

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/297913466>

# Contingency checking and self-directed behaviors in giant manta rays: Do elasmobranchs have self-awareness?

Article in *Journal of Ethology* · March 2016

DOI: 10.1007/s10164-016-0462-z

CITATIONS

25

READS

833

2 authors:



Csilla Ari

University of South Florida

55 PUBLICATIONS 735 CITATIONS

[SEE PROFILE](#)



Dominic P D'Agostino

University of South Florida

106 PUBLICATIONS 2,118 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Effect of ketone supplementation on CNS diseases [View project](#)



Non-adenosine nucleosides, LPS and WAG/Rij rats [View project](#)

# *Contingency checking and self-directed behaviors in giant manta rays: Do elasmobranchs have self-awareness?*

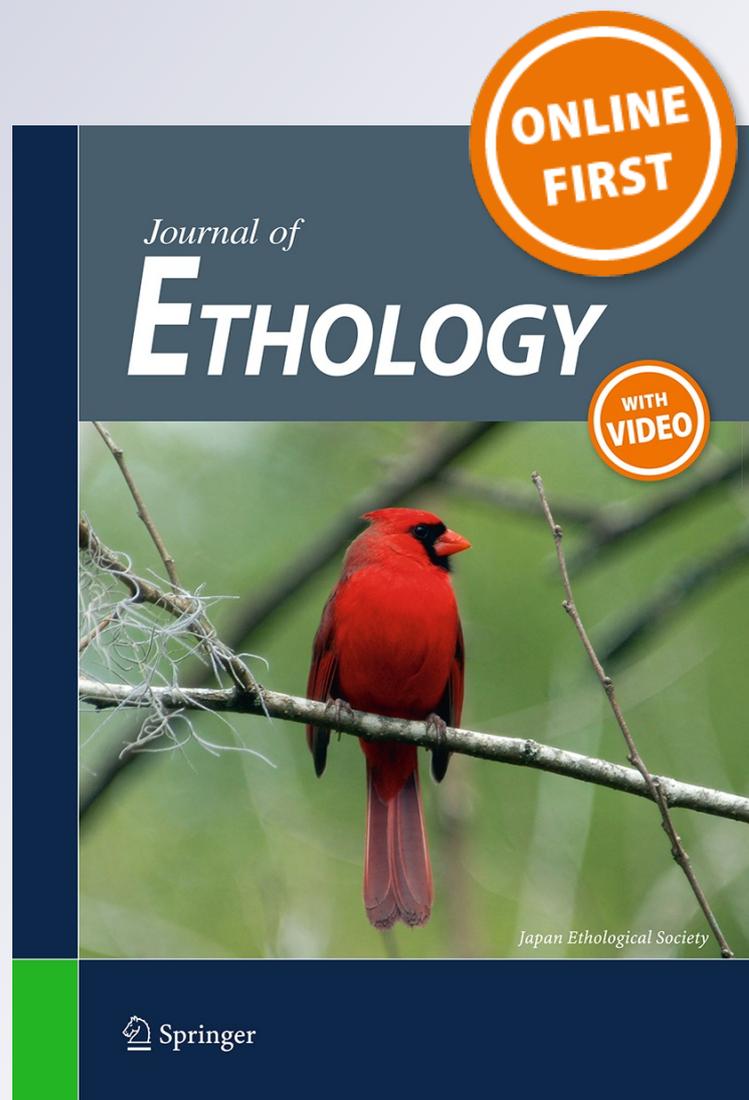
**Csilla Ari & Dominic P. D'Agostino**

**Journal of Ethology**

ISSN 0289-0771

J Ethol

DOI 10.1007/s10164-016-0462-z



**Your article is protected by copyright and all rights are held exclusively by Japan Ethological Society and Springer Japan. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Contingency checking and self-directed behaviors in giant manta rays: Do elasmobranchs have self-awareness?

Csilla Ari<sup>1,2,3</sup> · Dominic P. D'Agostino<sup>1,2,3</sup>

Received: 30 November 2015 / Accepted: 20 February 2016  
© Japan Ethological Society and Springer Japan 2016

**Abstract** Elaborate cognitive skills arose independently in different taxonomic groups. Self-recognition is conventionally identified by the understanding that one's own mirror reflection does not represent another individual but oneself, which has never been proven in any elasmobranch species to date. Manta rays have a high encephalization quotient, similar to those species that have passed the mirror self-recognition test, and possess the largest brain of all fish species. In this study, mirror exposure experiments were conducted on two captive giant manta rays to document their response to their mirror image. The manta rays did not show signs of social interaction with their mirror image. However, frequent unusual and repetitive movements in front of the mirror suggested contingency checking; in addition, unusual self-directed behaviors could be identified when the manta rays were exposed to the mirror. The present study shows evidence for behavioral responses to a mirror that are prerequisite of self-awareness and which has been used to confirm self-recognition in apes.

**Keywords** Self-recognition · Mirror test · Comparative cognition · Mobulidae · Cognition

**Electronic supplementary material** The online version of this article (doi:10.1007/s10164-016-0462-z) contains supplementary material, which is available to authorized users.

✉ Csilla Ari  
csari2000@yahoo.com

<sup>1</sup> Hyperbaric Biomedical Research Laboratory, Department of Molecular Pharmacology and Physiology, Morsani College of Medicine, University of South Florida, 12901 Bruce B. Downs Blvd., MDC 8, Tampa, FL 33612, USA

<sup>2</sup> Foundation for the Oceans of the Future, Budapest, Hungary

<sup>3</sup> Manta Pacific Research Foundation, Kona, HI, USA

## Introduction

Animal cognition is the process by which animals acquire, process, store and act on information gathered from the environment (Shettleworth 2010; Brown 2014). Consciousness includes sentience, intelligence and self-awareness (Brown 2014), or, in other words, awareness of internal and external stimuli, having a sense of self and some understanding of one's place in the world (Chandross et al. 2004; Bekoff and Sherman 2004; Brown 2014).

Animal consciousness has been a long-time interest and a debated field among cognitive ethologists (Heyes 1994, 1998; Povinelli et al. 1997). The mirror self-recognition (MSR) test initially developed by Gallup (1970) is considered to be a reliable behavioral index to show an animal's ability for self-recognition/self-awareness (SA; Platek and Levin 2004; Prior et al. 2008). Recognizing oneself in a mirror is a rare capacity among animals (Reiss and Marino 2001), while no species of fish has so far passed this test. There has been only one report on self-recognition in fish using chemosensory recognition (Thünken et al. 2009). However, studies conducted on other fish species reported that the response to their mirror images differed from responses to conspecifics (Verbeek et al. 2007; Desjardins and Fernald 2010; Suddendorf and Butler 2013; Balzarini et al. 2014). The only nonhuman species which demonstrated MSR are the great apes (i.e., chimpanzees, *Pan troglodytes*, *Pan paniscus*; orangutans, *Pongo pygmaeus*; gorilla, *Gorilla gorilla*), asian elephants (*Elephas maximus*), bottlenose dolphins (*Tursiops truncatus*) and a non-mammal species, the magpie (*Pica pica*) (Gallup 1970; Amsterdam 1972; Lethmate and Ducker 1973; Povinelli et al. 1993; Miles 1994; Patterson and Cohn 1994; Walraven et al. 1995; Prior et al. 2008).

Those species that passed the MSR test to date share common characteristics, such as large, complex and highly foliated brain, complex social behavior, cooperative and empathic behavior. The largest brain of all fish species is possessed by manta rays with high encephalization quotient and highly foliated cerebellum (Ari 2009, 2011), they often form large feeding aggregations suggesting complex social system, and are often referred to as being intelligent; therefore, manta rays may be considered the most likely candidates from any fish species to pass the MSR test. The universal use of this test has attracted controversy, because it is biased for vision, but not other sensory modalities. Although it has been suggested that olfactory recognition using chemical cues is more appropriate for fish (Thünken et al. 2009; Brown 2014), this might not be the case for Mobulids. Manta rays have exceptionally large optic tectum and telencephalon among elasmobranchs, and the high importance of vision during their foraging activity has also been recently described (Ari 2009, 2011; Ari and Correia 2008), which further supports the possibility that evaluating their self-awareness based on the MSR test is likely a suitable technique.

The definitive test of MSR is the mark test focusing the animal's behaviors on the newly marked area of their body when exposed to a mirror (Sarko et al. 2002). However, similarly to marine mammals, fish species also have the disadvantage that they are not able to touch the marked area of their body; therefore, it is more challenging to evaluate their behavioral response. Exploratory and social behavior can be observed at first when animals are exposed to a mirror, which stage is followed by contingency checking when the animals engage in highly repetitive or unusual movements to understand their own image. In the next stage, the animals might show self-directed behavior (e.g., dolphins blowing bubbles, chimpanzee picking teeth; Gallup 1970; Reiss 2012; Sarko et al. 2002; de Veer and van den Bos 1999), before the mark test would be initiated.

Mirror exposure experiments were conducted on two captive giant manta rays to document their responses to their mirror image in order to predict whether they would be a candidate for the mark test and whether they use a mirror to understand their own image. The present study shows evidence for manta rays' contingency checking and self-directed behavior when exposed to a mirror, which are the prerequisites of self-awareness.

## Materials and methods

### Subjects

Two giant manta ray specimens were exposed to a mirror at the Atlantis Aquarium, Bahamas, in March 2012 during a 16-day period. The first subject (M1) was a mature male

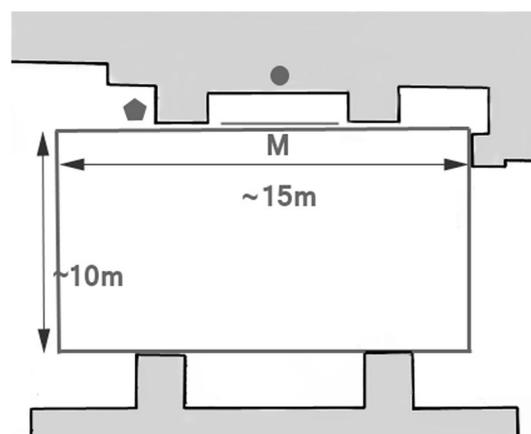
*Manta birostris* (estimated disc width 4.2 m) which had been living in the exhibit for over 2 years, while the second subject (M2) was a female (estimated disc width 3.3 m) that had been at the Aquarium for 1 year. This individual's taxonomical classification is uncertain to date, because her characteristics almost completely fulfill the criteria for *M. birostris*, except for a white mouth region, brownish back coloration and the lack of large white shoulder bars.

The two manta rays showed similar responses throughout the study, and therefore their data were merged in most cases during the representation of the results, unless there was significant difference between their behaviors, in which case their data are presented separately.

### Apparatus and procedure

The observation area (OA) was selected to be the widest area in the tank that was free of underwater decoration obstacles, where the animals were able to turn and maneuver comfortably when necessary (Fig. 1). The two manta rays' behavior was documented in a rectangular area of the tank (OA) that was approximately 10 m wide, 15 m long and 5.5 m deep, where the mirror was considered visible to the manta rays (Fig. 1).

Three experimental conditions were tested: (1) mirror placed in the water (MI); (2) control conditions when the mirror was either removed completely (MO), or (3) a mirror-sized, non-reflective white board was placed in the water (WB). Seven trials were performed in each experimental condition during 16 days. Each trial was conducted between feeding times and lasted for 10 min. The test was performed with a 0.9 m × 1.5 m mirror which was temporarily installed in a horizontal orientation on the side of



**Fig. 1** The observation area (OA, rectangle) of the tank is presented, where the mirror was considered visible to the manta rays, from dorsal view. The elongated tank continues on both sides for approximately 55 and 35 m (*M* mirror, *polygon* location of the underwater camera, *circle* location of the camera outside the tank)

the tank in the manta rays' regular swimming path,  $\sim 1$  m below water level. The placement of the mirror was made to ensure that the manta rays would have a frequent and predictable visual image of their reflection, and thus the potential to exhibit a behavioral response. The white board condition was achieved by reversing the mirror to the white surface facing the pool. The duration of the experimental sessions was between 10 and 50 min per day. The manta rays' behavior was video-recorded and viewed by two independent analysts. Observations during the study were recorded from inside the tank using a Canon S100 camera with Fisheye Fix S100 underwater housing and from outside the tank by using an Olympus FE360 camera.

The reported variables were determined as the total time spent in the observation area, number of cephalic fin movements and circling behavior in the observation area. A continuous record of the manta ray's behavior during each condition was also created for the total duration of the sessions, and the total time spent in the observation area was presented for every 10 min interval. The time of occurrence of specific behaviors, its onset (from a counter on the videotape), its duration and any additional comments were noted. The analysis of the video recordings were done by the independent observers.

Behavioral categories were identified, using the MSR test reported on bottlenose dolphins by Reiss and Marino (2001) and modified to manta ray specific behaviors, which are described in Table 1. Social behaviors (S) were defined when the animals were closely following, chasing or touching each other inside the OA. Surfacing behavior (when the animals swam up breaking the water surface) was considered to be feeding related behavior (F) independently of whether or not the mouth or cephalic lobes were open. Contingency checking behaviors (when the animal is testing to see whether, when it moves, the image also moves, CC) included performing unusual or repetitive body movements in front of the mirror while visually oriented to it (e.g., circling in front of the mirror, repetitive cephalic fin movements or bubble blowing in front of the mirror). Self-directed behavior (SD) occurs when a subject uses a mirror to investigate parts of its body that would not

be visible without the mirror while visually oriented to the mirror. Based on this definition which has been used in previous studies on dolphins, when a posture or movement exposing the ventral side to the mirror otherwise not visible to the animal could be observed, while the manta ray was visually oriented to the mirror, this behavior was identified as SD, while it could also be classified as CC. Other behaviors (O) that were unusual but not strictly classifiable included sudden speed or swimming direction change, stopping or twitching of fins.

Coding was done by two coders (C.A. and D.D.) who independently scored the same ten sessions. The coding of C.A. was considered the standard which was to be achieved by D.D. Coding was considered reliable when the sequence and duration of specific behaviors coded by C.A. and D.D. was of the same (duration could differ by a few seconds).

Statistical comparisons were made using an unpaired *t* test  $\pm$  standard error (SEM) with GraphPad Prism 6.

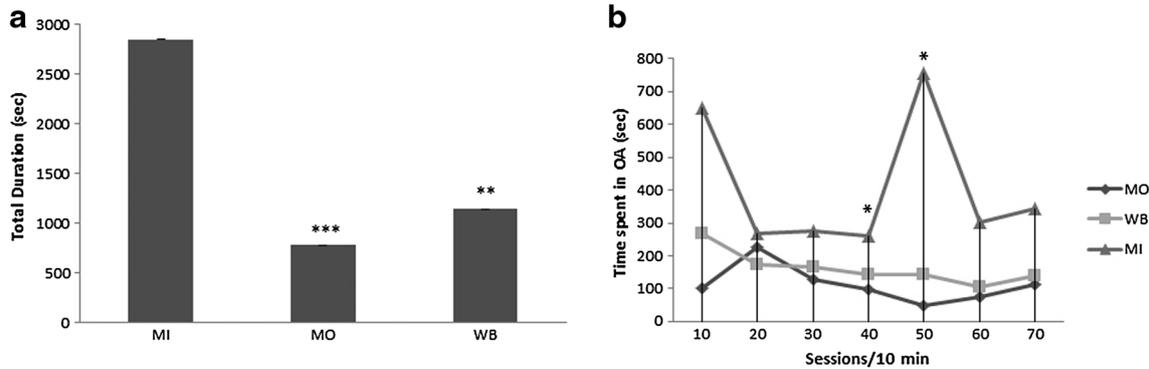
## Results

The manta rays spent 67.88 % of the total observation time in the OA when the mirror was in the tank, while they spent 18.54 % of the time in the OA when the mirror was not in the tank. Overall, the manta rays spent 265 % more time in the OA when the mirror was in compared to when the mirror was out of the tank (unpaired *t* test,  $P = 0.0001$ ,  $t = 4.086$ ,  $n = 28$ ; Fig. 2a). They also spent significantly more time in the OA than when WB was presented to them (unpaired *t* test,  $P = 0.0066$ ,  $t = 2.826$ ,  $n = 28$ ). The time the manta rays spent in the OA was not significantly different between the specimens, except when the white board was present (unpaired *t* test, MI:  $P = 0.384$ ,  $t = 0.879$ ,  $n = 28$ ; MO:  $P = 0.12$ ,  $t = 1.586$ ,  $n = 20$ ). In that condition, M2 spent more time in the OA compared to M1 (unpaired *t* test, WB:  $P = 0.0002$ ,  $t = 4.282$ ,  $n = 15$ ).

The average duration of time spent at the mirror was also measured for every subsequent 10-min interval. During the first 10 min, the manta rays spent 549 % more time at the mirror, which decreased during the 2–4th sessions.

**Table 1** Description of behavioral categories used during the study

Behavioral category	Abbreviation	Definition/examples
Social	S	Closely following, chasing or touching each other
Feeding related	F	Surfacing behavior
Contingency checking	CC	Unusual or repetitive behavior while visually oriented to the mirror, e.g., circling in front of the mirror, repetitive cephalic fin movement, bubble blowing
Self-directed	SD	Posture or movement exposing the ventral side/a body part to the mirror that otherwise would not be visible without the mirror while visually oriented to the mirror
Other behaviors not strictly classifiable	O	Sudden change in swimming speed or direction, body twitching



**Fig. 2 a** The manta rays (*Manta birostris*) spent significantly more time in the observation area when the mirror was placed in the water compared to control conditions. **b** During the first 10-min session, the manta rays spent 549 % more time at the mirror than without the mirror. The time spent in the OA was significantly more in the 3rd,

5th and 6th 10-min sessions when the mirror was present, compared to control conditions. *MI* mirror in the tank, *MO* mirror out of the tank, *WB* white board in the tank, \* $P < 0.05$ ; \*\* $P < 0.005$ ; \*\*\* $P < 0.0005$

Following the 4th session, the time increased again by more than 1400 % within the period of the 5th session which was significantly higher in the 4–5th sessions than in the control conditions (unpaired  $t$  test, 40 min MI/MO:  $P = 0.018$ ,  $t = 3.244$ ,  $n = 4$ ; 50 min MI/MO:  $P = 0.0297$ ,  $t = 2.641$ ,  $n = 5$ ; Fig. 2b).

During the time spent at the mirror, their cephalic fin movements were frequent, and they opened their cephalic fins significantly more often when the mirror was in the tank, compared to when the mirror was removed (unpaired  $t$  test, MI/MO:  $P < 0.0001$ ,  $t = 5.954$ ,  $n = 19$ ; MI/WB:  $P < 0.0001$ ,  $t = 4.677$ ,  $n = 19$ ; Fig. 3a). They also closed their cephalic fins more often when the mirror was in the tank, compared to when the mirror was removed (unpaired  $t$  test, MI/MO:  $P < 0.0001$ ,  $t = 6.142$ ,  $n = 18$ ; MI/WB:  $P < 0.0001$ ,  $t = 5.363$ ,  $n = 18$ ; Fig. 3a).

The manta rays showed significantly higher frequency of other repetitive behavior, such as circling at the mirror when the mirror was placed in the tank compared to either control conditions (unpaired  $t$  test, MI/MO:  $P = 0.0006$ ,  $t = 3.776$ ,  $n = 19$ ; MI/WB:  $P = 0.0012$ ,  $t = 3.51$ ,  $n = 19$ , Fig. 3b).

No aggressive displays by any of the specimens were seen towards the mirror. Social/sexual behaviors remained at a low frequency throughout the study with following each other at four occasions and touching each other by their cephalic fins two times. No rapid coloration changes were observed and the white markings on the back and head of the animals did not intensify in response to the mirror on either of the specimens (Fig. 4a, b), as previously reported to occur during feeding, intense social interaction and in response to the presence of a new individual (Ari 2014).

Feeding-related (MI:14; MO:3; WB:2), mirror-directed, self-directed, and other unusual behaviors together (MI:22;

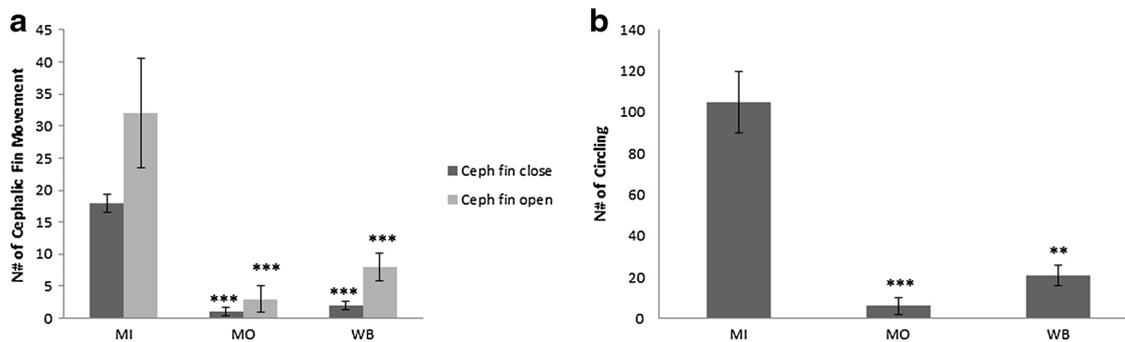
MO:2; WB:3) were more frequent when the mirror was present compared to when the mirror was absent (unpaired  $t$  test,  $P = 0.0294$ ,  $t = 2.539$ ,  $n = 6$ ) or when the white board was present (unpaired  $t$  test,  $P = 0.0251$ ,  $t = 2.631$ ,  $n = 6$ ; Table 2). Speed change was divided into unusually slow or fast swimming and stopping/stationing behaviors. More frequent slow swimming (MI:7; MO:0; WB:1) and even more frequent fast swimming (MI:17; MO:3; WB:0) could be observed when the mirror was present. Swimming up and surfacing behaviors happened more often when the mirror was present (MI:20; MO:4; WB:5).

Some contingency checking (CC) and SD behaviors were exclusively present when the mirror was in the tank, which included body turns into a vertical direction, exposing the ventral side of the body to the mirror while visually oriented to it (MI:3; MO:0; WB:0) and bubble blowing (MI:2; MO:0; WB:0) in front of the mirror, while other, repetitive behaviors were more frequent, such as cephalic fin movements and circling (Fig. 3). Figure 4 and Movies 1–5 of the Electronic Supplementary Material show some of the behaviors observed with and without the mirror.

These spontaneous CC and SD behaviors could be observed in both individuals except exposing the ventral side and bubble blowing which was performed by only one of them (M2).

## Discussion

The present study provides a qualitative and quantitative description of two manta rays' behavioral responses in front of a mirror by employing protocols adapted from primate and bottlenose dolphin MSR studies. Similar to that observed in primate studies, the manta rays showed



**Fig. 3** The frequency of repetitive behaviors: **a** cephalic fin movements and **b** circling in front of the mirror was significantly higher when the mirror was present compared to control conditions. *MI*

mirror in the tank, *MO* mirror out of the tank, *WB* white board in the tank,  $**P < 0.005$ ;  $***P < 0.0005$

exploratory, contingency checking and self-directed behavior when exposed to the mirror. Intelligence is often defined as behavioral flexibility, by abilities such as reasoning, planning, learning from past experiences and applying this knowledge to solve problems in novel contexts (Brown 2014). To assess the intelligence (cognitive complexity) of an animal, since it is difficult to measure mental states or feelings, subjective behavioral responses that imply consciousness are measured instead (Dawkins 2001; Brown 2014).

The presented data show that the manta rays gave selective attention to the mirror by displaying significantly more repetitive movements than in control conditions and several unusual contingency checking behaviors exclusively at the mirror. The manta rays' white markings on their back and head did not change; it was recently described that the white markings rapidly increase in intensity when a ray meets a new individual (Ari 2014). Therefore, we can speculate that the animals did not perceive their mirror image as a new individual, suggesting that the observed behaviors in the OA were not part of social behaviors towards the mirror. Aggressive behavior directed specifically toward the mirror could not be identified.

Social behaviors between the animals remained at extremely low frequency during exposure to the mirror which is similar to what was found with bottlenose dolphins (Reiss and Marino 2001). Gallup (1970) and Povinelli et al. (1993) also showed that, in chimpanzees, social responsiveness declines and contingency checking increases over time of exposure to the mirror.

Cephalic fin movements, especially on the side that was facing the mirror, increased greatly in frequency, which might suggest that manta rays used their cephalic fin movements for contingency checking (testing to see whether when it moves, the image also moves). It is also possible that the cephalic fin movements are helping the exploration of new objects, so their role is not exclusively

channeling plankton into their mouth during foraging. Bubble blowing behavior was never observed other than during *MI* condition, suggesting that bubble blowing while staying visually oriented to the mirror was possibly contingency checking.

Among other marine species, in killer whales (*Orcinus orca*) and false killer whales (*Pseudorca crassidens*; DeFleur and Marten 2001) the response to an applied mark on their body is likely not the only proof of SA, especially if indeed many levels of self-consciousness exist. An African Grey parrot (*Psittacus erithacus*) was described as exhibiting mirror mediated object discrimination in an earlier study (Pepperberg et al. 1995), while all monkey species so far tested (Anderson 1986; Itakura 1987) have been shown to exhibit mirror-guided behavior (i.e., using the mirror to guide a part of their body towards hidden food; Sarko et al. 2002), but no compelling evidence was found in these species for CC and/or SD responses. In humans and great apes, CC behaviors are represented as repetitive head or hand motions (Povinelli et al. 1993), while in dolphins CC behaviors usually involved head or body cocking, repetitive horizontal and vertical head movements, and head circling (Reiss and Marino 2001; Marino et al. 1994). In dolphins, SD behavior was represented as unusual neck stretching, body flexing and bubble blowing (Reiss and Marino 2001; Marino et al. 1994), a behavior which resembles manta rays exposing their ventral surface to the mirror and bubble blowing in front of the mirror. Contrary to studies of chimpanzees reported by Gallup (1970) and others, the manta rays showed a decrease in the amount of time at the mirror after the first two sessions, but after the 4th session it dramatically increased. This trend was similar to that observed in bottlenose dolphins (Sarko et al. 2002). In apes, SD behavior in response to a mirror has been taken as evidence of self-recognition (Prior et al. 2008); therefore, the recorded observations on manta rays possibly show their ability to self-awareness. However, to further confirm this



**Fig. 4** **a, b** Manta rays swim in front of the mirror; **c, d** Displaying the ventral side to the mirror while staying visually oriented; **e** surfacing behavior; **f** opening of cephalic fin in front of the mirror;

**g, h** Bubble blowing behavior in front of the mirror while displaying the ventral side and staying visually oriented (*M* the location of the mirror, *large arrows* point to bubbles)

possibility, a MSR mark test might need to be completed and more animals will need to be tested. Although the full MSR test could not be completed due to technical difficulties, previous studies suggest that those individuals that showed mark-directed behavior were the same that had shown a high interest in the standard mirror exploration test (Prior et al. 2008).

Primates, cetaceans and elasmobranchs all possess elaborated brains which show a dispersed morphological

convergence that may also be linked to cognitive convergence. Social intelligence is also believed to be an explanation for the evolution of the primate brain (Whiten and Byrne 1997). The brain of elasmobranchs has analogous structures and functions similar to other vertebrates; for example, the telencephalic dorsal pallium in fish, which is greatly enlarged in Mobulids (Ari 2011), is considered to be homologous to the tetrapod hippocampus, amygdala and neocortex (Broglio et al. 2011; Demski 2013; Brown

**Table 2** Summarized frequencies of feeding-related and other behaviors

	Feeding-related		Speed change				Stopping		Direction change			
	M1	M2	Slow		Fast		M1	M2	Up		Down	
			M1	M2	M1	M2			M1	M2	M1	M2
MI	5	9	1	6	10	7	1	1	7	13	1	0
MO	1	2	0	0	2	1	0	0	1	3	0	0
WB	2	0	0	1	0	0	0	0	3	2	0	0

Unpaired *t* test, MI/MO:  $P = 0.0294$ ,  $t = 2.539$ ,  $n = 6$ ; MI/WB:  $P = 0.0251$ ,  $t = 2.631$ ,  $n = 6$

MI mirror in the tank, MO mirror out of the tank, WB white board in the tank, M1 Manta1, M2 Manta2

2014). Those species with elaborated brains that have passed the MSR test to date, have large, complex and highly foliated brains, complex social behaviors, cooperative behaviors and the ability to empathize (Reiss 2012; Plotnik et al. 2006). If manta rays are entering the small group of species with self-awareness, we might speculate that they also share the same common characteristics and are able to perform complex social understandings, cooperative and empathic behaviors.

Self-recognition is also essential for the ability to use one's own experience to predict the behavior of conspecifics (Prior et al. 2008) which might be a unique ability for an elasmobranchs species. However, these findings should be interpreted with caution because of the small sample size and because the MSR test might demonstrate only a specific level of consciousness (Panksepp 2005; Brown 2014).

Studies on fish intelligence are largely restricted to bony fishes, while we have very little knowledge about the cognitive abilities of sharks and rays (Brown 2014). Therefore, these results on manta ray cognition are aimed at stimulating new research directions. In addition, the perception of an animal's cognitive abilities and intelligence influences the views and drives decisions about captive animal welfare and wildlife conservation. Therefore, our hope is that a greater understanding of manta rays' cognitive abilities will support the rationale for protective legislation in the future.

## Conclusion

This paper presents the first analysis of manta rays' behavioral response to a mirror, including the description of their contingency checking and self-directed behaviors which can serve as a basis for similar studies with manta rays and other elasmobranchs in the future. Further studies are needed to assess whether the mirror-induced, self-directed behavior is atypical or frequent in manta rays and whether manta rays are the first elasmobranch species to exhibit self-awareness, which would imply their potential

for an ability to higher order brain function, and sophisticated cognitive and social skills.

**Acknowledgments** This study was funded by the Save Our Seas Foundation. We are very grateful to Michelle Liu, Dave Wert and the staff of the Aquarium for the possibility and logistical support to conduct this research at the Atlantis Aquarium, Bahamas. The Divers Alert Network Europe and Dr. Huntington Potter provided essential support. The observations during this study were in compliance with all ethical standards and were approved by the Kerzner Marine Foundation and the Atlantis Aquarium, Bahamas. We thank three anonymous reviewers for their thoughtful comments on the manuscript.

## References

- Amsterdam B (1972) Mirror image reactions before age two. *Dev Psychobiol* 5:297–305
- Anderson JR (1986) Mirror-mediated finding of hidden food by monkeys (*Macaca tonkeana* and *M. fascicularis*). *J Comp Psychol* 100:237–242
- Ari C (2009) On the brain of cartilaginous fishes: cerebralization, astroglial architecture and blood-brain barrier composition. Lambert, Saarbrücken
- Ari C (2011) Encephalization and brain organization of mobulid rays (Myliobatiformes, Elasmobranchii) with ecological perspectives. *Open Anat* 3:1–13
- Ari C (2014) Rapid coloration changes of manta rays (Mobulidae). *Biol J Linn Soc* 113:180–193
- Ari C, Correia JP (2008) Role of sensory cues on the food searching behaviour of a captive *Manta birostris* (Myliobatiformes, Mobulidae). *Zoo Biol* 27(4):294–304
- Balzarini V, Taborsky M, Wanner S, Koch F, Frommen J (2014) Mirror, mirror on the wall: the predictive value of mirror tests for measuring aggression in fish. *Behav Ecol Sociobiol* 68:871–878
- Bekoff M, Sherman PW (2004) Reflections on animal selves. *Trends Ecol Evol* 19:176–180
- Broglio C, Gómez A, Durán E, Salas C, Rodríguez F (2011) Brain and cognition in teleost fish. In: Brown C, Krause J, Laland K (eds) *Fish cognition and behavior*. Wiley, Oxford, pp 325–358
- Brown C (2014) Fish intelligence, sentience and ethics. *Anim Cogn* 18:1
- Chandroo KP, Yue S, Moccia RD (2004) An evaluation of current perspectives on consciousness and pain in fishes. *Fish Fisheries* 5:281–295
- Dawkins MS (2001) Who needs consciousness? *Anim Welfare* 10(Suppl1):19–29

- de Veer M, van den Bos R (1999) A critical review of methodology and interpretation of mirror self-recognition research in non-human primates. *Anim Behav* 58:459–568
- Delfour F, Marten K (2001) Mirror image processing in three marine mammal species: Killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*) and California sea lions (*Zalophus californianus*). *Behav Process* 53:181–190
- Demski LS (2013) The pallium and mind/behavior relationships in Teleost fishes. *Brain Behav Evol* 82:31–44
- Desjardins JK, Fernald RD (2010) What do fish make of mirror images? *Biol Lett* 6:744–747
- Gallup GG (1970) Chimpanzees: self-recognition. *Science* 167:86–87
- Heyes CM (1994) Reflections on self-recognition in primates. *Anim Behav* 47:909–919
- Heyes CM (1998) Theory of mind in nonhuman primates. *Behav Brain Sci* 21:101–114
- Itakura S (1987) Mirror guided behavior in Japanese monkeys (*Macaca fuscata fuscata*). *Primates* 28:149–161
- Lethmate J, Ducker G (1973) Untersuchungen zum Selbsterkennen im Spiegel bei Orangutans und einigen anderen Affenarten. *Z Tierpsychol* 33:248–269
- Marino L, Reiss D, Gallup G (1994) Mirror self-recognition in bottlenose dolphins: Implications for comparative investigations of highly dissimilar species. In: Parker S, Boccia M, Mitchell R (eds) *Self-awareness in animals and humans: Developmental perspectives*. Cambridge University Press, New York, pp 273–290
- Miles HL (1994) Me Chantek: The development of self-awareness in a signing orangutan. In: Parker S, Boccia M, Mitchell R (eds) *Self-awareness in animals and humans: Developmental perspectives*. Cambridge University Press, New York, pp 254–272
- Panksepp J (2005) Affective consciousness: core emotional feelings in animals and humans. *Conscious Cogn* 14:30–80
- Patterson F, Cohn R (1994) Self-recognition and self-awareness in the lowland gorilla. In: Parker S, Boccia M, Mitchell R (eds) *Self-awareness in animals and humans: Developmental perspectives*. Cambridge University Press, New York, pp 273–290
- Pepperberg IM, Garcia SE, Jackson EC, Marconi S (1995) Mirror use by African Grey parrots (*Psittacus erithacus*). *J Comp Psychol* 109:182–195
- Platek SM, Levin SL (2004) Monkeys, mirrors, mark tests, and minds. *Trends Ecol Evol* 19:406–407
- Plotnik JM, de Waal FBM, Reiss D (2006) Self-recognition in an Asian elephant. *Proc Natl Acad Sci USA* 103:17053–17057
- Povinelli DJ, Rulf AB, Landau K, Bierschwale DT (1993) Self-recognition in chimpanzees. *J Comp Psychol* 107:347–372
- Povinelli DJ, Gallup GG, Eddy TJ, Bierschwale DT, Engstrom MC, Perilloux HK, Toxopeus IB (1997) Chimpanzees recognize themselves in mirrors. *Anim Behav* 53:1083–1088
- Prior H, Schwarz A, Güntürkün O (2008) Mirror-induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS Biol* 6(8):e202. doi:10.1371/journal.pbio.0060202
- Reiss D (2012) The dolphin in the mirror: exploring dolphin minds and saving dolphin lives. Houghton Mifflin Harcourt, New York
- Reiss D, Marino L (2001) Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proc Natl Acad Sci* 98:5937–5942
- Sarko D, Marino L, Reiss D (2002) A bottlenose dolphin's (*Tursiops truncatus*) responses to its mirror image: further analysis. *Int J Comp Psychol* 15(1):69–76
- Shettleworth SJ (2010) *Cognition, evolution, and behaviour*, 2nd edn. Oxford University Press, Oxford
- Suddendorf T, Butler DL (2013) The nature of visual self-recognition. *Trends Cogn Sci* 17:121–127
- Thünken T, Waltschyk N, Bakker T, Kullmann H (2009) Olfactory self-recognition in a cichlid fish. *Anim Cogn* 12:717–724
- Verbeek P, Iwamoto T, Murakami N (2007) Differences in aggression between wild-type and domesticated fighting fish are context dependent. *Anim Behav* 73:75–83
- Walraven V, van Elsacker L, Verheyen R (1995) Reactions of a group of pygmy chimpanzees (*Pan paniscus*) to their mirror images—evidence of self-recognition. *Primates* 36:145–150
- Whiten A, Byrne RW (1997) *Machiavellian intelligence II: extensions and evaluations*. Cambridge University Press, Cambridge