

# Visual lateralization in the bottlenose dolphin (*Tursiops truncatus*): evidence for a population asymmetry?

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## Abstract

A previous behavioural study with a single bottlenose dolphin had reported a right eye superiority in visual discrimination tasks, indicating a left hemisphere dominance for visual object processing. The presence of a functional asymmetry demonstrated with one individual shows that this function can be lateralized in this single animal, but cannot reveal if this represents a population asymmetry. Therefore, we conducted a series of visual discrimination experiments with three individuals of *Tursiops truncatus* under monocular conditions. The tested animals had to distinguish between simultaneously presented stimulus pairs of different patterns, whereby one stimulus was always defined to be correct. Additionally, the animals were observed for their free eye use during training and introduction of new items. The present data set revealed a right eye advantage (left hemisphere dominance) for all tested animals and a predominance of right eye use during daily activities. These results make it possible that bottlenose dolphins are lateralized for visual pattern discrimination at the level of a population asymmetry. Against the background of similar data in other vertebrates, a left hemisphere dominance for pattern discrimination points to the possibility that dolphins exploit local visual details instead of global configurational features to recognize and memorize visual stimuli. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** Cetecea; Interhemispheric transfer; Pattern discrimination; Monocular vision; Local; Global

## 1. Introduction

For a long time functional asymmetries have been regarded as a uniquely human characteristic. Only in the last decades there has been increased evidence of both structural and behavioural lateralization in nonhuman species suggesting that cerebral functional asymmetries might be a fundamental feature of all vertebrates [26]. However, only little information concerning functional asymmetries is available for aquatic mammals like cetecea. Although several studies have examined lateralization of motor function [20,24,27], findings about perceptual or cognitive asymmetries are relatively sparse. Two recent publications [7,18], however, examined visual asymmetries in pattern discrimination and visuospatial working memory and demonstrated a right eye dominance in both tasks. This accords with anecdotal observations also reporting a right eye preference in bottlenose

dolphins [25]. Due to the complete crossover of the optic chiasm in dolphins, a right eye superiority implies a left hemisphere dominance for visual object processes [17,28,29].

The study on visual asymmetries of pattern discrimination was conducted with a single animal [7]. A single-case study can provide an important hint for the presence of visual cerebral asymmetries but naturally falls short of showing that this fact can be extrapolated to the whole species. Additionally, a distinction between an individual and a population asymmetry is not possible. A population asymmetry is said to be present if more than half of a population is biased to one side. This is the case e.g. for handedness and speech in humans as well as for visual lateralization in birds [6,26]. An individual asymmetry, on the other side, implies that each or most individuals of a species are lateralized but that their preferred side is about equally distributed between left and right. This is the case, e.g. for pawedness in mice [3] or handedness for reaching in macaques [16].

To increase the number of tested animals we conducted a series of visual discrimination experiments with three individuals of *Tursiops truncatus*. The animals had to distinguish under monocular conditions between simultaneously

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presented pairs of different patterns, with one of them always defined to be correct. The numbers of trials until reaching 85% correct responses with each eye were used as a dependent variable. In the second experimental phase (transfer phase) the pattern pairs for the right eye were now presented to the left eye and vice versa. The performance of each naive eye was recorded and compared. We thus used an experimental design very similar to that of von Fersen et al. [7] to be able to closely compare our data to theirs.

## 2. Materials and methods

Three female bottlenose dolphins (*Tursiops truncatus*) named Cindy (approximately 20–21-year-old), Mery (approximately 20–21-year-old), and Gambi (8-year-old) were used. All animals underwent regular health controls. The eyes were examined by a veterinary surgeon and revealed no unusual conditions. They were housed together with two other bottlenose dolphins in a 13.5 m × 28 m outdoor pool

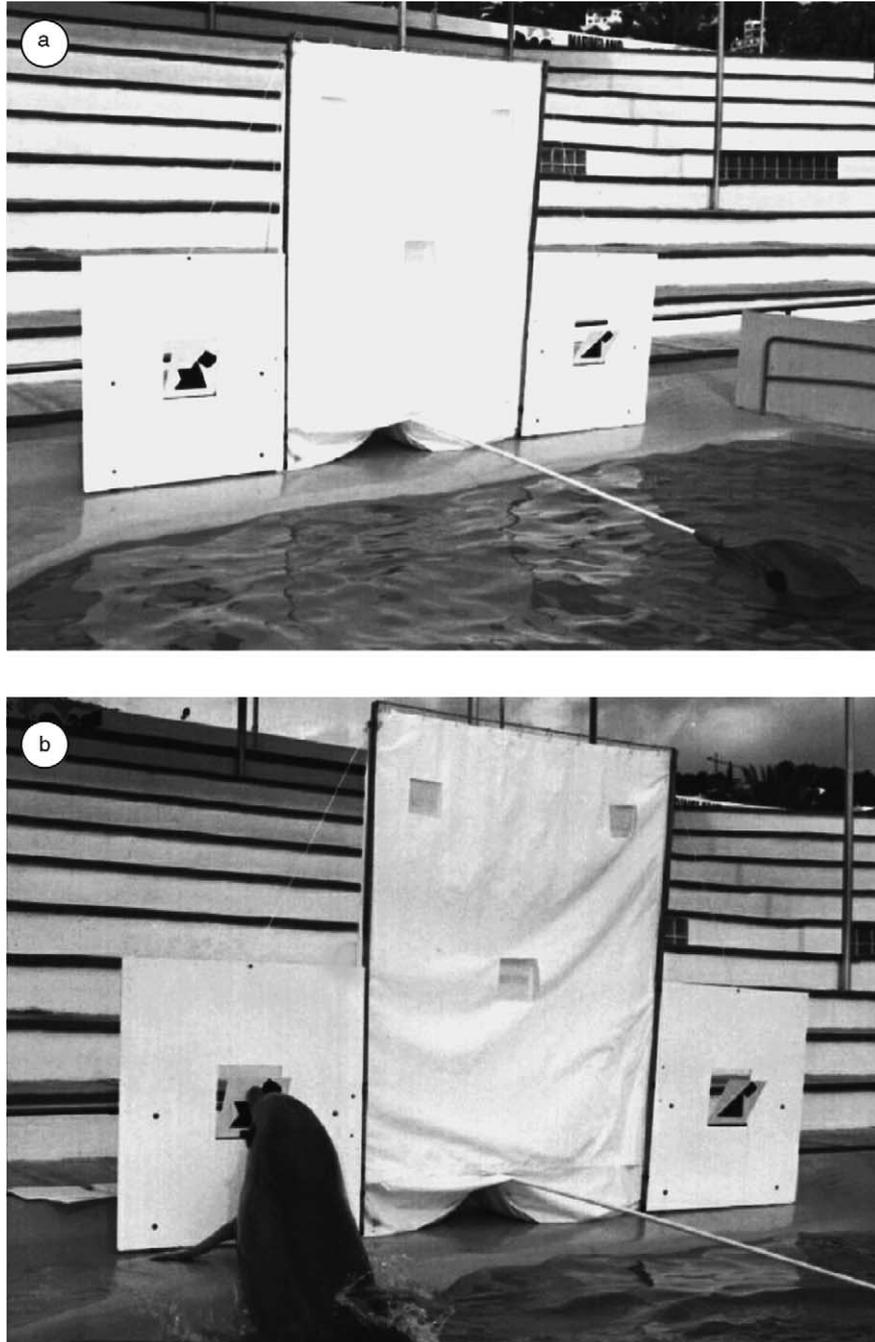


Fig. 1. (a) Overview of the testing situation with the apparatus, the stationing device and the position of the dolphin facing the revealed stimuli; (b) a dolphin touching one of the displayed stimuli with its rostrum.

of 4.5 m depth in Marineland Majorca (Spain). The experiments took place in an adjacent pool of 4.45 m width  $\times$  5.70 m length  $\times$  1.80 m depth where a single animal was separated for each session. The subjects who did not participate had no visual contact to the performing animal or the stimulus material.

### 2.1. Monocular discrimination learning of multiple stimulus pairs

At the start of an experimental session a rubber eyecup (9 cm diameter) was fixed by suction onto one of the subjects eyes and was removed at the end of the session. The dolphins could remove the eyecups easily if they wanted to, but did not show any sign of discomfort during the procedure. The animals had to discriminate between simultaneously presented pairs of different patterns (Fig. 1a) under monocular conditions. Successively, they learned to discriminate nine pairs of patterns of different complexity with each eye, whereby one pattern of each pair was always defined to be correct (Fig. 2). The stimuli consisted of 25 cm  $\times$  25 cm white PVC boards with a black pattern stuck onto it. Each stimulus was inserted in a window of a 1 m<sup>2</sup> white painted board such that a push with the nostril flipped the stimulus backwards (Fig. 1b). The white boards with the stimuli

were positioned to the left and right of the experimenter with an interboard distance of 1.50 m. During the discrimination process the experimenter was visually hidden from the subject through a plastic curtain. Each trial started with the animal being positioned at the tip of a 2.50 m target, above water level looking towards the apparatus (Fig. 1a). At this viewing distance dolphins have a high aerial acuity [14]. After positioning the animal, the experimenter revealed the covered stimuli and indicated four seconds later by a short whistle cue that the subject had to leave the target to touch one of the displayed stimuli with its rostrum. Only choices where one stimulus fell backwards were recorded. Additionally, the reaction time was recorded with a stopwatch. Correct responses were followed by a continuous whistle blow and reinforced with fish. Incorrect choices were indicated by non-continuous whistle blows and subsequently followed by correction trials. The left–right positions of the pattern were alternated quasi-randomly [9]. For each subject daily sessions were conducted, whereby each session consisted of 20 trials. The only exception was the very first presentation of a new stimulus pair, where a session consisted of 10 trials only, to minimize frustration. Criterion was reached after reaching 85% correct performance (17 out of 20 trials) within a session. In one session only a single stimulus pair was used.

### 2.2. Interocular transfer of learned discriminations

The general procedure was the same as described above. But in the second phase of the experiment, the stimulus pairs for the right eye were presented subsequently to the left eye and vice versa. With each stimulus pair only one session consisting of 20 trials was conducted and the animal's performance was recorded. In one session only one stimulus pair was used.

### 2.3. General observations of behaviour with emphasis on eye preference

After completion of the experiments, binocular observation-trials were run to record which eye the test subjects used in a free ranging task. Familiar and unfamiliar stimuli (e.g. toys, brush, stopwatch, buoy with rope) and situations (e.g. ballplay, people in water, training behaviour) were shown. Eye use was only recorded in cases where the animals clearly turned one eye to the situation or object. All occasions were excluded where the animal was looking with its binocular nasoventral visual field or where the preferred eye was unclear.

## 3. Results

An ANOVA with repeated measures was calculated using all nine stimulus pairs of all three animals. The parameters used were *viewing conditions* (left/right), *pattern*, as well as their statistical *interaction*. The test revealed a significant

Pair	Left eye	Right eye
1		
2		
3		
4		
5		
6		
7		
8		
9		

Fig. 2. The patterns used in the present study.

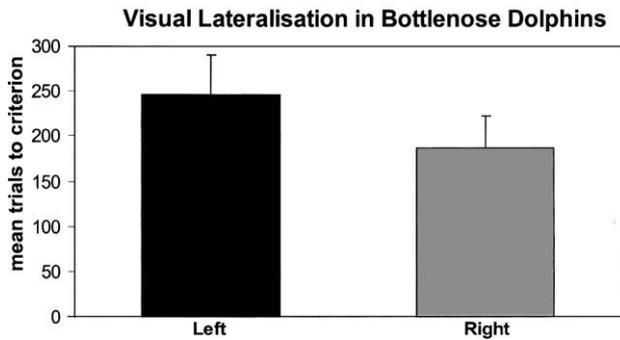


Fig. 3. Average trials to criterion for three dolphins and all nine stimulus pairs under monocular conditions, showing faster learning for the right eye. Bars depict standard error of mean.



Fig. 4. Individual average trials to criterion for each of three individual dolphins under monocular conditions. As visible, all animals showed faster learning scores with the right eye. Bars depict standard error of mean.

difference for *viewing conditions*  $F(1/2) = 24.33$ ,  $P < 0.05$  with an advantage for the right eye (Fig. 3). Furthermore, *patterns* differed significantly with respect to trials to criterion ( $F(8/16) = 8.5$ ;  $P < 0.001$ ). The interaction between *viewing conditions* and *pattern* was not significant ( $F(8/16) = 1.4$ , n.s.). A corresponding ANOVA run with

reaction time data revealed no eye difference ( $F(1/2) = 0$ , n.s.), no pattern-effect ( $F(8/16) = 0.56$ , n.s.) and no significant interaction ( $F(8/16) = 2.21$ , n.s.). These results reveal that the subjects showed on average a significant right eye superiority in learning speed but not in reaction times, whereby this learning advantage did not depend on the complexity of the different patterns. The average number of trials to criterion are depicted in Fig. 4 for each animal and eye condition. As shown, all three individuals showed a right eye superiority, albeit to different degrees.

For the transfer experiments we calculated an ANOVA with repeated measures for the variables *transfer direction* (left-to-right eye versus right-to-left eye), *patterns*, as well as their statistical *interaction*. The test revealed no significant difference for *transfer direction*  $F(1/2) = 15.87$ , n.s. (Fig. 5). Furthermore, *patterns* differed significantly with respect to trials to criterion ( $F(8/16) = 8.09$ ;  $P < 0.001$ ). The interaction between *transfer direction* and *pattern* was not significant ( $F(8/16) = 1.4$ , n.s.).

Observations of eye use during free swimming revealed a right eye preference which was not different for familiar or unfamiliar stimuli. Of 194 cumulative recorded cases of monocular eye use in all three animals, the dolphins used 138 times the right (71.1%), and 56 times the left eye (28.9%) ( $P < 0.001$ , binomial test). This was numerically also true for each individual and the right-eye bias was significant for two individuals (Cindy: L 26/R 77,  $P < 0.001$ ; Mery: L 24/R 50,  $P < 0.001$ ; Gambi: L 6/R 11, n.s.; binomial tests).

#### 4. Discussion

The present data shows that all three dolphins displayed a faster acquisition of a pattern discrimination task with their right eye. This visual stimulus learning asymmetry accords with a right eye preference during free observation sessions. Overall, these results are in close accordance with von Fersen et al. [7], indicating a left hemisphere superiority of visual object processing in dolphins. Although our sample is presently very limited, our results open the possibility of a population asymmetry for visual analysis in dolphins.

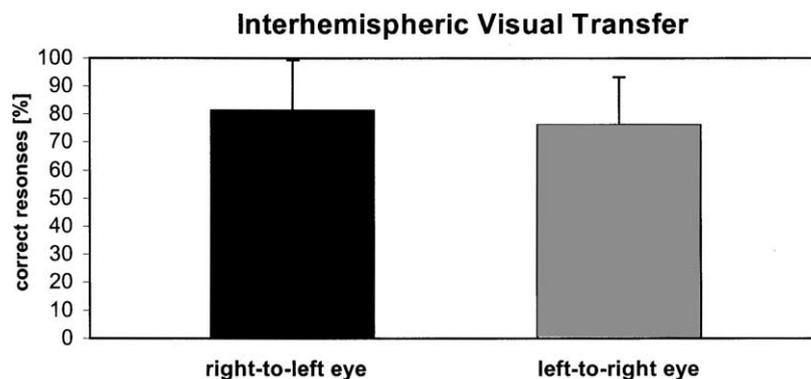


Fig. 5. Average interhemispheric transfer of pattern discrimination for all three dolphins. Bars depict standard error of mean.

The animals needed significantly different amount of trials to learn the discrimination between the nine pairs of patterns, indicating unequal demands to distinguish and memorize the stimuli. Since, however, the interaction between eye performance and patterns was not significant, visual asymmetry seems to create an overall effect on all discriminations. Due to the complete decussation of the optic nerve [17,28,29] this overall right eye superiority is possibly related to a left hemisphere dominance in recognising and/or memorising visual objects. The visual asymmetry probably also affects spontaneous eye use of the animals, since all of our individuals scrutinised interesting new and old situations or objects preferentially with their right eye. This is in accordance with previous studies in dolphins and other toothed whales ([24] and citations therein). We, therefore, assume that the counterclockwise swimming tendency often reported in dolphins [27] is probably secondary to their right eye visual superiority since the visual lateralization brings their right side to the outer rim of their pool. A motor asymmetry could not have influenced our discrimination data since the position of the positive stimuli were equally often to the left or to the right of the animals.

In humans, figural or face comparison tasks similar to the present one usually result in right hemisphere advantages [4,11,12,22]. A right hemisphere advantage for pattern or face discrimination tasks can also be observed in other mammalian species like monkeys, cats, rats, and sheep ([1,2,5,21,23,31,32], but see [10]). It is, however, likely that the right hemisphere is not dominant for pictorial material as such but only for a certain cognitive process underlying these discriminations: If a pattern is initially learned, the object's parts and their spatial relationships have to be encoded separately before creating a stored structural description. This process is dominated by the left hemisphere which is especially suited to analyse local details of stimuli [8,15,23]. However, once this form has become familiar, its global shape can be directly matched to information stored in memory by configurational analyses. This process is primarily guided by right hemisphere structures which are specialised to global stimulus analysis [13,19]. Consequently, shifts in hemispheric dominance depending on the amount of familiarity and the instruction is observed even without changes of the stimulus material [15,19]. This lateralized organisation seems to be true also for animals outside the mammalian order [26,30]. Thus, cerebral asymmetries for visual discriminations could be indicators for the cognitive strategy used by the animal. The left hemispheric dominance of our dolphins would then indicate that their strategy to distinguish and learn the patterns was to concentrate on local details which were subsequently matched with a stored representation of this stimulus. This may be also the reason why Kilian et al. [18] encountered a left hemisphere superiority in their visuospatial working memory task with dolphins. If the dolphins of this study would had utilised not the geometrical spatial position but local featural details of the position of the stimuli, a left hemispheric strategy

would indeed be expected. Taken together, we assume that the right eye/left hemisphere superiority of our dolphins represents the result of a cognitive strategy which primarily concentrates on local object features without exploiting the information provided by global and configural cues.

The design of the present study was virtually identical to that of von Fersen et al. [7]. Combining their single case with our three animals shows that four out of four dolphins tested under monocular pattern visual discrimination conditions displayed faster learning scores with the right eye/left hemisphere. At least within the limits of our small sample, this is an indication for a population asymmetry of visual object processing lateralization in bottlenose dolphins. A population asymmetry of visual object processing in dolphins might point to a common pattern of functional asymmetries shared by most, if not all vertebrates, with an emphasis on local feature analysis performed by the left hemisphere.

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### References

- [1] Bianki VL. Lateralization of functions in the animal brain. *Int J Neurosci* 1981;15:37–47.
- [2] Broad KD, Mimmack ML, Kendrick KM. Is right hemisphere specialization for face discrimination specific to humans? *Eur J Neurosci* 2000;12:731–41.
- [3] Collins RL. On the inheritance of handedness II. Selection for sinistrality in mice. In: Freeman WH, editor. *Left brain–right brain*. New York: Springer SP, Deutsch G; 1993. J Hered 1969;60:117–9.
- [4] Corballis PM, Funnell MG, Gazzaniga MS. Hemispheric asymmetries for simple visual judgements in the split brain. *Neuropsychologia* 2002;40:401–10.
- [5] Doty RW, Fei R, Hu S, Kavcic V. Long-term reversal of hemispheric specialization for visual memory in a split-brain macaque. *Behav Brain Res* 1999;102:99–103.
- [6] von Fersen L, Güntürkün O. Visual memory lateralization in pigeons. *Neuropsychologia* 1989;28:1–7.
- [7] von Fersen L, Schall U, Güntürkün O. Visual lateralization of pattern discrimination in the bottlenose dolphin (*Tursiops truncatus*). *Behav Brain Res* 2000;107:177–81.
- [8] Fink GR, Marshall JC, Halligan PW, Frith CD, Frackowiak RSJ, Dolan RJ. Hemispheric specialization for global and local processing: the effect of stimulus category. *Proc R Soc London B* 1997;264:487–94.
- [9] Gellermann LW. Chance orders of alternating stimuli in visual discrimination experiments. *Pedagogical Sem J Gen Psychol* 1933;42:206–8.
- [10] Hamilton CR, Vermeire BA. Complementary hemispheric specialization in monkeys. *Science* 1988;242:1691–4.
- [11] Hausmann M, Güntürkün O. Sex differences in functional cerebral asymmetries in a repeated measure design. *Brain Cogn* 1999;41:263–75.

- [12] Hausmann M, Güntürkün O. Steroid fluctuations modify functional cerebral asymmetries: the hypothesis of progesterone-mediated interhemispheric decoupling. *Neuropsychologia* 2000;38:1362–74.
- [13] Hellige JB. Hemispheric asymmetry: what's right and what's left. Cambridge, MA: Harvard University Press; 1993.
- [14] Herman LM, Peacock MF, Yunker MP, Madsen CJ. Bottlenosed dolphin: double-slit pupil yields equivalent aerial and underwater diurnal acuity. *Science* 1975;189:650–2.
- [15] Hillger LA, Koenig O. Separable mechanisms in face processing: evidence from hemispheric specialization. *J Cogn Neurosci* 1991;3:42–57.
- [16] Hörster W, Ettliger G. An association between hand preference and tactile discrimination performance in the rhesus monkey. *Neuropsychologia* 1985;23:411–3.
- [17] Jacobs MS, Morgane PJ, McFarland WL. Degeneration of the visual pathways in the bottlenosed dolphin. *Brain Res* 1975;88:346–52.
- [18] Kilian A, von Fersen L, Güntürkün O. Lateralization of visuospatial processing in the bottlenose dolphin (*Tursiops truncatus*). *Behav Brain Res* 2000;116:211–5.
- [19] Laeng B, Shah J, Kosslyn S. Identifying objects in conventional and contorted poses: contributions of hemisphere-specific mechanisms. *Cognition* 1999;70:53–85.
- [20] Marino L, Stowe J. Lateralized behavior in two captive bottlenose dolphins (*Tursiops truncatus*). *Zool Biol* 1997;16:173–7.
- [21] Morris RD, Hopkins WD. Perception of human chimeric faces by chimpanzees: evidence for a right hemispheric advantage. *Brain Cogn* 1993;21:111–22.
- [22] Nicholls MER, Bradshaw JL, Mattingley JB. Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size. *Neuropsychologia* 1999;37:307–14.
- [23] Peirce JW, Leigh AE, daCosta AP, Kendrick KM. Human face recognition in sheep: lack of configurational coding and right hemisphere advantage. *Behav Proc* 2001;55:13–26.
- [24] Ridgway SH. Physiological observations on the dolphin brain. In: Schusterman RJ, Thomas JA, Woods FG, editors. *Dolphin cognition and behavior: a comparative approach*. Hillsdale, NJ: Lawrence Erlbaum; 1986. p. 31–60.
- [25] Ridgway SH. The central nervous system of the bottlenose dolphin. In: Leatherwood S, Reeves RR, editors. *The bottlenose dolphin*. San Diego, CA: Academic Press; 1990. p. 69–97.
- [26] Rogers L, Andrew RJ, editors. *Comparative vertebrate lateralization*. Cambridge: Cambridge University Press; 2002.
- [27] Sobel N, Supin AY, Myslobodsky MS. Rotational swimming tendencies in the dolphin (*Tursiops truncatus*). *Behav Brain Res* 1994;65:41–5.
- [28] Supin AY, Mukhametov LM, Ladygina TF, Popov VV, Mass AM, Poliakova EG. Electrophysiological study of the dolphin brain. Moscow: Nauka; 1978 (from Ridgway, 1986).
- [29] Tarpley RJ, Gelderd JB, Bauserman S, Ridgway SH. Dolphin peripheral visual pathway in chronic unilateral ocular atrophy: complete decussation apparent. *J Morphol* 1994;222:91–102.
- [30] Tommasi L, Vallortigara G. Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. *Behav Neurosci* 2001;115:602–13.
- [31] Vermeire BA, Hamilton CR. Inversion effect for faces in split-brain monkeys. *Neuropsychologia* 1998;36:1003–14.
- [32] Vermeire BA, Hamilton CR, Erdmann AL. Right-hemispheric superiority in split-brain monkeys for learning and remembering facial discriminations. *Behav Neurosci* 1998;112:1048–61.