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REVIEW

Cognition of the manatee: past research and future developments

Yann Henaut[1] · Aviva Charles[2,3] · Fabienne Delfour[4]

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Abstract

In this paper, we present a review of the current knowledge related to the cognitive abilities of the manatee, with a focus on the Antillean manatee in situ and ex situ. Following a biocentric approach, we consider the animals' ecology, perception and sociality and we introduce future perspectives on their cognition. Scientific literature on the cognitive abilities of Antillean manatees' is limited and mainly linked to medical training and veterinary manipulations. To perceive and to interact with their social and natural environment (e.g. social interactions, foraging and traveling), manatees use visual, acoustic and tactile modalities that may be involved in a large range of cognitive abilities. Research on stimuli perception in manatees is scarce; however, these animals demonstrate abilities to learn and appear to show long-term memory. For example, to mate and/or to forage manatees travel at medium and large geographical scales; without doubt their movements entail the use of a set of stimuli and learning processes. Furthermore, their social skills (e.g. social organization, tactile and acoustic communications) are also poorly understood although their social interactions appear to be more complex than previously thought. Finally, as for many animals, temperament/personality may play a key role during their interactions with conspecifics and the environment. These aspects on manatee behavior and cognition are important for management and conservation purposes and help us understand the evolution of these marine mammals.

Keywords Antillean manatee · Cognition · Communication · Marine mammals · Perception

Introduction

Species and geographical range of manatees

There are four existing manatees' species described throughout the world: two species inhabit freshwater environments in the Amazon basin; the Amazonian manatee, *Trichechus inunguis,* and the dwarf manatee *Trichechus pygmaeus*. *T. pygmaeus* is a disputed species closely related to the Amazonian manatee that can only be found in the river Aripuaña (Rosas 1994; Vianna et al 2006; van Roosmalen 2015). The West African manatee *Trichechus senegalensis* is distributed from Senegal to Angola and as for *T. inunguis* and *T. pygmaeus*, it is poorly studied (Vianna et al 2006). Finally, the West Indian manatee (*Trichechus manatus*) lives mostly in shallow coastal areas, including rivers and estuaries and is distributed along Florida coasts to Brazil and around the Caribbean islands and divided in two subspecies. This work mainly focuses on the two *Trichechus manatus* subspecies, the Florida manatee (*Trichechus manatus latirostris*), the most studied, and the Antillean manatee (*Trichechus manatus manatus*) that are closely related. Information on *T.manatus latirostris*'s various aspects of biology and behavior may be useful in opening perspectives for the study of the Antillean manatee as well as for other understudied species, even though they are not the focus of this research. The endangered Antillean Manatee (*Trichechus manatus manatus)*, the southern subspecies of the West Indian manatee, is a large aquatic herbivore mammal living in coastal waters, estuaries or rivers from Mexico, Central America to Brazil (Lefebvre et al. 2001). The other subspecies, the Florida manatee (*Trichechus manatus latirostris*), inhabits a more

✉ Yann Henaut
yhenaut@ecosur.mx

1 Laboratorio de Conducta Animal, GAIA-BIO, El Colegio de la Frontera Sur (ECOSUR), Av. del Centenario Km. 5.5, C.P. 77014 Chetumal, Quintana Roo, Mexico

2 Centre d'Ecologie et des Sciences de la Conservation (CESCO, UMR 7204, CNRS, MNHN, Sorbonne-Université, MNHN), Paris, France

3 ZooParc de Beauval and Beauval Nature, 41110 Saint Aignan, France

4 Ecole Pratique des Hautes Etudes, 75005 Paris, France

restrictive geographical range, predominantly along the coasts of Florida (Lefebvre et al. 2001). The two subspecies are separated morphologically (Domning and Hayek 1986) and genetically, and according to genetic studies, rare individual migrations occur between the Florida and the Antillean manatees (Nourisson et al. 2011). For example, a recent observation during the winter 2020–2021 showed that one individual from Florida visited the Mexican coast close to Cancún (Castelblanco-Martínez et al. 2021). On the other hand, the Antillean manatee inhabit a diverse range of ecosystems. For example, in the Caribbean Coast of Mexico and Belize, the subspecies lives in clear saltwater, visiting reefs, freshwater lagoons and rivers while in other areas (e.g. Tabasco states, Chiapas or along the coasts of South America) they live in fresh or salt waters with poor visibility (Corona Figueroa et al. 2021; Castelblanco-Martínez et al. 2012; Rodas-Trejo 2008). Manatees (all species) eat a large range of aquatic plants (Alves-Stanley et al. 2010) such as sea grasses (for example: *Halodule wrightii* and *Thalassia testudinum*) or red mangrove (*Rhizophora mangle*) (Castelblanco-Martínez et al. 2009). Their presence and movements are highly dependent on food resources and freshwater availability, both playing an important role in their distribution across seasons (Favero et al. 2020).

Perception

Manatees' vision appears to be dichromatic: they distinguish blue and green from greys (Griebel and Schmid 1996) and they possess the ability to discriminate brightness (Griebel and Schmid 1997). Studies on Florida manatees suggest that they may use vision at medium and long distances (Bauer et al. 2003). A study conducted on an Antillean manatee showed that they appear to use their vision to detect and to discriminate underwater geometrical forms at short distances (Henaut et al. 2020). The West Indian manatees' audiogram shows wide auditive capacities, previously considered through anatomical studies (Gerstein and Gerstein 1999). Their high-frequency sensitivity may be an adaptation to shallow water where low-frequency sound propagation is limited (Gerstein and Gerstein 1999). Manatees not only respond to underwater sounds, but are able to detect aerial sounds as observed with drones (Antillean ssp, Landeo-Yauri et al. 2021). Considering their olfactory abilities, male Florida manatees appear to use chemoreception to detect females in estrus, their anal gland being the principal source of signal expression (Bills et al. 2013). Taste also seems to be an important perceptive component for manatees' sensory system as they seem able to detect salt gradients, freshwater and a sense of bitter related to toxic food (Barboza and Larkin 2020). Tactile sense is one of the most important sensory channels in manatees, with the presence of vibrissae on the snout, body and around the mouth (Fig. 1). Tactile sensors

Fig. 1 Vibrissae present around the mouth and on the overall body

are also present on their lips and tongue (Lucchini et al. 2021). Perioral bristles are used during grasping but are also involved together with lips for manipulating objects, termed "oripulation" (Reep et al. 2001) (Video 1). The vibrissae are also used in tactile exploration to discriminate various object textures (Gaspard III et al. 2013; Bauer et al. 2012). Exploration and manipulation are not the only functions of vibrissae, manatees seem to be able to detect water movements (i.e. hydrodynamic stimuli) using their facial vibrissae (Gaspard et al. 2013; Reep et al. 2011) a characteristic found in several mammals such as semi-aquatic otters for underwater hunting. Manatees' sense of touch is involved not only in environment exploration or feeding, but also in self-maintenance (i.e. parasite removal) and in social interactions especially but not exclusively between mothers and calves (Lucchini et al. 2021) (Fig. 2). In captive Antillean manatees, tactile behavior frequencies may be influenced by the sex of individuals and are observed during social interactions (e.g. body/mouth/snout/tail/flipper touching, embracing, pushing), exploration (e.g. interacting with wall/gate, hanging objects, checking objects, slapping water) and self-maintenance behaviours (e.g. spinning, chewing flippers, moving mouth) (Lucchini et al. 2021).

Sociality

Manatees are generally considered as a solitary or a semi-social species, and their social organization remains unclear. The only social units in manatees are constituted by mother-calf pairs, with calves displaying nursing behavior until they reach 4 years old (Anderson 2002). During winter, they gather in warm waters, as observed in Florida manatees with groups of several hundred individuals, or around fresh water or food sources with groups frequently observed reaching 5 individuals (Henaut Y. personal observations on Antillean manatees in Mexican Caribbean). In Florida manatees, mating herds of up to 22 individuals have been observed with

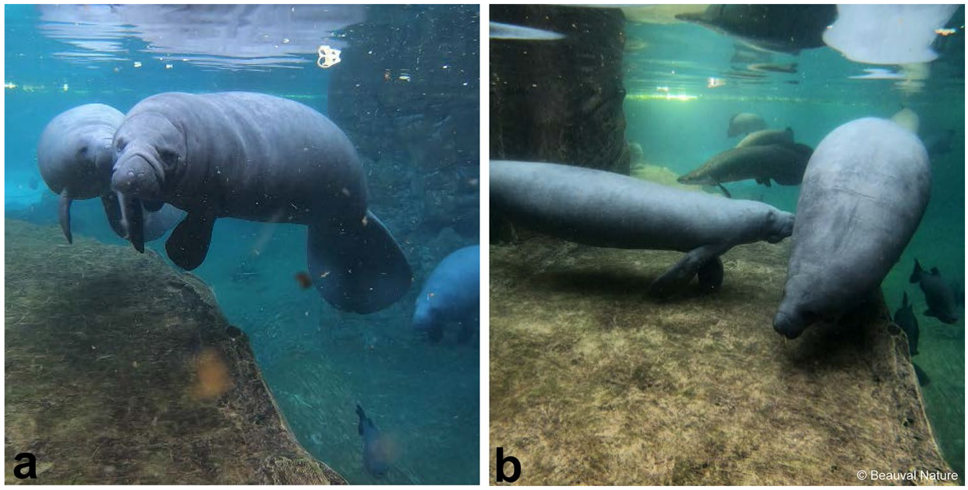

Fig. 2 Tactile interaction between (**a**) an adult female and a young Antillean manatee and (**b**) between two male Antillean manatees

groups of males following one receptive female (Reep and Bonde 2006; Rathbun et al. 1995). Flight surveys in Belize and Chetumal Bay (Mexico) showed that solitary manatees represent 62,8% of observations and 37.2% of individuals were observed in groups of 2 (including mother and calf pairs) to 11 individuals (Morales-Vela et al. 2000). There is a dearth of studies related to manatees' social interactions in the wild and papers found in the scientific literature are conducted mostly in captive settings. For example, captive female Florida manatees associate and interact with specific individuals, tend to form subgroups within the same pool and appear to display long-term associations (Harper and Schulte 2005). These strong associations between adults have also been observed in wild manatees in Sarasota bay (Florida). A high level of interactions between captive adult Antillean manatees, whether males or females, has also been observed (Henaut et al. 2010). For both subspecies (*T.m. latirostris* and *T.m. manatus*), agonistic interactions were rarely reported between individuals, suggesting a high degree of tolerance. These studies describing the high occurrences of social interactions between individuals suggest that manatees may be more social than previously considered.

Evolution

Manatees and dugongs remain the only representatives of the Sirenian order and are evolutionary close to elephants (*Elephantinae*) (Murata et al. 2003). They diverged from their common ancestor when placental mammals were separated after the K/T boundary (Murata et al. 2003). Even if manatees and cetaceans (i.e. dolphins, whales and porpoises) present morphological similarities probably due to similar environmental pressures, cetaceans are more closely related to hippos, ruminants and pigs than manatees but diverged at the same time during the Cenozoic era (Murata et al. 2003). In keeping with public perception, elephants are reported to have good cognitive capacities (Byrne et al. 2009) and are known for their excellent memory and cognitive maps. However, there is also a common perception that manatees are not very intelligent giants: they are for example called "sea cow" and cows supposedly show low intelligence (Davis and Cheeke 1998). In Crystal River (Florida), first observations of Florida manatees concluded that they do not need to perform complex behaviors because of the lack of natural predators and their evolution in areas with abundant food and stable conditions (Hartman 1979). Compared to other marine mammals, the brain of a West Indian manatee is small and represents 0.04% of their body weight (1.038% for *T. truncatus*) but in Sirenians, body size reflects the necessity of a large gut to process food, independent of the brain size (Würsig 2009). According to scientific and conservationist research, public perception on manatees is changing and manatees are now considered as friendly, shy, inoffensive, curious or intelligent (Goedeke 2004).

Aims of the paper

The growing number of research papers on the ecology and behaviour of the Antillean manatee is changing perspectives of the cognitive abilities of these animals. Despite the importance of cognition studies for the management and conservation of these aquatic mammals, there is little research related to cognition on West Indian manatees and it is particularly rare for the Antillean subspecies. Recent research on several aspects of manatee cognition (i.e. learning abilities, spatial cognition, or individual recognition) offer new perspectives on the implication of these potential cognitive abilities for manatee ecology and behavior. The Darwinian perspective is an important approach for the understanding of animal cognition, considering sociality, ecology and life history of one given species. This biocentric view on animal cognition allows us to avoid an anthropocentric viewpoint that would limit perspectives and generate experimental biases (see Bräuer et al. 2020). This viewpoint emphasizes the significance of ecological, perceptive and social perspectives of one given species to test hypothesis and to design experiments for cognitive studies (Byrne and Bates 2007). Consequently, the aim of this paper is to provide a detailed review on manatees' cognition, with a focus on Antillean manatees. More specifically, we explore the current knowledge on manatee life history, socio-ecology and the few existing studies on cognition, to construct assumptions related to the evolution of cognitive abilities in these aquatic mammals and finally to generate future perspectives.

We also discuss the relevance and implications of past and future research on manatees' cognition in the fields of animal welfare and conservation as well as their contribution to our understanding of cognition evolution across species.

Evidence for associative learning in manatees

According to animal caretakers working in zoos (Y. Henaut, personal observations), manatees are easier to train than bottlenose dolphins (*Tursiop truncatus)*, despite the general consideration that dolphins are intelligent and possess a large brain which is often compared to the human brain (Würsig 2009; Herman 2006; Lima et al. 2005). The manatees' trainability might be linked to their motivation for food and to their docility (Lima et al. 2005). Nevertheless, the decrease in session duration across sessions (i.e. decreasing learning curve) suggests that manatees are capable of learning, i.e. to associate a particular behavior to its reward. Sirenians display learning abilities and play behaviours in zoos but not at the same level as dolphins (Würsig 2009). However, this might be difficult to ascertain as mentioned by this author, due to the lack of studies on sirenians compared to other aquatic mammals such as dolphins. Several studies using trained behaviors in Florida manatees to investigate their perceptive abilities (mainly tactile and auditive) (Griebel and Schmid 1997, 1996; Gaspard et al. 2013) revealed that manatees possess excellent learning capacities (Gerstein 1994). In Antillean manatees, behavioral training based on positive reinforcement is used to facilitate veterinary manipulations and biological sample collections by inducing specific body positions. The training is primarily reinforced with food but also with verbal praise and sound (e.g. whistle) (Lima et al. 2005). The caretakers' personality, attitude and behaviors also appeared to be linked to the manatees' performance during training (Lima et al. 2005). In a study conducted on one single Antillean manatee, Henaut et al. (2020) observed that the animal was very curious, visually inspecting and touching geometrical forms underwater. It quickly learned to associate a specific visual form with a food reward, using the information acquired in other contexts (for example in another area) and after long periods of time (i.e. 1 year). The association between particular geometrical forms and food presence lasted one year without reinforcement, indicating a long-lasting memory capacity in manatees. However, there are very few studies on learning and memory abilities in manatees (both Florida and Antillean species) in comparison with other aquatic mammals (Henaut et al. 2020; Würsig 2009).

Ecological drivers for spatial cognition: navigation, location memory, mapping

Manatees are widely distributed, meaning that they are distributed over a large geographical area. Manatees, and especially Antillean manatees, are well adapted to navigate in various aquatic habitats. This ability could be linked to their use of multiple sensory channels: vision, hydrodynamic detection of water movement (e.g. currents), sensitivity to water chemical quality, salinity or other stimuli that involve chemoreception or audition. Their multisensorial integration may allow them to orient themselves and to travel in various environments with different chemical characteristics, currents or with variability in underwater visibility (Corona Figueroa et al. 2021; Castelblanco-Martínez et al. 2012; Rodas-Trejo 2008). In addition to these sensory drivers, cognitive abilities (e.g. memorization, learning abilities, mapping) might be applied to find conspecifics, food and fresh water to survive. These abilities are commonly observed in mammals, as in the case of their relative (i.e. elephants) which use a range of stimuli and possess cognitive mapping skills linked to a very well-developed memory for locations (Byrne et al. 2009). As observed in several animal species, patterns of displacements probably imply cognitive skills such as memorization and mapping during navigation (Geva-Sagiv et al. 2015; Byrne et al. 2009; Janson and Byrne 2007). For instance, elephants are able to maintain and regularly update information on the location of other group members during group movements based on their urine deposits (Byrne et al. 2009). Since Antillean manatees are often observed in groups (Morales-Vela et al. 2000), we may expect them to build cognitive maps involving spatial learning processes to visit conspecifics or to regroup around resource areas (see next paragraphs about sociality). With regard to the Florida manatee, the existence of spatial cognition is mentioned when considering their displacements and decision-making but has not been formally studied (Flamm et al. 2005, 2013). Authors have suggested that the Florida subspecies is able to maintain a mental map of warm water sites (Flamm et al. 2005, 2013). This knowledge may determine site selection during the cold season since they were observed making a rapid change from their preferred sites to alternative sites, rather than making random choices. In the wild, Antillean manatees (especially males) travel over long distances of up to 240 km with round trips from the north of Chetumal Bay (Mexico) to the south of Belize (Castelblanco-Martínez et al. 2012). Also, they perform short distance displacements around the Chetumal bay involving mostly but not exclusively females. This suggests the use of cognitive mapping processes potentially differing according to sex that requires further research.

Social behavior

Sociality (i.e. relationship with conspecifics) is evolutionary linked to intelligence and involves cognitive abilities such as social mapping, judgments on relationships with conspecifics or social learning (Lee and Moss 2014; Kamil 2004; Rendell and Whitehead 2001). Sociality in Caribbean manatees seems more complex than previously considered, with high levels of interaction between adults (especially during night time) and preferred associations between individuals for contacts (Henaut et al. 2010). In this study (Henaut et al. 2010), manatees appeared to be highly tolerant towards conspecifics, particularly when considering the acceptance and high levels of tolerance males display towards calves. For example, the authors observed in a captive group consisting of a large male, two females and a young male calf, that half of the diurnal and a third of the nocturnal adult male's social interactions were with the calf. These interactions included "kissing" with mouth-mouth contact, "embracing" with contact between one manatee's flippers and the other manatee's body, "nuzzling" with a body-body contact and "mouthing" when one manatee touches another with the mouth (Henaut et al. 2010). Calf behavior and constant interactions with several individuals may be linked to social play. Social play behaviors and object play behaviors have been described in wild Florida manatees (Hartman 1979) and observed in zoological settings (A. Charles, personal observations). Play behavior is observed in a wide range of taxa and is thought to enhance motor-training, neural connectivity and to help developing social skills (Lee and Moss 2014). For example, in elephants, play is a mechanism highly linked to sociality since it helps juveniles to experience diverse social partners and to experience and learn from unexpected events in their environment (Lee and Moss 2014). In manatees, play behavior may contribute to develop a range of learning abilities that will help individuals to face and cope with social or environmental challenges. This hypothesis is supported by the persistence of the bond between mothers and calves until 4 years old that may allow social learning processes associated with food selection and freshwater resource location for instance. For example, in spotted dolphins (*Stenella frontalis*), teaching behaviors from mothers to their calves have been observed during foraging (Bender et al. 2009). Sociality in Caribbean manatees can be studied within a large-scale geographic context, opening up the possibility of studies that consider the movements of individuals that socialize and associate temporally. On the other hand, scientific effort may focus on social learning between mother and calf in manatees (Würsig 2009). This author (Würsig 2009) also mentions that play is not considered in manatees and sirenians in general and suggests that long-term studies are essential if we are to gain a better understanding of these mammals.

Vocal behavior and individual recognition

Vocal communication represents an interesting research area in social cognition, with the investigation of cognitive processes underlying call production, call use and their perception by other individuals (Schwartz et al. 2020). Vocalizations play an important role in mother and calf communication in manatees (Wells et al. 1999), and recent studies emphasize the significance of the acoustic dimension in manatee communication (Ramos et al. 2020; Sayigh et al. 1999). Manatees produce different types of calls which have previously been classified as tonal, noisy or both (Fig. 3) (Brady 2021). Although vocalization function is not clearly understood, it could bring new insights into the understanding of a manatees' mind. A recent study on wild Florida manatees aimed to classify their calls and to link call types to group behavior contexts, found that calls with a hill shaped frequency contour were correlated to calf presence and that longer calls were produced during stressful contexts (Brady 2021). To our knowledge, this type of data on Antillean manatees is non-existent; however, research on the acoustic interactions of this species could help us associate call types to individual and social contexts. As observed in whales and dolphins (Musser et al. 2014; Reiss and Cowan 1993), it has been suggested that vocalizations produced by manatees may be related to the identification of an individual thus allowing individual recognition. Individual recognition allows animals to discriminate among individuals and categorize them as familiar *versus* unfamiliar, and as offspring, social or sexual partners. This mechanism involves other cognitive skills such as learning and memorization of the features associated to individuals (Yorzinski 2017). In mother and calf Amazonian manatees (*Trichechus inunguis*) vocal patterns look similar between mother and calf despite fundamental differences according to age and sex (Sousa-Lima et al. 2002). Shared genetics could be partly responsible for this similarity between mothers and their calves although the recognition through vocalizations hypothesis is also mentioned in this study (Sousa-Lima et al. 2002). Taking these

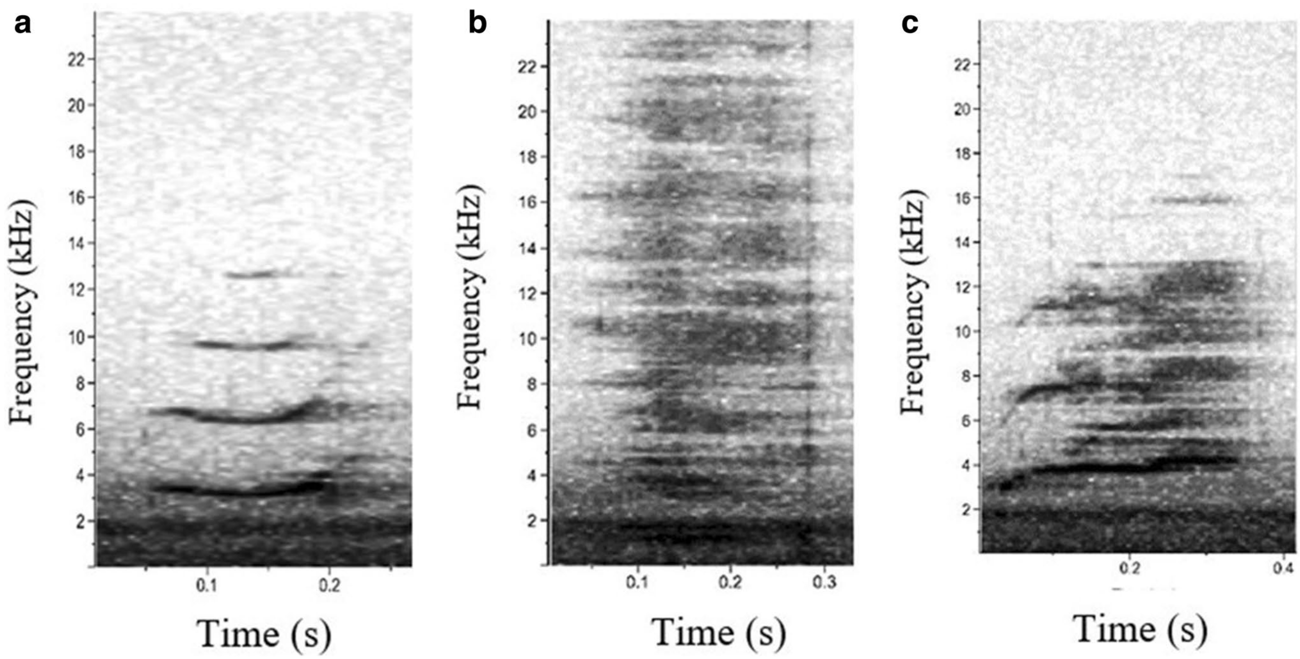

Fig. 3 Spectrograms (FFT 1024, 50% overlap, Hamming window) of each type of vocalization produced by captive Antillean manatee: calls with tonal component (**a**), noisy calls (**b**), call with tonal and noisy components (**c**)

observations into consideration, we would expect calves to use social learning to acquire an individual signature with acoustic features similar to their mothers', although there is no data yet to support these hypotheses. Individual recognition also hypothesizes relatively high inter-individual and low intra-individual differences in acoustic features. Low intra-individual variations in several acoustic parameters (i.e. peak frequency, call structure, frequency range) have been found in both Antillean and Florida subspecies (Alicea-Pou 2001) and it has been suggested that some acoustic traits might remain constant over long periods (O'Shea and Poché 2006). Since manatees sometimes travel in pairs and show preferential associations in captivity (A. Charles, personal observations), they must be able to find and keep contact with their social partners in large groups of hundred individuals, as observed in Florida, or in water with extremely poor visibility. For example, in cape fur seals (*Arctocephalus pusillus pusillus*) which live in dense colonies, a high degree of individual stereotypy is found in the species vocal repertory (Martin et al. 2021). Therefore, we may expect that individual recognition through vocalizations in Antillean manatees is a reasonable possibility, although further studies (e.g. conspecifics' playback) are needed.

The acoustic communication of the manatee may be more complex than previously thought, with vocalizations varying according to internal and external factors. These modifications of acoustic properties depending on individual and/or context open up perspectives on the existence of vocal and contextual learning processes in manatees.

Interactions between cognition, emotions and personality: implications for the welfare and conservation of the manatee

The implications of emotions on animal cognitive processes are widely acknowledged since an increasing body of work has shown that emotions could temporarily induce biases in attention and memory of judgement processes (Boissy 2014). The complex interaction between cognition and emotion is also observed in behavioral lateralization, i.e. how animals display specific behaviors using predominantly either the left or right side of their body (Leliveld et al. 2013). Laterality has been linked to intelligence with the assumptions that an efficient division of functions between the two brain hemispheres increases cognitive capacity (Barnard et al. 2017; De Boyer Des Roches et al. 2008). Behavioral laterality seems particularly relevant in the field of animals' emotions and ultimately their welfare. Visual and motor laterality might be in some cases good indicators of how animals process information and especially emotions (see Leliveld et al. 2013 for a review). Laterality and emotional states have been studied in marine mammals such as dolphins and whales (Hill et al. 2017; Karenina 2013; Siniscalchi et al. 2012; Thieltges et al. 2011). In bottlenose dolphins, behavioral laterality seems to vary according to emotional contexts, and visual and motor laterality could be a potential welfare indicator (Charles et al. 2021; Delfour and Charles 2021). Lateralized behaviors have also been described in wild Asian elephants (*Elephas maximus*) where mothers prefer to keep their young in their left visual field, therefore in their left side when walking side by side (Karenina et al. 2018). This bias in the calves' position has also been observed in killer whales (*Orcinus orca*) with mothers preferring to position calves on their left side during threatening situations (Karenina et al. 2013). A study on lateralization in Florida manatees provided evidence of body lateralization, with more injuries on the left part of the body, suggesting a side bias when approaching or fleeing boats (Tyler-Julian et al. 2016). This study also identified an individual but not population bias and suggests a possible behavioral laterality during feeding, with a left flipper preference. Laterality might therefore represent an interesting approach for researching the cognition and brain processes of manatees and therefore provide new insights on animals' emotions; however, research about emotions in manatees is necessary considering the lack of information for sirenians. Another factor that could modulate the complex interaction between cognition and emotions is the animals' personality, defined as inter-individuals' differences that are consistent across time and contexts (Réale et al. 2007). Personality or temperament influences the way animals perceive and respond to their environment (see Dougherty and Guillette, 2018 for a meta-analysis) and has implications for animal welfare, management and conservation (Cassola et al. 2020; Merrick and Koprowski 2017; Réale et al. 2007). Studies on the personality of marine mammals are becoming more common, focusing predominantly on dolphins (Birgersson et al. 2014) and pinnipeds: grey seals (Frick et al. 2017), California sea lions (Ciardelli et al. 2017), Galapagos fur seals (De Rango et al. 2019) and harbor seals (de Vere 2018). Those later works highlight the necessity to develop studies on personality in several aquatic mammal families, including Sirenians. Elephant and manatees are closely related, and studies focusing on personality in proboscideans have already been conducted (Frick et al. 2017) and interesting for manatees' perspective. For example, in captive Asian and African elephants, specific personality traits (i.e. aggressiveness and activity) were good predictors to problem-solving strategies, with individuals showing these behavioral traits being more efficient in the cognitive task (Barrett and Benson-Amram 2021). To our knowledge, only one recent study has been carried out on sirenian personality and focused on Antillean manatees under human care, offering methods to determine boldness and shyness traits in manatees (Charles et al. 2021). In this work, bolder manatees were also the most sociable and the most participating in keepers' interactions (i.e. hand-feeding sessions). These authors, along with Ubeda et al. (2021) discuss the relevance of integrating personality rating into conservation and welfare studies since it could drive ecological traits (i.e. exploration, sociality), and influence animals' perception and response to environment (Ubeda et al. 2021). In manatees, there are still no studies on lateralization and its link to emotions, personality and welfare. Studying these multifactorial interactions as a more complete approach, would increase our understanding on how manatees process information, as well as learning more about their behavior.

Evolutionary significance

Since manatees are socially tolerant and experience low natural predation and low feeding competition, they would be ideal candidates when analyzing social, ecological, life-history and predation-based hypotheses of the evolution of cognition. One prediction is that social learning tends to increase with species longevity, and particularly when a species shows long periods of juvenile dependence (Street et al. 2017). Manatees can live up to 60 years with a strong bond between the mother and the young until 2 to 4 years of age (Hartman 1979). Although their foraging strategies are not particularly developed and do not require developed cognitive skills, manatees often travel long distances to find good sites to forage and/or to regroup that they potentially have to remember over time (Castelblanco-Martínez et al. 2013). It is reasonable to assume that juvenile dependency might facilitate the acquisition and social transmission of survival skills from mothers to offspring (Szabo et al. 2022). Another social hypothesis emphasizes that social learning increases with group size (Street et al. 2017), and when considering observations of manatees' group, they are not expected to show particularly developed cognitive skills. However, although manatees do not seem to form large stable groups in a limited area as other gregarious species (e.g. birds), they may form part of a more complex social world occurring at a larger geographic scale, with perhaps knowledge on the locations of conspecifics (i.e. cognitive maps). This knowledge might allow individuals to temporally visit and interact with conspecifics distributed over a large area, as potentially observed with the Antillean subspecies (Y. Henaut, personal observations). This uncertainty on manatees' level of sociality might be explained by their evolutionary history. Manatees may have been more gregarious during their evolutionary path than today, but due to habitat fragmentation and consequently the dispersion of their resources, individuals may have begun to spread out over a more extensive area (Castelblanco-Martínez et al. 2012). Another ecological driver for the loss of gregarious behaviors is the absence of predation in their natural habitat, resulting in a lesser need to gather in their living areas. However, some aspects of this gregarious life would have been conserved such as the high tolerance between individuals or grouping behaviors around resources. The potential existence of individual recognition through vocalizations (not only between the mother and calf) in manatees also suggests that social interactions might be more stable and/or complex than previously thought. These hypotheses appear phylogenetically reasonable since manatees appear to share similar social behaviors with their cousins, the elephants, such as grouping when encountering a threatening situation (Henaut 2020). Considering the recent advances in manatee research, some initial predictions on their social and cognitive life may be incorrect or incomplete, this could be due to many factors, including a misunderstanding of their ecological context and a lack of efficient study methods (i.e. use of telemetry and drones) (Ramos et al. 2022). Moreover, manatee behavior has often been compared, perhaps wrongly, to cetacean species, due to their obvious convergent evolution in aquatic habitats (Hartman 1979). However, considering their phylogeny and recent studies on their behavior, manatees might share more social and cognitive skills with elephants than cetaceans, and we suggest further studies to address this possibility. Although all described hypotheses on sirenian evolution remain highly speculative, learning more about these behaviors and skills not only has welfare and conservation implications, but also contributes to our understanding on the evolution of cognition across species.

Conclusion

We highlighted in this paper that navigation (i.e. cognitive mapping and spatial learning), sociality (i.e. social leaning), communication (i.e. vocal production and individual recognition) and their link to emotional states and/or personality all have to be explored if we want to improve our understanding of the cognitive adaptations of manatees. More specifically, research on the movements of manatees in their habitats, aspects of their social behavior (e.g. play behavior, acoustic behavior) together with experimental studies on learning and/or memory abilities would be highly worth conducting to obtain some answers on the cognitive adaptations of these understudied animals. Though the ecology and biology of manatees are relatively well studied, there is a lack of scientific data on manatee cognition compared to their relatives the elephants and other aquatic mammals such as cetaceans. These research fields have a direct link to manatee welfare, conservation and management and overall, they contribute to our understanding of the evolution of cognition across species. This paper suggests some potentially relevant points of interest that merit further research, to gain more knowledge on these popular, but still poorly understood, aquatic mammals. We fervently suggest increasing future research on manatees, particularly with a focus on their behavior and cognition based on their ecological context, using a biocentric approach. This approach, differing from anthropogenic considerations on animal cognition, appears to be more adapted to the socio-ecology of this species and offers new perspectives and working hypothesis on manatee cognition.

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