere mechanisms in mammals and birds [42]. Against the background of this pattern stretching over two classes of vertebrates, the deviation in the organization of cerebral asymmetries in dolphins for visuospatial working memory (present study) and object recognition [10] makes it likely that the evolutionary line leading to cetacea encompassed drastic changes of the functional neural architecture.

Acknowledgements

We are very grateful to the staff of the dolphinarium at the Zoo Nürnberg for their continuous help during experimental sessions, and to the Director of the Zoo Nürnberg, Dr Peter Mühling, for his approval on the conduct of the study. Our thanks also go to the dolphins Emy and Anke for their incessant motivation during the experiment.

References

- [1] Adelstein A, Crowne DP. Visuospatial asymmetries and interocular transfer in the split-brain rat. *Behav Neurosci* 1991;105:459–69.
- [2] Bradshaw JL, Rogers LJ. *The Evolution of Lateral Asymmetries, Language, Tool Use, and Intellect*. San Diego: Academic, 1993.
- [3] Bianki VL. Lateralization of functions in the animal brain. *Int J Neurosci* 1981;15:37–47.
- [4] Bianki VL. Simultaneous and sequential processing of information by different hemispheres in animals. *Int J Neurosci* 1983;22:1–6.

- [5] Caldwell MC, Caldwell DK, Siebenaler JB. Observations on captive and wild bottlenosed dolphins, *Tursiops truncatus*, in the Northeastern Gulf of Mexico. LA County Museum Contrib Sci 1965;91:1–10.
- [6] Clapham PJ, Leimkuhler E, Gray BK, Mattila DK. Do humpback whales exhibit lateralized behaviour? Anim Behav 1995;50:73–82.
- [7] Clayton NS, Krebs JR. Memory for spatial and object-specific cues in food-storing and non-storing birds. J Comp Physiol A 1994;174:371–9.
- [8] D'Eposito M, Aguirre GK, Zarahn E, Ballard D, Shin RK. Functional MRI studies of spatial and nonspatial working memory. Cogn Brain Res 1998;7:1–13.
- [9] Fersen von L, Güntürkün O. Visual memory lateralization in pigeons. Neuropsychologia 1990;28:1–7.
- [10] Fersen von L, Schall U, Güntürkün O. Visual lateralization of pattern discrimination in the bottlenose dolphin (*Tursiops truncatus*). Behav Brain Res 2000;107:171–81.
- [11] Güntürkün O. Avian visual lateralization — a review. NeuroReport 1997;6:1–2.
- [12] Hatschek R. Sehnervenatrophie bei einem Delphin. Arb Neurol Inst Univ Wien 1903;10:223–9.
- [13] Hausmann M, Güntürkün O. Sex differences in functional cerebral asymmetries in a repeated measure design. Brain Cogn 1999;41:263–75.
- [14] Hellige JB. Hemispheric asymmetry for components of visual information processing. In: Davidson RJ, Hugdahl K, editors. Brain Asymmetry. Cambridge (MA): MIT Press, 1995:99–121.
- [15] Hoese HD. Dolphin feeding out of water in a salt marsh. J Mammol 1971;52:222–3.
- [16] Hopkins WD, Morris RD. Laterality for visual-spatial processing in two language-trained chimpanzees (*Pan troglodytes*). Behav Neurosci 1989;103:227–34.
- [17] Jacobs MS, Morgane PJ, McFarland WL. Degeneration of visual pathways in the bottlenosed dolphin. Brain Res 1975;88:346–52.
- [18] King R, Corwin JV. Spatial deficits and hemispheric asymmetries in the rat following unilateral and bilateral lesions of posterior parietal or medial agranular cortex. Behav Brain Res 1992;50:53–68.
- [19] Klinckert H-J, Thale B. Digestible Eyecups for Dolphins. Freeport, Bahamas: 20th Annual Conference of the IMATA, 1992.
- [20] Laeng B, Peters M. Cerebral lateralization for the processing of spatial coordinates and categories in left- and right-handers. Neuropsychologia 1995;33:421–39.
- [21] LaMendola NP, Bever TG. Peripheral and cerebral asymmetries in the rat. Science 1997;278:483–6.
- [22] Lorincz E, Fabre-Thorpe M. Shift of laterality and compared analysis of paw performances in cats during practice of a visuo-motor task. J Comp Psychol 1996;110:307–15.
- [23] Maguire EA, Frackowiak RSJ, Frith CD. Learning to find your way: a role for the human hippocampal region. Proc R Soc Lond B 1996;263:1745–50.
- [24] Maguire EA, Frackowiak RSJ, Frith CD. Recalling routes around London: activation of the right hippocampus in taxi drivers. J Neurosci 1997;17:7103–10.
- [25] Marino L, Stowe J. Lateralized behavior in two captive bottlenose dolphins (*Tursiops truncatus*). Zoo Biol 1997;16:173–7.
- [26] Marino L, Stowe J. Lateralized behavior in a captive beluga whale. Aq Mammals 1997;23:101–3.
- [27] McDaniel WF, Via JD, Smith JS, Wells DL. Unilateral injury of posterior parietal cortex and spatial learning in hooded rats. Behav Brain Res 1995;70:165–79.
- [28] Morgane PJ, Jacobs MS, Galaburda A. Evolutionary morphology of the dolphin brain. In: Schusterman R, Thomas J, Wood F, editors. Dolphin Cognition and Behavior: A Comparative Approach. Hillsdale, NJ: Lawrence Erlbaum, 1986:5–29.
- [29] Neville HJ, Hillyard SA. Neurophysiological approaches, state of the art report. In: Griffin DR, editor. Animal Mind-Human Mind. Berlin: Springer, 1982:333–53.
- [30] Norris KS, Dohl TP. The structure and functions of cetacean schools. In: Herman LM, editor. Cetacean Behavior: Mechanisms and Functions. NY: Wiley, 1980:211–61.
- [31] Nunn JA, Polkey CE, Morris RG. Selective spatial memory impairment after right unilateral temporal lobectomy. Neuropsychologia 1998;36:837–48.
- [32] Prior H, Ulrich C, Lipp HP, Güntürkün O. Zur Lateralisation der visuell-räumlichen Orientierung bei Tauben. In: Lachnit H, Jacobs A, Rösler F, editors. Experimentelle Psychologie. Lengerich: Pabst Science, 1998:265–6.
- [33] Rashid N, Andrew RJ. Right hemisphere advantage for topographical orientation in the domestic chick. Neuropsychologia 1989;27:937–48.
- [34] Ridgway SH. Physiological observations on the dolphin brain. In: Schusterman R, Thomas J, Wood F, editors. Dolphin Cognition and Behavior: A Comparative Approach. Hillsdale, NJ: Lawrence Erlbaum, 1986:31–59.
- [35] Ridgway SH. The Central Nervous System of the Bottlenose Dolphin. In: Leatherwood S, Reeves RR, editors. The Bottlenose Dolphin. San Diego: Academic, 1990:69–97.
- [36] Ridgway SH, Brownson RH. Relative brain sizes and cortical surface areas of odontocetes. Acta Zool Fennica 1984;172:149–52.
- [37] Rommel S. Osteology of the bottlenose dolphin. In: Leatherwood S, Reeves RR, editors. The Bottlenose Dolphin. San Diego: Academic, 1990:29–50.
- [38] Silber GK, Fertl D. Intentional beaching by bottlenose dolphins (*Tursiops truncatus*) in the Colorado River Delta, Mexico. Aq Mammals 1995;21:183–6.
- [39] Sobel N, Supin AY, Myslobodsky MS. Rotational swimming tendencies in the dolphin (*Tursiops truncatus*). Behav Brain Res 1994;65:41–5.
- [40] Supin AY, Mukhametov LM, Ladygina TF, Popov VV, Mass AM, Poliakova EG. Electrophysiological Study of the Dolphin Brain. Moscow: Nauka, 1978 (from Ridgway, 1986).
- [41] Ulrich C, Prior H, Duka T, Leshchins'ka I, Valenti P, Güntürkün O, Lipp H-P. Left-hemispheric superiority for visuospatial orientation in homing pigeons. Behav Brain Res 1999;104:169–78.
- [42] Vallortigara G, Rogers LJ, Bisazza A. Possible evolutionary origins of cognitive brain lateralization. Brain Res Rev 1999;30:164–75.
- [43] Vaclair J, Fagot J. Manual and hemispheric specialization in the manipulation of a joystick by baboons (*Papio papio*). Behav Neurosci 1993;107:210–4.