



Short report

## Left hemispheric advantage for numerical abilities in the bottlenose dolphin

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### Abstract

In a two-choice discrimination paradigm, a bottlenose dolphin discriminated relational dimensions between visual numerosity stimuli under monocular viewing conditions. After prior binocular acquisition of the task, two monocular test series with different number stimuli were conducted. In accordance with recent studies on visual lateralization in the bottlenose dolphin, our results revealed an overall advantage of the right visual field. Due to the complete decussation of the optic nerve fibers, this suggests a specialization of the left hemisphere for analysing relational features between stimuli as required in tests for numerical abilities. These processes are typically right hemisphere-based in other mammals (including humans) and birds. The present data provide further evidence for a general right visual field advantage in bottlenose dolphins for visual information processing. It is thus assumed that dolphins possess a unique functional architecture of their cerebral asymmetries.

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### 1. Introduction

Over the last decades, a large body of experimental studies has accumulated, demonstrating that functional asymmetries are not unique to humans, but represent a characteristic that many vertebrate species have in common (Rogers and Andrew, 2002). This growing

evidence for perceptual and cognitive lateralizations in animals also provides the basis for understanding the biological foundations of hemispheric specializations. So far, only few studies have focused on lateralizations in marine mammals like dolphins. Apart from findings on lateralized motor functions in the bottlenose dolphin (Norris and Dohl, 1980; Marino and Stowe, 1997), first investigations on cerebral functional asymmetries were carried out by von Fersen et al. (2000) and Kilian et al. (2000) demonstrating a right eye dominance in two different visual tasks for their subjects. Due to the complete decussation of the optic nerves in dolphins

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(Ridgway, 1990; Tarpley et al., 1994), this right eye dominance relates to a left hemispheric advantage. Recently, Yaman et al. (2003) have produced evidence that this cerebral asymmetry for visual pattern discrimination is population-based in the bottlenose dolphin and possibly is the basis for the right eye preference of these animals in observing objects or situations, substantiating earlier anecdotal observations (described in Ridgway, 1990). In the present study, we investigated whether this right visual field advantage could also be found for cognitive visual processes where behaviour is based on relational comparisons between visual objects.

This was tested during experiments where a bottlenose dolphin discriminated visual stimuli differing in numerosity. The results as regards the animal's accomplishment of the task were published recently (Kilian et al., 2003). It was demonstrated that the dolphin represented ordinal relations among numerosities, but that his performance was affected by non-numerical stimulus attributes during initial experimental phases. The data presented here give the results of test series conducted during two different phases of this experiment where numerosity stimuli were presented to the animal under monocular conditions. This enabled us to reveal possible hemispheric specializations for discriminating relational features between visual stimuli as required for tests of numerical abilities.

## 2. Materials and methods

### 2.1. Subject

The tests were carried out with a male bottlenose dolphin, Noah, 7 years of age, born and housed at the dolphinarium of the Zoo Nürnberg. Experimental sessions took place indoors in a circular tank 14 m in diameter (depth 4.7 m).

### 2.2. Apparatus and stimuli

The numerosity stimuli consisted of elements (pieces of white adhesive film) that were stuck on black square panels (1 m side length; 6 mm thickness) of synthetic material. The elements differed in form and size (see Fig. 1 for examples). The panels were hung underwater in stainless steel frames, which were fixed by

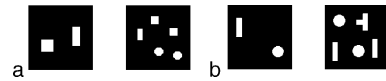


Fig. 1. Example for a stimulus pair in Test 1 (a). Compared to the stimulus pairs used prior to this test (b, example), the stimulus parameter 'overall surface area of elements' is now controlled.

hooks to the tank side. The distance between the frames and, thus, the stimuli was fixed at 1 m.

### 2.3. Procedure

In a two-choice discrimination paradigm, the dolphin had to choose between two simultaneously presented stimuli. One trial of a session went as follows: the dolphin's right or left eye was covered with an eyecup made of a special gelatine mixture (Klinckert and Thale, 1992). He was then sent to a stationing point at the opposite side of the tank. While waiting there with his head held above water, the experimenter hid behind the tank walls and two stimuli were placed in the water by an assistant. A starting signal (whistle blow) prompted the dolphin to swim towards the stimuli. He made his choice by touching one of the panels with the tip of his snout and pushing it slightly upwards. The chosen panel would move above the water surface which was observed by the experimenter. Thereafter, depending on the subject's choice, there were two possibilities of feedback. In a correct trial, the dolphin would choose the stimulus with the lower number of elements, which was followed by a continuous whistle blow (secondary reinforcer) and food (primary reinforcer). An incorrect choice, in which the animal would choose the stimulus with the higher number of elements, was followed by a specific non-continuous whistle blow without food being provided. In both cases, the eyecup was removed directly after the correct/incorrect signal.

Each session consisted of six trials. Right and left monocular conditions alternated within a session as well as for the first trial in successive sessions. The positions of the correct stimuli changed in a quasirandom sequence for each session (Fellows, 1967), but were balanced across the two monocular conditions.

The dolphin underwent regular medical examinations by a veterinary surgeon including a check-up of the eyes. These revealed that the animal was in good health. Before running the monocular tests, the dol-

phin had training sessions where his eyes were alternately covered by an eyecup. His behavioural reactions to subtle familiar hand signals showed no differences according to the viewing conditions. Therefore, any acuity differences of the eyes are unlikely.

2.4. Test 1

This test was conducted after the dolphin was choosing correctly between two stimuli representing different numerosities (either 2 or 5). At this experimental stage, the non-numerical feature ‘overall surface area of elements’ covaried with numerosity. To test whether the subject’s choice behaviour was influenced by these stimulus dimensions, we introduced stimuli with an overall equal surface area of elements. Each stimulus consisted of elements of different forms but identical sizes, combined in such a way that, in every choice, the overall surface area for the two presented stimuli was the same (either 0.072 or 0.125 m<sup>2</sup>). This novel stimulus set, where the attribute ‘overall surface area of elements’ was controlled, was first presented under monocular conditions. An example for a novel stimulus pair is depicted in Fig. 1a; for comparison, Fig. 1b shows a stimulus pair of the set used in the preceding binocular sessions. In the monocular test, 12 sessions consisting of six trials each were conducted, resulting in an overall of 36 right eye and 36 left eye trials.

2.5. Test 2

This monocular test was carried out after confounding stimulus dimensions were controlled and the dolphin then based his choice on stimulus numerosity. In binocular sessions, he had achieved a successful transfer to new stimulus pairs consisting of intervening numerosities (e.g., 3 versus 4). These new number pairs had been introduced in non-rewarded test trials. Thereafter, we introduced monocular trials presenting the number pairs 2 versus 5 and 3 versus 4 (see Fig. 2) with a normal feedback and reward procedure. For each of

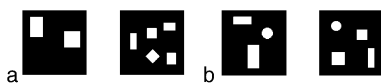


Fig. 2. Examples for stimulus pairs presented in Test 2: (a) 2 vs. 5; (b) 3 vs. 4.

these pairs, there were seven sessions with six trials each, that is, 42 right eye and 42 left eye trials in all. Note that the set of stimulus pairs for the numerosities 2 versus 5 is virtually identical to that used in Test 1.

3. Results

3.1. Test 1

The dolphin achieved 69.4% correct responses for the right eye trials, whereas his performance when seeing with his left eye was 47.2% which is close to the chance level of 50% (see Fig. 3). This difference between the viewing conditions was significant (Wilcoxon-test,  $Z = 2.0, T = 0, P < 0.05$ ).

3.2. Test 2

The results of this test are depicted in Fig. 4. For the number pairs 2 versus 5, the dolphin achieved 81% (right eye) and 76.2% (left eye) correct responses. There were no significant differences between the viewing conditions (Wilcoxon-test,  $Z = 0.4, T = 6, P > 0.6$ ). In the sessions with numerosities 3 versus 4, his right eye performance (85.7%) differed significantly from his left eye performance (61.9%), Wilcoxon-test,  $Z = 2.0, T = 0, P < 0.05$ .

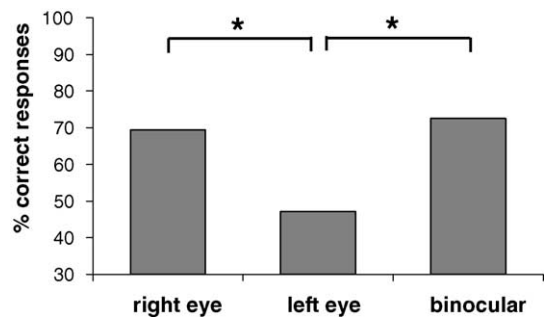


Fig. 3. Performances in the two monocular conditions with the numerosity pairs 2 vs. 5 with an overall equal surface area of elements (Test 1). The column ‘binocular’ depicts the performance over four binocular sessions with the same stimulus set carried out directly after the monocular tests. Asterisks indicate significant differences at the 5% level.

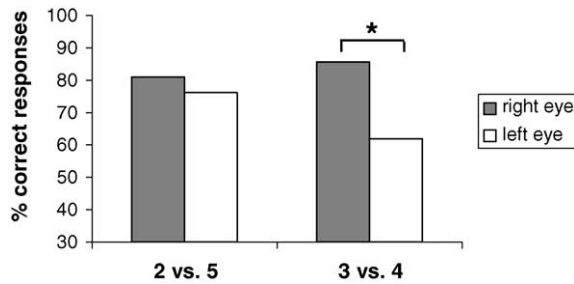


Fig. 4. Performances with the stimulus pairs 2 vs. 5 and 3 vs. 4 in the two monocular conditions (Test 2). Asterisks indicate significant differences at the 5% level.

#### 4. Discussion

The present study reveals a visual asymmetry in the bottlenose dolphin for discriminating relational dimensions between stimuli differing in numerosity. The overall right visual field advantage suggesting a dominance of the left hemisphere is in accordance with all recent findings on lateralized visual functions for this species (von Fersen et al., 2000; Kilian et al., 2000; Yaman et al., 2003).

In Test 1 and for the number pairs 3 versus 4 in Test 2, the subject demonstrated a significantly better performance level when using his right eye. However, no difference between the monocular conditions was found for the number pair 2 versus pair 5 in Test 2, a stimulus set virtually identical to that used in Test 1. We assume that the absence of a significant asymmetry is due to a ceiling effect. As a result of the ongoing training sessions between Tests 1 and 2, Noah was meanwhile familiar with more demanding discriminations between stimuli differing in numerosity. Therefore, his performance for the 2 versus 5 discrimination was higher for both eyes, reducing the possibility to find a significant lateralization. A dependence of asymmetry displays on the amount of stimulus familiarity was also reported in other studies (Fagot and Vaclair, 1994; Doty et al., 1999; Laeng et al., 1999). Thus, overall both test series demonstrate an advantage of the right visual field for analysing relational stimulus attributes which presumably implies a left hemisphere superiority for these processes.

Lateralization studies in humans mostly use only very brief stimulus exposure times and require their subjects to respond very quickly. This is due to the im-

PLICIT assumption that stimulus information projected to one hemisphere is quickly disseminated throughout the brain. This assumption does not even completely hold for humans, where asymmetrical responses can be elicited after lengthy periods of lateralized visual exposure (Wittling and Roschmann, 1993). Different from humans, dolphins evince a complete chiasmatic crossing, and their corpus callosum is comparatively minor relative to the extent of their cerebral hemispheres (Tarpley and Ridgway, 1994). Therefore, this study, like several previous ones (von Fersen et al., 2000; Kilian et al., 2000; Yaman et al., 2003), was able to observe asymmetrical response levels during monocular testing that very likely are due to asymmetries of visual processing. This is in line with studies in a large number of avian species that also have a complete chiasmatic decussation and have the commissura anterior for interhemispheric exchange (Güntürkün, 2002). Thus, the presence of anatomical means for interhemispheric exchange does not necessarily imply that lateralized visual information has to be quickly transferred to the non-stimulated hemisphere.

An alternative interpretation of the right eye superiority of Noah could be the existence of acuity differences between the eyes. While we are unable to completely exclude this possibility, we believe this interpretation to be unlikely for four reasons. First, Noah's eyes were regularly checked by a veterinary surgeon who would have detected at least major problems. Second, Noah showed no asymmetry in understanding even subtle hand cues. Third, the asymmetry for the first stimulus pair disappeared after training – a result unlikely to happen if acuity differences had determined the lateralized response. Fourth, previous experiments had used in total six adult bottlenose dolphins and in all of them an asymmetrical visual performance was demonstrated. In one of these studies (Kilian et al., 2000), the animals were allowed to approach and grasp the objects, making a lateralized performance due to acuity differences unlikely. Taken together, we are inclined to believe that the asymmetrical performance of Noah was due to lateralized visuocognitive processes and not due to acuity differences between the eyes.

Yaman et al. (2003) suggested that the left hemispheric dominance for object pattern discrimination in the bottlenose dolphin is due to a strategy of analysing local features of stimuli. This asymmetry display would then accord with the lateralized pattern in humans,

other mammals, and birds which also demonstrate a right visual field advantage for encoding local details (Fink et al., 1997; Hopkins, 1997; Peirce et al., 2001; Tommasi and Vallortigara, 2001). However, this explanation does not hold for the present results. A successful discrimination of relational dimensions between the stimuli presented here could not be accomplished by analysing and comparing local details, consequently, we should not expect an advantage of the left hemisphere. In humans, the right hemisphere is advantaged for magnitude judgements and for non-verbal assessments of numerosity during subitizing (Boles, 1986; Klein and McInnes, 1988; Nicholls et al., 1999; Pasini and Tessari, 2001). Contrary to this, our data suggest a specialization of the left hemisphere for these processes in the bottlenose dolphin.

A general pattern that emerges from all the results on lateralized functions in the bottlenose dolphin, including the present results, is a consistent right visual field advantage for visually guided behaviours. This is very likely due to a dominance of the left hemisphere for several different visual processes. As against this pattern, other mammals (including humans) and birds display complementary specializations of the hemispheres in encoding visual information, with left–right advantages depending on the stimulus nature and the cognitive strategy applied (Hellige, 1996; Vallortigara et al., 2001; Güntürkün, 2002; Rogers and Andrew, 2002; Jager and Postma, 2003). Recent findings including the present data suggest an overall left hemisphere superiority of dolphins for visual processing which could thus represent a remarkable deviation of their functional cerebral asymmetries.

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