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ORIGINAL PAPER

Detection of hydrodynamic stimuli by the postcranial body of Florida manatees (*Trichechus manatus latirostris*)

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Abstract Manatees live in shallow, frequently turbid waters. The sensory means by which they navigate in these conditions are unknown. Poor visual acuity, lack of echolocation, and modest chemosensation suggest that other modalities play an important role. Rich innervation of sensory hairs that cover the entire body and enlarged somatosensory areas of the brain suggest that tactile senses are good candidates. Previous tests of detection of underwater vibratory stimuli indicated that they use passive movement of the hairs to detect particle displacements in the vicinity of a micron or less for frequencies from 10 to 150 Hz. In the current study, hydrodynamic stimuli were created by a sinusoidally oscillating sphere that generated a dipole field at frequencies from 5 to 150 Hz. Go/no-go tests of manatee postcranial mechanoreception of hydrodynamic stimuli indicated excellent sensitivity but about an order of magnitude less than the facial region. When the vibrissae were trimmed, detection thresholds were elevated, suggesting that the vibrissae were an important means by which detection occurred. Manatees were also highly accurate in two-choice directional discrimination: greater than 90% correct at all frequencies tested. We hypothesize that manatees utilize vibrissae as a three-dimensional array to detect and localize low-frequency hydrodynamic stimuli.

Keywords Manatee · Sirenian · Tactile · Hydrodynamic · Vibrissae

Abbreviations

FSC Follicle-sinus complex
F Frequency (Hz)

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Introduction

Florida manatees are obligate aquatic mammalian herbivores that spend substantial time in habitats with low visibility. They have poor visual acuity (Bauer et al. 2003; Mass et al. 2012) and lack active echolocation. In addition, the neurobiological evidence suggests modest chemosensory abilities (Mackay-Sim et al. 1985; Levin and Pfeiffer 2002). In contrast, manatees have exquisite tactile sensitivity (Bauer et al. 2012; Gaspard et al. 2013) and a system of sensory hairs distributed over the entire body (Reep et al. 2001, 2002). These observations have led to the hypothesis that this system of hairs functions as a mammalian version of the lateral line system to detect water movements and features of the underwater environment. Such a capacity would provide a basis for spatial orientation and navigation.

Mammalian sensory hairs are specialized to detect movement, either through direct contact with an object or through passive deflection by the fluid medium in which they are immersed. These hairs are also known as vibrissae, tactile hairs, sinus hairs, or whiskers. Each externally visible sensory hair is part of a follicle-sinus complex (FSC),

defined as having an outer dense connective tissue capsule, circumferential blood sinus, and dense innervation (Rice et al. 1986). Multiple types of innervated mechanoreceptors are distributed along the membranous wall surrounding the proximal shaft of the sensory hair (Rice et al. 1986, 1997). When the hair shaft moves and contacts the membranous wall of the FSC with sufficient energy, it excites mechanoreceptors that transduce mechanical deformation into electrical signals that propagate along axons and enter the central nervous system.

Among marine mammals, pinnipeds and cetaceans have sensory hairs on the face only (Ling 1977). Pinnipeds exhibit morphological elaborations of the sensory hairs that are associated with prey capture and benthic foraging (Marshall et al. 2006; Ginter et al. 2010). Baleen whales have 30–100 sensory hairs on the upper and lower jaws (reviewed in Mercado 2014). In most odontocete cetaceans, hair is present only as prenatal sensory hairs which atrophy, resulting in vibrissal crypts, which are electroreceptive in some taxa (Ling 1977; Czech-Damal et al. 2012). An important exception is the freshwater river dolphin, which has well-developed sensory hairs along the upper and lower jaws that may be used in prey localization (Layne and Caldwell 1964; Ling 1977). As first described by Dosch in dugongs and later verified for manatees, sirenians are unusual in having sensory hairs distributed over the entire body, and this is the only type of hair they possess (Dosch 1915; Bryden et al. 1978; Kamiya and Yamasaki 1981; Sokolov 1986; Reep et al. 1998, 2001, 2002).

In the aquatic environment, facial sensory hairs are involved in exploration, either through direct contact (active touch) or by detecting hydrodynamic stimuli. The Australian water rat uses its long mystacial sensory hairs to locate prey when it is underwater. While on land, it dips its sensory hairs into the water, presumably to sample the hydrodynamic environment prior to diving after prey with its eyes closed (Woollard et al. 1978; Dehnhardt et al. 1999). Walruses use their stiff sensory hairs to explore the benthic substrate in search of shellfish and are able to discriminate objects at a small scale (Fay 1982; Kastelein and van Gaalen 1988). Seals and sea lions are able to discriminate fine differences in objects and can accurately track the hydrodynamic trails generated by moving prey (Dehnhardt 1994; Dehnhardt and Kaminski 1995; Dehnhardt and Dücker 1996; Dehnhardt et al. 1998, 2001; Schulte-Pelkum et al. 2007; Glaser et al. 2011; Hanke et al. 2013). Manatees use their facial sensory hairs to investigate food items and novel objects and to grasp aquatic vegetation and convey it into the oral cavity (Hartman 1979; Marshall et al. 1998; Bachteler and Dehnhardt 1999; Bauer et al. 2012). Recent work has demonstrated that manatees can also detect hydrodynamic stimuli using the facial sensory hairs (Gaspard et al. 2013).

We have hypothesized that manatees in the wild use their postcranial sensory hairs as a mammalian version of the lateral line system of fishes to detect hydrodynamic stimuli created by tidal flows, river currents, other animals moving in the aquatic environment, and changes in their own flow field due to the presence of stationary objects (Reep et al. 2002). The present study tests the plausibility of this hypothesis by defining under what conditions a dipole hydrodynamic stimulus is detectable by manatees using the postcranial body.

Materials and methods

Subjects

The subjects were two male Florida manatees (*Trichechus manatus latirostris*) housed at Mote Marine Laboratory and Aquarium in Sarasota, Florida, USA. Buffett and Hugh, 23 and 26 years of age, respectively, at the initiation of the study, had an extensive training history in husbandry behaviors and psychophysical methods (Colbert et al. 2001, 2009; Bauer et al. 2003, 2012; Mann et al. 2005; Gaspard et al. 2012, 2013).

Experiment 1: sensitivity to hydrodynamic stimuli

The results from this experiment established the detection thresholds for hydrodynamic stimuli with frequencies ranging from 5 to 150 Hz. The upper limit was selected to minimize the possibility that detection of the stimuli by hearing confounded tactile measurements (see audiograms in Gerstein et al. 1999; Gaspard et al. 2012).

Equipment

A dipole vibration shaker (Data Physics – Signal Force, Model V4, San Jose, CA, USA) with a 5.7 cm diameter rubberized sphere connected via a rigid stainless steel extension rod was used to generate the stimuli (Coombs 1994; Dehnhardt et al. 1998). The dipole shaker generates a localized flow that decreases in amplitude as $1/\text{distance}^3$, as opposed to a monopole source that decreases in amplitude as $1/\text{distance}^2$ (Kalmijn 1988). To minimize any unwanted vibrational transfer between the shaker and the manatee, the stationing apparatus and the shaker mount were separate pieces of equipment buffered with shock absorbing foam between each frame and the wall of the tank. We were unable to detect any vibration with 3-dimensional (3-d) accelerometer attached to the frame or human touch on the stationing apparatus when the shaker was activated.

The stimuli were generated digitally by a Tucker-Davis Technologies (TDT) Enhanced Real-Time Processor

(RP2.1, Alachua, FL, USA; sample rate 24.4 kHz), attenuated with a TDT Programmable Attenuator (PA5) to control level, and amplified with a Samson Power Amplifier (Servo 120a, Hauppauge, NY, USA). The signal generating equipment was controlled by a program in MATLAB® (MathWorks®, Natick, MA, USA) in conjunction with a graphical user interface (TDT Real-Time Processor Visual Design Studio). A digital output on an RP2.1 was used to control the LED that indicated the start of a trial. A separate D/A channel was used to generate the acoustic secondary reinforcer, which was presented through an underwater speaker (Clark Synthesis, Model AQ-39, Littleton, CO, USA) when the manatee was correct on a trial. The speaker was located >1 m away from the subject and also presented noise (151 dB re 1 μPa; 12.2 kHz bandwidth with a falloff at 10 Hz) constantly through the session to mask any auditory artifacts from the generation of the hydrodynamic stimulus, which was verified from underwater recordings with a hydrophone at the position of the manatee auditory meatus. These signals were amplified by a separate amplifier (American Audio, Model VLP 300, Los Angeles, CA, USA) to avoid crosstalk.

For stimulus analysis and calibration in the tank environment, six underwater hydrophones (HTI-96-MIN, Gulfport, MS, USA; sensitivity −164 dBV/μPa; 2 Hz–37 kHz) with one on each face of a cubic frame (20 cm apart on the X, Y, and Z axes) were used to measure pressure gradients of the stimulus as well as to monitor any concurrent hydrodynamic noise generated by the equipment. The pressure gradient was, therefore, composed of the primary stimulus presented by the vibrating sphere, as well as simultaneous contributions originating from vibrations of the shaker, shaker frame, and wall. The cube was placed, so that the center was the same distance from the sphere as the surface of the manatee during testing and aligned with the axis of the vibrating sphere (Fig. 1). To calculate the pressure gradient, dipole signals were recorded simultaneously on all hydrophones. Pressure signals from each pair of hydrophones representing the three axes (X, Y, and Z) were subtracted and divided by the distance between them to calculate the pressure gradient. The pressure gradient was divided by the water density to calculate the particle acceleration. For sinusoidal signals, particle velocity is the particle acceleration divided by 2πf (where, f = frequency), and particle displacement is particle velocity divided by 2πf. All values are expressed as RMS levels. To monitor stimuli during animal testing, a 3-d accelerometer (Dimension Engineering, Model DE-ACCM3D, Akron, OH, USA) was embedded into the sphere to measure its movement. MATLAB® was used to calculate, plot, and log the stimulus for each trial. The accelerometer was used to monitor the proper functioning of the equipment (i.e., to make sure a stimulus was delivered on every trial). It was not used for estimating the signal level at the location of the manatee. Given the environment, we measured the actual received field at the location of the manatee. This would include all the sources of signal from the system. Furthermore, the sphere did not oscillate with a perfect sinusoidal motion in only one axis; it had more of an ovoid three-dimensional motion with most, but not all, of the energy in the vector along the rod.

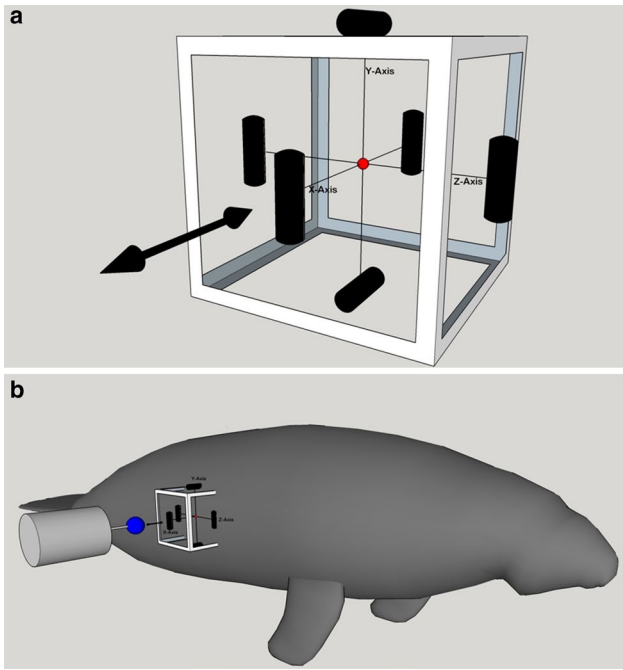

Fig. 1 **a** Schematic of the cube used to calibrate particle flow. The black cylinders represent the position of the six hydrophones. To calculate the pressure gradient, dipole signals were recorded simultaneously on all hydrophones. Pressure signals from each pair of hydrophones representing the three axes (*X, Y*, and *Z*) were subtracted and divided by the distance between them to calculate the pressure gradient. The red dot represents the point at which the pressure gradient was measured. **b** Schematic of the position of the cube relative to the surface of the manatee. The manatee was not present during calibration, but the position of the center of the cube represents the distance from the vibrating sphere to the manatee during testing

To ensure that the test subjects were not cued during testing, a number of protocols and measurements were conducted. The research trainer responsible for verifying the position of the manatee and providing the primary reinforcement was blind to whether the ensuing trial was a stimulus-present or stimulus-absent trial. This trainer was also out of the manatee's direct line of sight and remained motionless until the trial sequence was complete.

Two underwater laser pointers (Lasermate SL6505M, Camino De Rosa, CA, USA) were attached on either side of the shaker apparatus by ball mounts and positioned to converge at 20 cm in-line with the center of the stimulus generating sphere. Convergence of the lasers on the manatee

indicated the appropriate test distance of the manatee from the vibrating sphere. The laser locations were monitored either via a submersible video camera (HelmetCamera, Fredricksburg, VA, USA) and recorded using a portable DVR unit (DTY Industrial, V5, Guangdong, China), or monitored by direct observation of a trainer out of the subject's sight. The lasers were also out of eyesight of the subjects.

Procedures

The manatees were trained utilizing operant conditioning through positive reinforcement to signal the detection of hydrodynamic stimuli directed at their postcranial sensory hairs. A go/no-go procedure was used to determine stimulus detection. If the stimulus was detected, the manatee responded by withdrawing from a horizontal stationing bar and touching a response target on the same side that the stimulus was presented with its muzzle (Fig. 2). The response target was located 1 m lateral to the head of the subject. If no stimulus was detected, the manatee remained at station for a minimum of 10 s. Correct responses were followed by an auditory secondary reinforcer, a digitized whistle from an underwater speaker, followed by primary reinforcement, mixtures of preferred food items: pieces of apples, carrots, beets, and monkey biscuits. A staircase method (Cornsweet 1962) was used in which eight reversals were averaged to calculate a threshold. After a correct response on a vibrational signal present trial, the level of the stimulus was attenuated by 3 dB. If the manatee was incorrect on a signal present trial, the level of the stimulus was increased by 3 dB. Four "warm-up" trials were conducted prior to testing to assess the motivation and performance levels of the manatees with the stimulus at the same frequency and highest level that was to be tested. A criterion of 75% correct on "warm-up" trials had to be met in order for testing to occur during that particular session. If the subject failed to meet criterion on the first set of warm-up trials, a second warm-up set was conducted. Testing was not conducted if the subject failed to meet criterion on the second warm-up block.

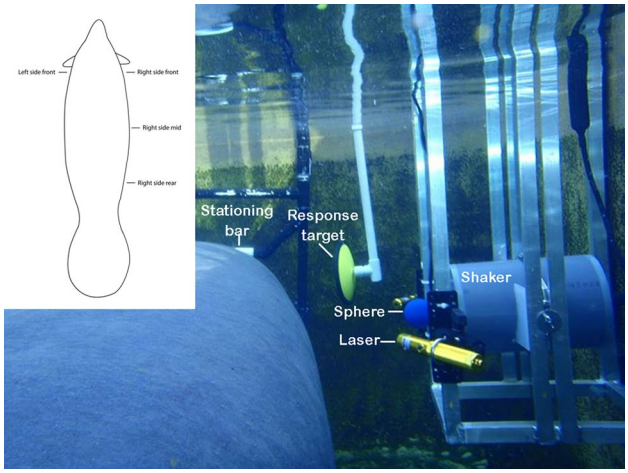

Fig. 2 Manatee is at the underwater station, prepared for a test trial of the right-side mid-postcranial region. The stationing bar, response target, shaker, sphere, and laser are labeled in the figure. The inset shows a schematic diagram showing the four locations tested to determine sensitivity to hydrodynamic stimuli

The subjects were trained to station by placing their postnasal crease on a horizontal PVC bar (2.5 cm diameter) at a depth of 0.75 m. A tri-cluster LED signaled the initiation of every trial. The LED was illuminated for a duration of 1 s, followed by a 0.5 s delay prior to both vibrational signal present and vibrational signal absent windows. The signal was always presented immediately after the 0.5 s delay. The vibrational stimuli were generated by a 5.7 cm sinusoidally oscillating sphere driven by a computer-controlled calibrated vibration shaker. The sphere was connected to the shaker via a rigid stainless steel rod. The shaker and attachment rod were oriented horizontally in the water column. The shaker was housed in a water-tight cylindrical housing with the rod passing through a sealed silicone barrier. The stimuli were 3 s in duration with $\cos^2$ rise–fall times of 300 ms and ranged from 5 to 150 Hz. Signal present versus signal absent trials were counterbalanced using a 1:1 ratio. Daily sessions (weekdays) were conducted with each session focused on a single frequency, encompassing 18–48 trials. A single frequency was tested over the course of two separate staircase sessions conducted on consecutive days to confirm thresholds. If the thresholds were not within a factor of two (i.e., 6 dB) of each other, a third session was conducted and the thresholds were averaged.

Four locations were tested on each manatee's postcranial body, all dorso-ventrally centered: three on the right side (forward third, middle third, and rear third) and the forward third of the left side (Fig. 2, inset). The manatees were trained to maintain each of the four locations 20 cm from the vibrating sphere.

To ensure that the same region of the manatee was tested on different days, the position of the equipment was marked and repeated during each regional test. This was done for each manatee as they differed in size.

Experiment 2 trimmed hairs

Experiment 1 established the detection thresholds for various low-frequency vibrations, but it did not determine the contribution of the sensory hairs to that process. In Experiment 2, one frequency was tested, 75 Hz, using the same procedures as Experiment 1, except that the subjects were located 40 cm from the vibrating sphere. After establishing the detection threshold, again, we trimmed the hairs in a 50 cm square at the right-side forward location. The

borders of the square were marked with a wax pen, so that the same area could be trimmed each day. The hairs were trimmed using a waterproof trimmer (Wahl Mustache and Beard Trimmer—Model 5537-420, Sterling, IL, USA). Because of the rough skin of the manatees, the trimming left a short stubble. Assessment after the experiment of distance of the subject from the vibrating sphere indicated a mean distance of 37.1 cm, sd = 4.0 cm (N = 28 trials) for Buffett and 41.0 cm, and sd = 6.3 cm (N = 21 trials) for Hugh.

Experiment 3 directional discrimination

Directional discrimination was tested using a shaker on each side of the body, aimed at the front region (Fig. 3). The shakers were calibrated to produce identical detectable stimuli at four selected frequencies (25, 50, 75, and 125 Hz). Each trial involved presentation of a suprathreshold stimulus from either the right or left shaker, or no stimulus (catch trial). The subject correctly indicated detection of a suprathreshold stimulus by withdrawing from the stationing apparatus and pressing a laterally positioned response target located on the same side as the shaker that generated the stimulus. Correct response to a catch trial was defined operationally as not touching a response target for a 10 s period after the initiation of a signal absent trial. A total of 112 trials were run for both Hugh and Buffett, with 25% catch trials. Similar procedures were used as in the previous experiment, including beginning each trial with a 1 s duration light followed by a 0.5 s delay. The shakers were aligned to direct the stimuli at the same front body location on opposite sides at the same depth in the water column. Each shaker was supported by identical hardware and software as described for Experiment 1. All other procedures were as described for Experiment 1.

Fig. 3 Manatee is shown at underwater station, prepared for a test trial of directionality discrimination. Shakers and response targets are equidistant from either side of the manatee

Results

Particle displacement thresholds were similar across the three body regions (front, middle, and rear) (Fig. 4a), and therefore, these results were combined (Fig. 4b). Because of differences in subject participation, there were variable numbers of thresholds available for some frequencies. All data were averaged to generate the detection threshold at each frequency. The manatees responded to all frequencies tested. Comparison between the right front and left front regions revealed no apparent difference in sensitivity (Fig. 4c). The mean false alarm rate for Buffett was 14% and for Hugh, 9%, with a low of 0% and high of 25% for both manatees. Velocity and acceleration show the same pattern, because they are linearly related to displacement for sinusoidal stimuli. Both subjects displayed thresholds near or below one micron of particle displacement for frequencies above 50 Hz. At 150 Hz, Buffett detected particle displacement near 10 nm using the postcranial body. Sensitivity was positively correlated with frequency, with an increase in sensitivity observed at higher frequencies. Both manatees demonstrated similar thresholds.

Trimming the hairs raised the detection thresholds for both manatees by approximately threefold (Table 1). There was no overlap in threshold values for any of the trim and no-trim sessions (i.e., all trim sessions had a higher threshold). Buffett had a false alarm rate of 8% for the no-trim trials and 7% for the after-trimming trials. Hugh had a false alarm rate of 11% for the no-trim trials and 13% for the after-trimming trials. Low and high ranges for Buffett were 0 and 13% and for Hugh, 11 and 13%.

Both manatees determined the direction (left or right) of the hydrodynamic stimuli at well above chance levels (Table 2). They correctly identified the direction of the stimulus and responded correctly to catch trials at over 90% at all frequencies tested. The mean false alarm rate for both subjects was 4% with a low of 0% and a high of 13%, highlighting the conservative strategy that both manatees appeared to employ.

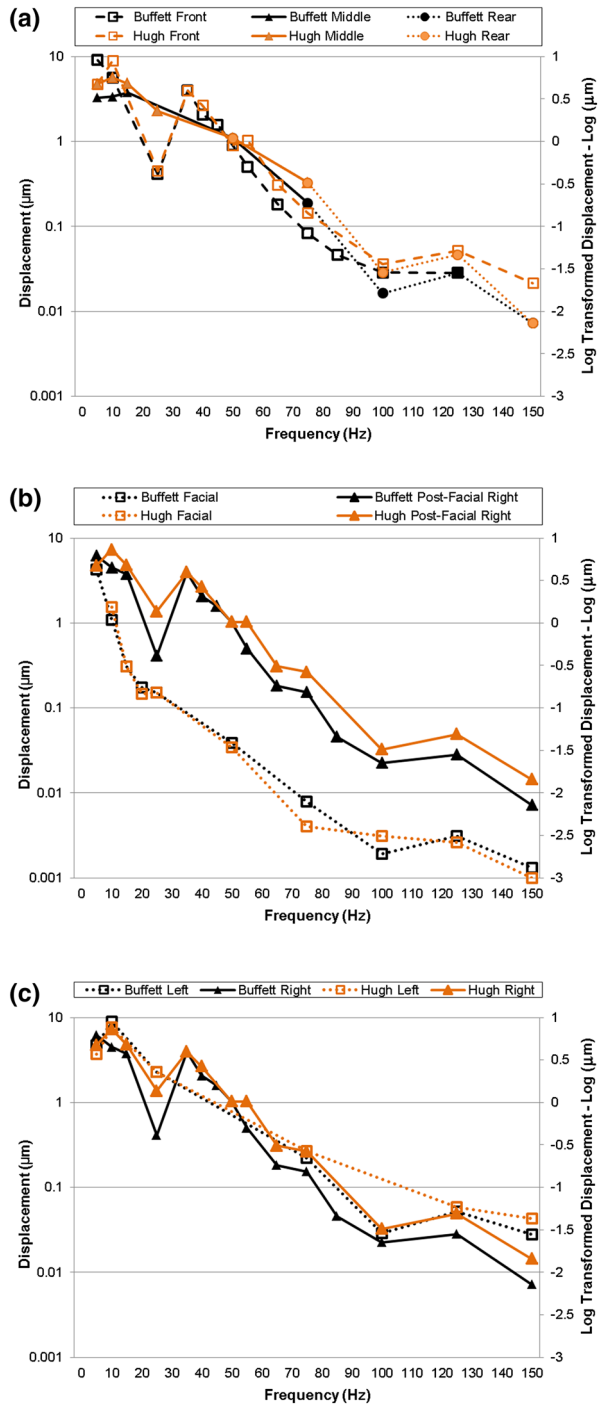

Fig. 4 **a** Experiment 1. Particle displacement thresholds (µm) for Buffett and Hugh are shown for three locations on the right side. All frequencies were tested on the front right location, but only a subset was tested at the other locations. Manatees detected the stimulus for all frequencies tested. **b** Experiment 1. Particle displacement thresholds (µm) were averaged over the three *right*-side locations: front, middle, and rear. The *top* two curves plot the thresholds for the postcranial region for each manatee. The *bottom* two curves plot the facial thresholds reported in a previous publication (Gaspard et al. 2013). **c** Experiment 1. A comparison of particle displacement at front *left* and *right* sides for Hugh and Buffett shows similar thresholds (µm)

Discussion

Our principal finding is that the postcranial body demonstrates high sensitivity to hydrodynamic stimuli across a wide range of frequencies. The postcranial threshold sensitivity curves are remarkably similar to comparable data from the facial region of the body (Gaspard et al. 2013), except that the postcranial region is less sensitive by about an order of magnitude across all frequencies (Fig. 4b). Although we report that particle displacement detection thresholds decreased at progressively higher frequencies, we do not know the stimulus actually detected by the manatee (i.e., displacement, velocity, or acceleration). It may be that they detect all three: displacement, velocity, and acceleration. If manatees sense velocity or acceleration, the thresholds would increase proportionally to frequency for velocity and to frequency squared for acceleration. Regardless of which stimulus characteristics were actually detected, both manatees demonstrated similar threshold sensitivity curves and directional discrimination, suggesting that these results may be a reasonable representation of the abilities of manatees generally. As noted by others (Bleckmann et al. 2001), natural selection has demanded successful operation of sensory systems in noisy environments, whereas we have tested manatee detection using an unnatural stimulus in low-noise conditions.

Based on our findings in Experiment 2 (Trimmed hairs), we hypothesize that detection of hydrodynamic stimuli by the postcranial body is mediated by the sensory hairs. Although increasing the distance from the manatee to the sphere for the hair trimming experiment from 20 to 40 cm might have changed some stimulus characteristics (e.g., the form of the wave front and angular differences in water motion across the field), the critical focus for this study was the difference in detection thresholds with and without sensory hairs. That difference indicated a roughly three-fold increase in threshold when hairs were trimmed. Because trimming attenuated but did not eliminate detection, the residual hair stubble could have been sufficient to detect the stimuli. In addition, hairs outside the 50 cm trimmed square (right-side forward location) may have been stimulated or other unknown skin receptors that mediate detection of hydrodynamic stimuli might be involved.

The amplitude measured at the location of the manatee surface was a measure of a composite stimulus (e.g., sphere, shaft, shaker, frame, and wall). That the stimulus was not also meaningfully conveyed by the stationing apparatus is suggested by the confluence of several lines of evidence. Human touch and accelerometer measurements did not indicate transfer. Although these measures are not probative by themselves, the differences between the trim and no-trim conditions in Experiment 3 (directional discrimination), in which the same stimulus magnitudes were used,

Table 1 Postcranial detection threshold values at 75 Hz for the right side, trim versus no-trim conditions for Buffet and Hugh

Subject	Displacement (μm)		Velocity (mm/s)		Acceleration (mm/s^2)	
	Trim	No trim	Trim	No trim	Trim	No trim
Buffett	0.041	0.013	0.019	0.006	9.088	2.956
Hugh	0.065	0.022	0.030	0.010	14.328	4.917

Table 2 Percentage correct on directionality test trials based on the presentation of the stimuli directed at the subjects' left or right-side trials

Frequency (Hz)	*N*	Buffett		Hugh	
		Left (%)	Right (%)	Left (%)	Right (%)
125	16	100	100	100	100
75	32	92	100	100	92
50	32	92	100	83	100
25	32	100	100	100	100

False alarm rate was 4% overall for each subject and less than 13% for each session

indicate that the hairs substantively mediated the difference without transfer from the stationing apparatus.

The known functional anatomy of manatee follicle-sinus complexes (FSCs) parallels the sensitivity differences seen between facial and postcranial sensory hairs. These anatomical features include hair density, FSC size, innervation, and receptor composition. The greater density of sensory hairs on the facial region (~30x compared to the postcranial body; Reep et al. 1998, 2002) may account for the increased sensitivity demonstrated by facial sensory hairs, because greater hair density produces greater receptor density per unit area of skin. Furthermore, the facial sensory hairs include perioral bristles and bristle-like hairs of the oral disk; both exhibit larger FSC size and greater hair length and width than the postcranial hairs. In addition, there are more axons per facial FSC than for postcranial FSCs (Reep et al. 2001, 2002). Facial FSCs also possess more receptor types than do postcranial sensory hairs (Sarko et al. 2007b). Along with the functional shift from a predominance of active touch (facial sensory hairs) to passive detection (postcranial sensory hairs), the bristle-like hairs of the oral disk possess intermediate numbers of receptors and axons, and are involved in both detection scenarios.

Information from the sensory hairs enters the central nervous system, and a large amount of the manatee brainstem, thalamus, and cortex appears devoted to processing somatosensory information, including that related to hydrodynamic stimuli (Reep et al. 1989, 2002; Marshall and Reep 1995; Sarko and Reep 2007; Sarko et al. 2007a). Information regarding postcranial sensory hairs is conveyed from ~3,300 FSCs and their associated ~100,000 axons to the central nervous system (Reep et al. 2002). There is prominent representation of somatosensation in the brainstem and thalamus that appears to represent the fluke, flipper, tactile hairs of the postcranial body, perioral face, and the oral disk topographically (Sarko et al. 2007a). The presumptive somatosensory cortex is more extensive than the auditory or visual cortex, and represents ~25% of the total cortical area (Sarko and Reep 2007). Cortical representations of the postcranial hairs are hypothesized to be localized in the small Rindenkerne in area CL2 (Reep et al. 1989, 2002). Rindenkerne are neuronal aggregations found in layer VI in five cortical areas (Marshall and Reep 1995); they may be similar to the somatosensory barrels of layer IV in other taxa.

Hydrodynamic reception in other taxa

Hydrodynamic reception appears to be of great ecological value, as evidenced by the widespread distribution of this capability throughout animal taxa. Spatially elongated structures associated with mechanoreceptors that respond to hydrodynamic stimuli are found in a wide variety of invertebrate and vertebrate taxa (Budelmann 1989; Bleckmann 1994; Leitch and Catania 2012; Mercado 2014). More broadly, such structures also include hair-like appendages in insects and spiders, used as flow sensors to detect air movement (Barth 2014), and hairs that sense airflow in bats (Sterbing-D'Angelo and Moss 2014).

The lateral line system of fishes detects hydrodynamic stimuli in the frequency range of 1–150 Hz (Bleckmann 1994; Coombs and Montgomery 1999). Some form of the lateral line system was present in early craniates, and appears in most extant anamniotes (Northcutt 1989). Behavioral studies of the lateral line system in several species of fish have reported detection thresholds similar to those we found for the manatee facial area (Gaspard et al. 2013). Oscars (*Astronotus ocellatus*), goldfish (*Carassius auratus*), and toadfish (*Opsanus tau*) display particle displacement detection thresholds near or less than 1 nm (RMS) (Fay and Olsho 1979; Fay 1984; Fay et al. 1994), with the sensitivity of manatees being slightly higher at 100 Hz. Detection thresholds for the postcranial body of the manatee were higher than those reported for fish, approximately an order of magnitude higher than the manatee facial area.

In non-mammals, hydrodynamic sensors spread over the body surface record the spatial distribution of a stimulus,

and thus extract important three-dimensional information (Teyke 1989; Bleckmann 1994). For example, many fish use the lateral line for discrimination and avoidance of objects in the aquatic environment (Hassan 1986). The blind cavefish utilizes self-produced hydrodynamic stimuli to detect objects as they near or pass them (Campenhausen et al. 1981; Weissert and Campenhausen 1981; Hassan 1989). Stationary underwater objects change the flow fields generated by animals moving through water, and this conveys information about object size and distance that is detected by the lateral line system of fish through analysis of the velocity distribution of the flow field over the entire body (Hassan 1989; Bleckmann 1994; Windsor 2014). These capacities may be enhanced in manatees due to their large body size and the widespread distribution of sensory hairs.

Individual neuromasts of the lateral line system are directionally selective (Bleckmann 1994), whereas a manatee sensory hair may not be. Each postcranial manatee sensory hair is innervated by ~30 axons that supply mechanoreceptors of various types (Reep et al. 2002; Sarko et al. 2007b). Because single axons are highly branched and innervate multiple mechanoreceptors distributed around the cylindrical wall of the FSC, this would suggest that single axons convey no directional information. However, a recent report demonstrates that single branched mechanosensory axons may indeed convey directionally selective responses (Pruszynski and Johansson 2014), so this question remains unresolved for manatee sensory hairs. It is possible that regionalized clusters of axons for a group of vibrissae may generate receptive fields via bundling.

It seems plausible that the efference copy mechanism that fish employ, allowing the organism to differentiate between externally generated stimuli versus those resulting from its own actions, may also be utilized by aquatic mammals (Bell 1982; Coombs et al. 2002).

A mammalian lateral line?

The postcranial sensory hairs of manatees are anatomically specialized and are utilized to detect low-frequency hydrodynamic stimuli, 5–150 Hz in these experiments, supporting the hypothesis that they act as a sensory array analogous to the lateral line system of the fish. The ability of manatees to detect hydrodynamic stimuli having displacements below a micron and down to a nanometer suggests the hypothesis that manatees utilize their system of hairs to navigate.

Manatees are large-bodied aquatic mammals and are often found in turbid water. It is not known what cues they use for orientation as they navigate through their environment and migrate between summer and winter refugia. However, tracking of manatee movements suggests that individuals are well aware of the spatial configuration of their environment and utilize preferred paths to navigate (Slone et al. 2012). One example of a complex environment navigated by manatees is the Ten Thousand Islands area of southwest Florida that features numerous small islands with narrow channels between them.

The present findings suggest that the sensory hairs on the body of a manatee constitute a three-dimensional array capable of aiding navigation. Based on its multiplicity of mechanoreceptors, substantial neural investment, and elaborations of the somatosensory processing regions of the central nervous system (Sarko and Reep 2007; Sarko et al. 2007a, b), we hypothesize that the array of manatee sensory hairs computes the intensity and direction of water displacements and low-frequency vibrations impinging on the body surface. This information would be useful for detecting and localizing approaching conspecifics, other animals, water currents, and tidal flows. We are not the first to make such a suggestion. Hartman (1979) hypothesized that the body hairs were used to sense water movements. He suggested that this may allow detection of approaching conspecifics, and could also be the means by which a group of animals resting on the substrate with their eyes closed rises in unison to breathe. Reynolds (1979) also made a similar conjecture, and used the term "lateral line" as an analogy to describe the presumed function of the postcranial hairs. Based on their study of manatee auditory capabilities, Gerstein et al. (1999) proposed that manatee postcranial sensory hairs might detect low-frequency acoustic energy in the form of near-field particle displacements. They found that improved detection at low frequencies when the manatee oriented its postcranial body towards the stimulus and occurred within the range of frequencies (0.1–0.2 kHz) that correspond to lateral line detection in fish.

Manatee postcranial sensory hairs may also be used to detect and localize fixed objects in the underwater environment, including limestone formations and boundaries, such as river banks and sand bars. Objects in aquatic media produce a boundary layer and they generate turbulence when introduced in flow fields. Manatees may be able to detect these perturbations and utilize them as orientation and/or navigational cues. As mentioned above, hydrodynamic reception in other taxa allows for information about object size and distance to be detected. If the distributed system of postcranial sensory hairs in the Florida manatee is used in a similar way, the large body size of manatees might facilitate this capability by providing a larger detector array.

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