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RESEARCH ARTICLE

Role of Sensory Cues on Food Searching Behavior of a Captive *Manta birostris* (Chondrichtyes, *Mobulidae*)

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This study reports on the first experimental research designed specifically for *Manta birostris* behavior. The authors attempted to learn about the feeding behavior and environmental cues influencing this behavior, as well as general cognitive ability. The preconditioned Manta's ability to identify food, on the basis of a fraction of the ordinary food signal complex, was tested. The opening of cephalic fins was considered a good indicator of feeding motivation level. The study subject animal used its biological clock to predict time and also associated a specific location with food, suggesting an ability to build up a cognitive map of its environment. Both underwater visual stimuli and olfactory stimuli had a very intense effect on food searching behavior over a 30 m distance, in contrast to visual signs from above the water surface. In addition, although an underwater visual signal resulted in a more intense response than from an olfactory signal, the specimen did not discriminate between different objects tested on the basis of visual sensation. It could therefore be suggested that food searching behavior of Mantas are governed by triggering stimuli, including smell or visual recognition, and modulated by the cognitive spatial map stored in their long-term memory. These findings will hopefully prove useful while devising protecting policies in the natural environment and/or while keeping these animals in captivity. Zoo Biol 27:294–304, 2008. © 2008 Wiley-Liss, Inc.

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INTRODUCTION

This study is the first behavioral experiment on a captive *Manta birostris* [Donndorff, 1798]. *M. birostris* is the largest of all rays [Nelson, 1994; Compagno, 1999; Myers, 1999], and can be found worldwide in almost all tropical seas [Compagno, 1973, 1999; Last and Stevens, 1994; Homma et al., 1999].

Many populations of this species are in need of protective measures, with multiple results suggesting they are rapidly decreasing toward extinction because of commercial fishing and by-catch in various countries [Compagno and Last, 1999; Homma et al., 1999; Alava et al., 2002]. The International Union for the Conservation of Nature and Natural Resources (IUCN) lists these animals under category "Near Threatened" [IUCN, 2006] on its Red List.

Despite its widespread distribution there is limited information on the basic biology, population dynamics, social behavior, sensory and learning capabilities of this species Yano et al., 1999. Like other pelagic, big bodied, free-swimming species, the study of Manta rays in the wild presents multiple logistical and financial difficulties. Captive animals are also not abundant and their stay on public displays is usually not long. Furthermore, they are sensitive to different environmental cues and have very low fecundity [IUCN, 2006].

A captive immature male *M. birostris*, displayed at the Oceanário de Lisboa (Lisbon Oceanarium), was the subject of a series of trials conducted with the objective of answering the following research questions:

- Is the position of the cephalic fins an indicator of to the motivational level of feeding?
- It is commonly known that Manta rays leap out of the water [Coles, 1916; Homma et al., 1999] occasionally, so does the presence of people and/or objects over the surface influence this behavior? In other words, does *M. birostris* sense and evaluate activity above the surface?
- Does it have a biological inner clock? Is it able to predict periodical events with its biological clock? How does time influence food-searching behavior?
- Does it have a cognitive spatial map of feeding places and can it differentiate objects and situations indirectly linked to food exposure?
- How important are underwater visual cues and how efficiently can it differentiate between these?
- Are underwater visual or olfactory stimuli stronger motivational cues in food-searching behavior?
- Is it able to perform associative learning and build up long-time memory?

The tests conducted were designed to improve the general understanding about this species' behavior. This understanding will hopefully prove helpful when designing both protective measures in the wild and husbandry protocols for captive specimens.

MATERIALS AND METHODS

An immature male *M. birostris* (1.6 m wide) was captured on 13 November 2002 in a set-net off Tavira, South of Portugal, and immediately transported to the Oceanário de Lisboa. Transport was done by road, inside a 1.6 m wide round polyethylene vat, and lasted for 4 hr. During transport the water was mechanically and chemically filtered with one Jacuzzi® (Jaccuzi Inc., Chino, CA) cartridge filter powered by a 12 V Rule® (ITT Industries, Inc., Gloucester, MA) 2000 GPH bilge pump mounted on the lid; each cartridge consisted of multiple laminated sheets of filter paper with the addition of one bag of activated carbon in the center. Two water changes of approximately 40% of the total volume, each, were conducted during the trip. Oxygen saturation was maintained above 150% through the use of a small 12 V Rule® 500 GPH bilge pump, used as an atomizing device and coupled to a medicinal compressed oxygen cylinder. The transport method generally followed the technique described, and previously used, by Correia in publications such as Correia [2001], Young et al. [2002], Smith et al. [2004] and Correia et al. [2008].

The animal was kept in the square-shaped Open Ocean tank, measuring 30 × 30 m wide × 7 m deep, which also housed 68 other shark, ray and teleost species. The tank contained 4,700 m^3 of artificial seawater cycled through a closed circuit consisting on 16 pressurized sand filters, 4 ozone contact chambers, 1 protein skimmer and a reverse up-flow of water through a 20 cm thick gravel bed. Water temperature was maintained constant and averaged 21.9°C. Average oxygen saturation was 91%, salinity 32.7 ppt and pH 8.0. The Open Ocean tank receives natural daylight through four glass windows mounted on the ceiling and also from 301,000 W metal halogen lamps, which were turned on at 08.00 and turned off at 20.00 hr. Water parameters remained fairly constant throughout the study and there were negligible variations in other chemical parameters, such as ammonia, nitrite and nitrate concentrations.

Behavioral conditioning began the day after the Manta was introduced into the tank. The primary objective was to train the Manta to feed at a specific location. Food was presented to the individual in a white plastic bucket, with horizontal black lines painted on it, by an observer standing on a walkway over the tank. The bucket had small holes drilled on the bottom, which allowed for some liquid food "extract" to dissolve into the water, providing visual and olfactory information of food simultaneously. The Manta would quickly recognize the bucket and approach it, slightly elevating the anterior part of the body while taking up the food from the bucket, which was literally dumped inside the Manta's open mouth.

This technique was used to feed the Manta ray 1 kg of frozen Euphausiid shrimp (*Palaemonetes varians*) at 08.00 and 13.00 hr and 2 kg at 16.00 hr daily, except for Sundays when no food was given.

Data were collected from three observation spots, when the Manta was in two areas bordered by fiberglass walkways (Fig. 1(1)). These two areas were labeled as "feeding area" and "other area." Both areas were 11.6 m long × 6.2 m wide. The observation spots were defined as follows:

(A) The observer was on the walkway above the "feeding area," recording the Manta's behavior in the "feeding area."
(B) The observer was hidden behind a structural pillar, recording the Manta's behavior in the "feeding area."
(C) The observer was on the walkway above the "other area," recording the Manta's behavior in the "other area."

The following variables were recorded during each trial conducted on any of the three observation spots, by using EthoLog 2.2 software [Ottoni, 2000]:

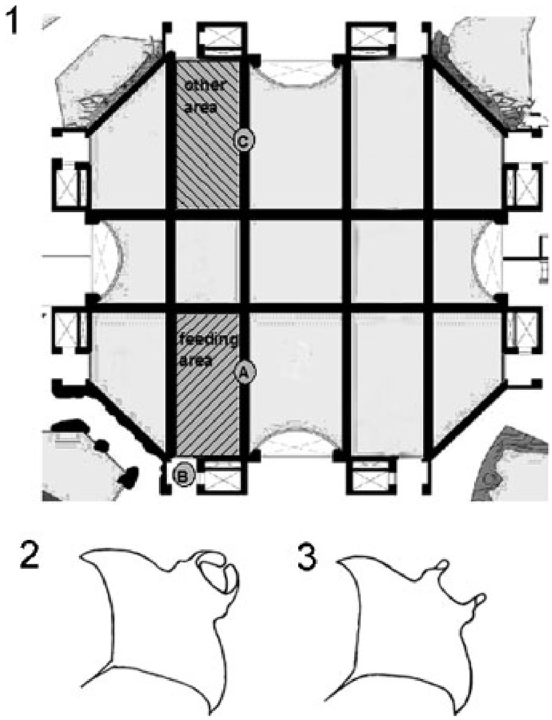

Fig. 1. (1) Top view of the Open Ocean tank at the Oceanário de Lisboa. Black lines: fiberglass walkways over the tank (1 m above water surface): (**A**) position where person would offer food on the bridge; the observer could be seen by the animal; (**B**) position where observer could observe the animal while remaining unseen from the water; (**C**) position on the bridge in "other area," not used for feeding, the observer could be seen by the animal. (2) Top view of *Manta birostris* with opened cephalic fins. (3) Top view of *M. birostris* with closed cephalic fins.

- Time spent in the observed area (in case of A and B the observed area was the "feeding area," in case of C it was the "other area").
- Time spent with opened cephalic fins (Fig. 1(2)) in the observed area.
- Time spent with closed cephalic fins (Fig. 1(3)) in the observed area.
- Number of times when the head and upper jaw were slightly elevated out of water in the observed area, which was labeled as "head-out-of-water" behavior.

"Head-out-of-water" behavior could be regularly observed before starting the series of trials and exclusively during normal feedings. This very prominent elevation of the head was consistently observed immediately before food was placed in the ray's mouth. This behavioral element was therefore used as an index of high motivation level in food searching.

The fact that the ray was conditioned to associate the placement of the bucket in the water with feeding, allowed for small changes to some of these variables and the observation of the Manta ray's responses. Different stimulus fractions built up complex stimuli pattern of the feeding procedure. Feeding was decomposed to stimulus fractions, such as the presence of people, out-of-water visual cues, underwater visual cues, olfactory cues, time, location and others. Using different treatments, tests were conducted to assess whether the animal was able to detect the selected stimulus components. The empty feeding bucket and a different bucket (different in color, pattern and size) were used as underwater visual cues. A 0.3 L shrimp extract was used as an olfactory cue. The Manta's ability to identify food on the basis of a fraction of the ordinary food signal complex was also tested.

Data on the Manta's behavior were collected daily during 15 min observation periods, which occurred at feeding time, but were also conducted at random times between 07.30 and 18.00 hr. After measuring the variables during different trials, the Manta got its regular feeding. On two Sundays the observations were continued at feeding times without any treatment. During 2 weeks of observations, a total of 25 hr of data were collected. Trials are described in Table 1. A minimum of seven replicates per trial were conducted. The abbreviations of the trials will be used from now.

Each comparison involved two or three trials. The length of time spent in the "feeding area" or in the "other area" after different treatments was compared between two or three trials, and the length of time spent with opened cephalic fins in the "feeding area" was compared between the two or three trials.

Pairs of trials were compared using Mann–Whitney's test, as the data did not meet the assumptions of normality. When comparing three trials, Kruskal–Wallace's test was used as the data were also not normally distributed ($P<0.05$). Statistical analysis was performed using GraphPad Instat software.

RESULTS

Comparative trials made on *M. birostris* behavior and perception are presented in Table 2. Measured variables during the different trials are shown graphically as well in Figure 2(1–6).

TABLE 1. Description of the trials conducted while analyzing the feeding behavior of one captive *Manta birostris* at the Oceanário de Lisboa

Abbreviations of trial conducted	Observed area	Observer's position	Observation time	Treatment
fa.br.rt	Feeding area	On the bridge(A)	Random time	—
hidp.rt	Feeding area	Hidden (B)	Random time	—
fa.br.ft	Feeding area	On the bridge(A)	Feeding time	—
otha.br.rt	Other area	On the bridge(C)	Random time	—
fa.emptyb.ft	Feeding area	On the bridge(A)	Feeding time	Empty bucket in the water
fa.diffb.ft	Feeding area	On the bridge(A)	Feeding time	Different bucket in the water
fa.soup.ft	Feeding area	On the bridge(A)	Feeding time	Shrimp extract in the water
fa.feeding	Feeding area	On the bridge(A)	Feeding time	Normal feeding
otha.emptyb.ft	Other area	On the bridge(C)	Feeding time	Empty bucket in the water
otha.soup.ft	Other area	On the bridge(C)	Feeding time	Shrimp extract in the water
Sunday	Feeding area	On the bridge(A)	Feeding time	No food reward

The abbreviation of a trial is composed of the first letters of the important features that describe the trial. The first abbreviation is about the area observed, than the position of the observer or the treatment used and the last abbreviation labels the time of the observation. Example: fa.empty.ft means that the measured variable is the time spent in the feeding area when the observer collects data while putting the empty feeding bucket in the water at feeding time.

Figure 2(1) shows the influence of the observer's position during random time, comparing variables taken from the feeding bridge and from a place where the observer is out of the Manta's view. No significant difference was found between time spent in the feeding area and in other areas. Time spent with closed cephalic fins was longer in both cases than that with opened fins, regardless of the position of the observer.

To test the effect of feeding time variables from the feeding bridge, at random times and at feeding times, were compared. Figure 2(2) shows the comparison of results obtained during random time and feeding time. A significant difference in

TABLE 2. Comparative trials conducted, and statistical results, while analyzing the feeding behavior of one captive *Manta birostris* at the Oceanário de Lisboa

Comparative trials	Test used	P value	Signif.
Visual sign from out of the water			
fa.br.rt. op/hidp.rt. op	Mann–Whitney	$P = 0.1973$	ns.
fa.br.rt. (op+cl)/hidp.rt. (op+cl)	Mann–Whitney	$P = 0.2237$	ns.
Time			
fa.br.rt.op/fa.br.ft. op	Mann–Whitney	$P = 0.0009$	[a]
fa.br.rt. (op+cl)/fa.br.ft. (op+cl)	Mann-Whitney	$P = 0.0064$	[b]
Place			
fa.br.rt. (op+cl)/otha.br.rt. (op+cl)	Mann–Whitney	$P = 0.2588$	ns.
fa.emptyb.ft.(op+cl)/otha.emptyb.ft. (op+cl)	Mann–Whitney	$P = 0.0006$	[a]
fa.soup.ft. (op+cl)/otha.soup.ft (op+cl)	Mann–Whitney	$P = 0.0047$	[b]
Underwater visual sign			
fa.br.ft. op/fa.emptyb.ft. op	Kruskal–Wallis	$P < 0.05$	[c]
fa.br.ft. op/fa.diffb.ft.op		$P < 0.01$	[b]
fa.emptyb.ft.op/fa.diffb.ft.op		$P > 0.05$	ns.
fa.br.ft. (op+cl)/fa.emptyb.ft. (op+cl)	Kruskal–Wallis	$P < 0.01$	[b]
fa.br.ft. (op+cl)/fa.diff.ft.(op+cl)		$P < 0.05$	[c]
fa.emptyb.ft. (op+cl)/fa.diff.ft.(op+cl)		$P > 0.05$	ns.
Underwater visual and/or olfactory sign			
fa.feeding. op/fa.emptyb.ft. op	Kruskal–Wallis	$P < 0.01$	[b]
fa.feeding. op/fa.soup.ft.op		$P < 0.01$	[b]
fa.emptyb.ft. op/fa.soup.ft.op		$P > 0.05$	ns.
fa.feeding. (op+cl)/fa.emptyb.ft. (op+cl)	Kruskal–Wallis	$P < 0.01$	[b]
fa.feeding. (op+cl)/fa.soup.ft(op+cl)		$P < 0.01$	[b]
fa.emptyb.ft. (op+cl)/fa.soup.ft(op+cl)		$P > 0.05$	ns.
"Head-out-of-water" behavioral element			
fa.emptyb.ft/fa.diffb.ft	Kruskal–Wallis	$P > 0.05$	ns.
fa.emptyb.ft/fa.soup.ft		$P < 0.05$	[c]
fa.diffb.ft/fa.soup.ft		$P < 0.05$	[c]
Sunday			
Morning (op+cl)/Daytime (op+cl)	Kruskal–Wallis	$P > 0.05$	ns.
Morning (op+cl)/afternoon(op+cl)		$P < 0.001$	[a]
daytime(op+cl)/afternoon(op+cl)		$P > 0.05$	ns.

[a] The difference is extremely significant between the two trials (i.e. $P < 0.001$).

[b] The difference is very significant between the two trials (i.e. $0.001 < P < 0.01$).

[c] The difference is significant between the two trials (i.e. $0.01 < P < 0.05$).

Trials compared are labeled by their abbreviations and separated by "/". Example: fa.br.rt.op/hidp.rt.op means that the results on the measured variable "time spent in the feeding area with opened cephalic fins and with the observer on the bridge at random time" was compared with those results when the observer was hidden and collected data in the feeding area at random time. op+cl, total time spent in the observed area (with opened and closed cephalic fins together); signif., significance; ns., no difference could be proven between the two trials (i.e. $P > 0.05$).

behavior between feeding (fa.br.ft) and random times (fa.br.rt) was observed. During feeding time, time spent in the feeding area and also time spent with opened cephalic fins was longer than at random times. During random times, the ray spent more time with closed cephalic fins than with opened fins. On the contrary, during feeding time the ray's cephalic fins were opened longer than closed.

Figure 2(3) shows the influence of location during random time and feeding time. No significant difference between measured variables at random times were observed. However, there was a marked difference during feeding time between performance of the ray in the feeding location and other locations, demonstrated by either presenting shrimp "soup" or the empty feeding bucket. Time spent with opened and closed cephalic fins was also significantly different and the ray spent considerably longer time in the feeding place. The ray responded similarly to shrimp "soup" and empty bucket in each location.

To test the effect of different underwater visual stimuli, observations in the feeding square, with the traditional and a different feeding bucket, were compared with those from the feeding bridge (Fig. 2(4)). When any of the buckets were placed in the water, the Manta spent significantly more time in the feeding area with cephalic fins opened more often. However, there was no significant difference in the behavioral response to the two buckets (i.e. traditional and different). During this study 49 "head-out-of-water" actions were recorded when only the empty feeding bucket was placed into the water, whereas 43 were observed when the empty different bucket was placed in the water. This difference was not significant.

Figure 2(5) shows results obtained by varying stimulus modalities (smell or vision). Variables were compared during normal feedings, using the empty feeding bucket, and when the extract of shrimp was placed in the water separately in the feeding area at feeding times. When the visual or the olfactory stimulus was present, the Manta spent significantly more time in the feeding area, and the cephalic fins were opened more often. There was no significant difference in time spent in the feeding area when food, or an empty feeding bucket, was presented. There was significant difference in the "head-out-of-water" behavior response to different underwater stimuli. During this study, six "head-out-of-water" actions were recorded when only shrimp soup was presented and 49 were recorded when only the empty feeding bucket was placed into the water.

There were differences between time intervals spent in the feeding area in the three feeding times (morning, daytime, afternoon) on Sundays (i.e. when the animal was not fed). However, this set of trials consisted on a limited number of measurements (Fig. 2(6)). Even if there was no food at the time of the first feeding, the animal searched for food in the feeding area. In the two following feeding times, on the same day, the Manta was more motivated by hunger, but spent less time at the feeding area than at the first feeding time.

The combination of all trials allowed for the conclusion that the Manta spent more time with opened cephalic fins before feeding times than at random times and more in the "feeding area" than in the "other area."

DISCUSSION

This study focused on the elements of a captive *M. birostris*' feeding behavior and what environmental cues influence this behavior and also trying to determine its general cognitive abilities. The way visual and olfactory cues affect its food searching

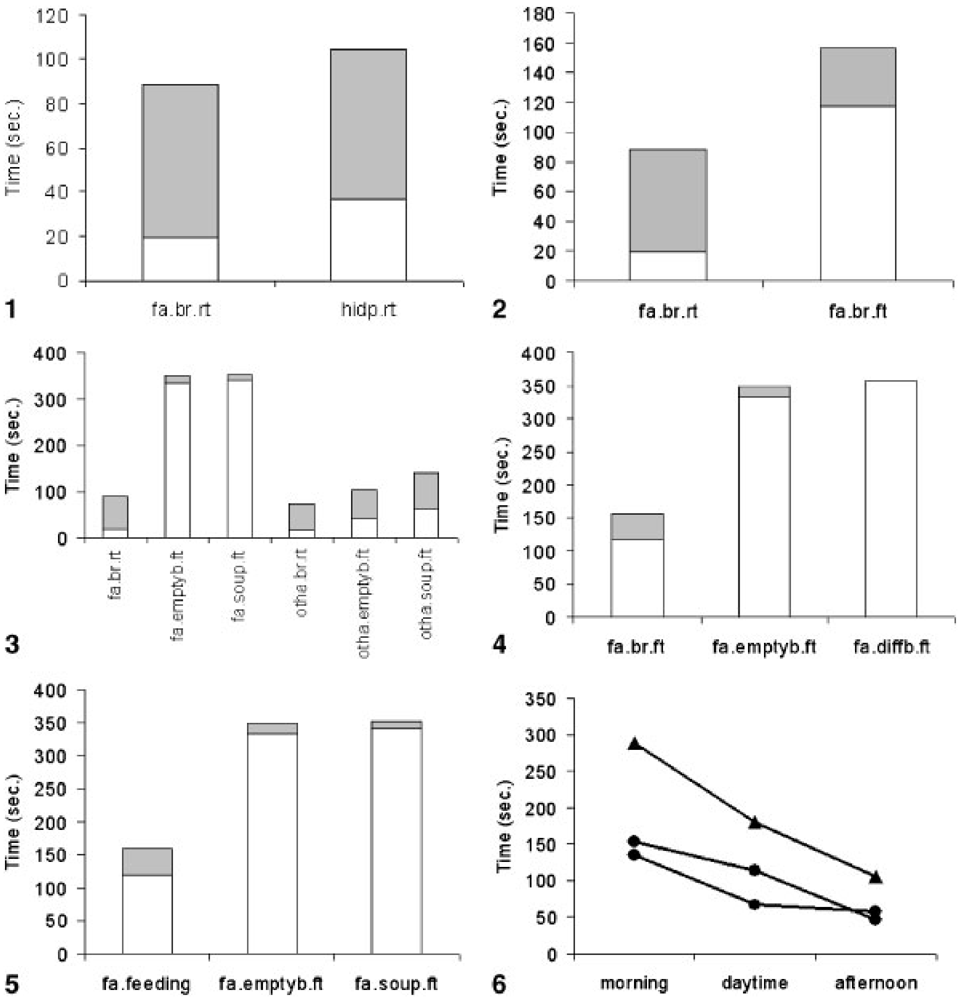

Fig. 2. Observations on feeding behavior of captive *Manta birostris*. White areas: time spent in the observed area with opened cephalic fins; Gray areas: time spent in the observed area with closed cephalic fins. Circles show the recorded time spent in the feeding area during each observation ($n = 2$); triangles show their summation.

behavior were studied; how it was able to memorize time and location and whether it had visual perception through the surface of the water.

Results revealed that the opened and closed position of the cephalic fins have significant meaning, which was interpreted as a good indicator of feeding motivation level. The opened cephalic fins represented higher motivational level of feeding, as compared to partially opened or closed cephalic fins, which defined medium or low feeding motivational levels, respectively.

No significant differences were found in the Manta's behavior in response to visual stimulus from above the surface of the water. Additional studies are required to determine what sensory cues are used when leaping out of the water or to predict what the effect of other objects (such as dive boats) above the surface might have on these animals' behavior. It should be noted that, during this study, the Manta did not leap out of the water under any circumstance.

This Manta ray was able to differentiate feeding time from other times regardless of the location of the observer. These results suggest that the individual used its biological clock to predict time of feeding. During feeding time, the frequency and duration of the Manta ray's stay in the feeding area was significantly higher, independently of the observer's position, which suggests exact time recognition from these rays.

The Manta associated a specific location (i.e. feeding area) with food, suggesting an ability to memorize places. This, in turn, suggests the individual was able to build up a cognitive map of its environment. It is, however, unclear whether it used experience from spatial exploration or a biological compass for location recognition. Cognitive spatial map building is supported by the recurrent observation that the animal successfully, and consistently, avoided a particularly large higher (i.e. shallower) rock in the tank even at night. This cognitive map creation most likely maximized the ray's survival in the tank's spatially limited environment. Location sensitivity and spatial map formation is a typical hippocampal function in mammals [Bingman et al., 2003; Strösslin et al., 2005]. These trials, therefore, suggest conducting spatial orientation experiments on rays from this taxon.

Recognition of the bucket, as a visual stimulus for feeding, is the result of learned behavior. However, it is unclear whether it associated food with the shape, color or pattern of the bucket. Results from measured variables suggest that the Manta could not discriminate between the empty feeding bucket and a different bucket. Nevertheless, it is noteworthy that the Manta gave the highest motivational level indication, "head out-of-water" responses, most frequently when the empty feeding bucket was used. To specify what sensory cues (color, pattern, size) Mantas use for discrimination between buckets requires focused experiments on differential conditioning.

Visual and olfactory elements of stimuli were separated by the Manta ray, although it did not discriminate any of them as key stimulus for feeding. This fact was interpreted as a result of previous training of the ray, focusing on feeding time and feeding area, but not on distinction between smell and image of food. The Manta ray associated certain fractions of feeding stimulus pattern with food (e.g. smell of shrimp without image of shrimp) as a behavioral trigger. This is most likely an innate association memory capacitance. The reaction to smell was very positive, being able to detect 0.3 L of shrimp extract in 4,700 m^3 of water. However, for location the Manta most likely used its long-term spatial memory, thus moving immediately to the feeding area, independent of the source of the olfactory stimulus.

The underwater visual and olfactory stimuli had a similar effect on the Manta's food searching behavior over a 30 m distance. However, the analysis of "head-out-of-water" behavior revealed that visual cues had a greater influence on the ray's behavior. The importance of the underwater vision in the food searching behavior is interesting because these rays usually feed in plankton rich waters where visibility is often poor.

It is also intriguing that the behavioral response was different on Sundays, when there was no feeding. This may suggest that the capacity for time estimation of Manta ray is so highly developed that it extended for several days and allows estimation of certain days. This explanation could be questionable, so it was assumed that the missing food reward on Sunday changed the ray's behavior after a single trial. The first missing food reward made the ray unresponsive to the feeding location during the next feeding times of that same day. This led to the conclusion that Manta's conditioned feeding behavior can be modified easily by one missing reward, suggesting good learning capacities.

Methodological Considerations

It should be noted that other fish living together in the same tank as this Manta did not seem to influence the Manta ray's food searching behavior. Small fish were certainly attracted by the empty feeding bucket but not so much by the shrimp smell. The Manta ray's response to both of those was however equally intense.

As the noise generated by the water circulation system (which delivers some of the returning filtered water above the surface of the tank) was a lot stronger than the noise caused by putting the bucket into the water gently, it was assumed that the splash caused by dipping the bucket into the water most likely did not have an effect on the Manta ray's behavior.

Feeding is an important component of the daily routine, hence time and location of feedings were not changed during this study. The fact that the ray was conditioned to be fed in a specific time and location, using a specific utensil, allowed for experimental manipulation of these variables and observe the Manta ray's responses. This is a typical behavioral conditioning paradigm, and it was used to explore sensory capacities and space-temporal rules of the animal.

CONCLUSION

This study supports the assumption that feeding behavior and food searching behavior of the Manta are governed by triggering stimuli, such as smell or visual recognition and modulated by the cognitive spatial map stored in their long-term memory. These results should contribute, in a positive fashion, toward the betterment of captive Manta ray husbandry and may also assist future studies on captive Manta rays.

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