RESEARCH ARTICLE

Active touch in sea otters: in-air and underwater texture discrimination thresholds and behavioral strategies for paws and vibrissae

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ABSTRACT

Sea otters (*Enhydra lutris*) are marine predators that forage on a wide array of cryptic, benthic invertebrates. Observational studies and anatomical investigations of the sea otter somatosensory cortex suggest that touch is an important sense for detecting and capturing prey. Sea otters have two well-developed tactile structures: front paws and facial vibrissae. In this study, we use a two-alternative forced choice paradigm to investigate tactile sensitivity of a sea otter subject's paws and vibrissae, both in air and under water. We corroborate these measurements by testing human subjects with the same experimental paradigm. The sea otter showed good sensitivity with both tactile structures, but better paw sensitivity (Weber fraction, $c=0.14$) than vibrissal sensitivity ($c=0.24$). The sea otter's sensitivity was similar in air and under water for paw ($c_{air}=0.12$, $c_{water}=0.15$) and for vibrissae ($c_{air}=0.24$, $c_{water}=0.25$). Relative to the human subjects we tested, the sea otter achieved similar sensitivity when using her paw and responded approximately 30-fold faster regardless of difficulty level. Relative to non-human mammalian tactile specialists, the sea otter achieved similar or better sensitivity when using either her paw or vibrissae and responded 1.5- to 15-fold faster near threshold. Our findings suggest that sea otters have sensitive, rapid tactile processing capabilities. This functional test of anatomy-based hypotheses provides a mechanistic framework to interpret adaptations and behavioral strategies used by predators to detect and capture cryptic prey in aquatic habitats.

KEY WORDS: Tactile sensitivity, Haptic, Amphibious, Relative difference threshold, Two-alternative forced choice, *Enhydra lutris*

INTRODUCTION

A predator's ability to filter sensory information to capture prey represents a key constraint on diet; however, sensory capabilities and search strategies used by many top predators are poorly understood. Different habitats and prey characteristics often require different sensory modalities for efficient foraging. Large or conspicuous prey in open habitats may be detected visually, whereas small or cryptic prey in terrestrial habitats may be detected via chemoreception or audition. In aquatic habitats, visual cues can be limited at depth, at night or in periods of high turbidity.

Although underwater olfaction has been documented for two air-breathing vertebrates in aquatic habitats (Catania, 2006; Catania et al., 2008), such specialized abilities are uncommon. Both passive and active hearing may assist in prey detection, but at close range, taction has emerged as a primary sense among aquatic and semi-aquatic taxa, especially when hunting buried invertebrates or fishes (Dehnhardt and Mauck, 2008). For example, many shorebird species probe the tidally flooded substrate with touch structures at their beak tips (Piersma et al., 1998); star-nosed moles seek prey in subterranean streams using specialized appendages around their nostrils (Catania and Kaas, 1997; Catania and Remple, 2004); and seals, sea lions and walruses detect and pursue prey using their vibrissae while diving (Dehnhardt and Mauck, 2008; Dehnhardt et al., 2001; Kastelein and van Gaalen, 1988; Kastelein et al., 1990; Niesterok et al., 2017).

Sea otters are amphibious mammals that dive <100 m to capture invertebrate prey along the north Pacific coastline (Bodkin et al., 2004; Thometz et al., 2016a). As apex predators in nearshore ecosystems, sea otters consume prey occurring in diverse subtidal and intertidal habitats (Riedman and Estes, 1990) and exert strong direct and indirect effects on ecosystem structure and function (Estes and Duggins, 1995; Estes and Palmisano, 1974; Hughes et al., 2013; Watson and Estes, 2011). Although their prey occur in micro-habitats where visual detection is difficult or impossible, sea otters nonetheless maintain a remarkably high rate of prey capture, consuming over a quarter of their own body mass each day (Costa and Kooyman, 1982). Sea otters hunt at the sea floor, but they return to the surface after each foraging dive to breathe and consume captured prey. Because sea otters rest on their backs at the surface while handling prey, direct observation of prey manipulation and consumption is possible; as a result, they have become a model species for diet composition and foraging behavior studies (Elliott Smith et al., 2015; Estes et al., 2003; Newsome et al., 2015; Thometz et al., 2016a; Tinker et al., 2007, 2008, 2012). Although much is known about their prey handling at the surface, basic cognitive and sensory mechanisms integral to prey search and capture remain unknown.

Behavioral observations and morphological patterns suggest that sea otters rely to some degree on touch during foraging. Telemetry-based field studies reveal that sea otters forage equally day and night, when visual cues may be reduced or absent (Bodkin et al., 2007; Gelatt et al., 2002; Ralls et al., 1995; Tinker et al., 2008). Unique among marine mammals, sea otters have two enhanced, complementary tactile structures that can be controlled with dexterity: flexible paws and a complex array of facial vibrissae (Fig. 1). At the surface, sea otters use their paws to manipulate hard-shelled prey directly and indirectly using tools (Fujii et al., 2015), as well as to regularly groom their fur. Their use of vibrissae at the surface is less clear. Although observations of underwater use of

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List of symbols and abbreviations

2AFC	two-alternative forced choice
AICc	Akaike information criterion corrected for small sample size
c	Weber fraction
CI	credible interval
GLMM	generalized linear mixed model
LOOIC	leave-one-out cross-validation information criterion
MCMC	Markov chain Monte Carlo
MCS	method of constant stimuli
MOL	method of limits
s	test session
S−	incorrect discriminative stimulus; subject's choice of this does not receive reinforcement
x_t	difference between the standard and S− on trial t
α	position of the psychometric curve along the abscissa
β	slope of the psychometric curve
γ	poorest performance expected by chance (0.50)
ΔLOOIC	change in LOOIC from the best-supported model
ΔS	discrimination threshold
ε_s	random effects associated with test session s
λ	lapse rate

vibrissae are sparse, sea otters can use their paws and face to dig into soft substrate in pursuit of burrowing invertebrates (Hines and Loughlin, 1980; Shimek, 1977). In support of these observations, sea otter vibrissae, like those of walruses (Fay, 1982), exhibit evidence of wear – particularly in soft-sediment habitats where infaunal bivalves are hunted (Marshall et al., 2014; M. T. Tinker unpublished observations) – which may result from active functional use or passive incidental contact with abrasive sediment.

Sea otter neural architecture provides additional clues indicating the importance of tactile information. The area of the somatosensory cortex representing paws and vibrissae is disproportionately enlarged compared with terrestrial mustelids (Radinsky, 1968), suggesting that sea otters have good tactile sensitivity with both structures. However, a higher proportion of this enlarged cortical area is dedicated to receiving paw input, which suggests that paws may have greater functional relevance than vibrissae in sea otters.

Radinsky (1968) noted the same pattern in other species of invertebrate-eating otters but the opposite pattern in species of fish-eating otters, from which he suggested that the location of enlargement may correspond to mode of prey pursuit and capture – paw-based for invertebrate-eating otters or mouth-based for fish-eating otters.

The gross morphologies of both paws and vibrissae in sea otters seem suited for dexterous touch, consistent with Radinsky's (1968) suggestion. The paws' palmar surfaces are hairless, the digit and palm pads are fused, and the skin has a leathery granular texture (Fig. 1). The neural morphology of sea otter paws has not been described. The structure of the sea otter vibrissal array suggests that substantial blood flow – and thus energetic investment – is directed to these sensory organs to process information in cold, aquatic environments (Marshall et al., 2014). The vibrissae are highly innervated, with a tripartite blood sinus system that more closely resembles aquatic pinnipeds than terrestrial mustelid relatives (Marshall et al., 2014). The vibrissae are smooth, as in otariids (Ginter et al., 2012), some phocids (Berta and Sumich, 1999; Ginter et al., 2012; Marshall et al., 2006), walruses (Berta and Sumich, 1999), water rats (Dehnhardt et al., 1999) and terrestrial mammals (Hyvärinen et al., 2009). Hanke et al. (2013) suggest that smooth vibrissae are advantageous during active touch, i.e. subject-controlled tactile exploration (Gibson, 1962). Active touch is required of benthic foragers, as opposed to mid-water foragers that likely rely on hydrodynamic wake detection. Similar to benthic foragers such as walruses and bearded seals (Fay, 1982; Marshall et al., 2006), the sea otter vibrissal bed is rostrally oriented and comprises microvibrissae and macrovibrissae (Fig. 1).

Despite these behavioral and morphological indications of enhanced tactile sensitivity, fine-scale mechanics of how sea otters use their tactile system to gather information about physical objects or hydrodynamic cues are unknown. Neither absolute nor comparative functional sensitivities of paws and vibrissae have been measured in this species. As sensory perception is inherently probabilistic – influenced by an individual's external environment and internal state – obtaining such data requires controlled conditions with experienced captive subjects trained for psychophysical procedures.

Fig. 1. The right paw and vibrissal region of the sea otter used in the present study. Left panel: sea otter's paw delineated (white dashed lines) into digits (a), upper paw pad (b) and lower paw pad (c). Calipers visible at top of photo; scale bar, 20 mm. Right panel: sea otter's rostrally oriented vibrissal region. Microvibrissae are located medially, and macrovibrissae are located laterally from the midline. The microvibrissae are shorter and more rostrally directed than the macrovibrissae. Scale bar, 20 mm. Photo collection authorized under USFWS research permit MA186914-2. Photo credits: S. M. Strobel and A. Friedlaender.

Here we describe the performance of the sea otter tactile system – paws and vibrissae – in air and under water. To obtain tactile discrimination thresholds (ΔS), we trained and tested an individual sea otter in a behavioral two-alternative forced choice (2AFC) paradigm (Gescheider, 1997) using textured stimuli. To complement these data, we report the sea otter's decision-making strategy, including speed and explorative movement, as well as the effect of testing medium (in air or under water). In addition, we trained and tested four human subjects using their hands in air with the same experimental paradigm to compare the sea otter's abilities with those of a known tactile specialist. These data allowed us to directly compare performance metrics and decision-making strategy between species, assess whether our approach produced comparable results to published studies of humans, and interpret comparisons of the sea otter's performance metrics with published values from marine and terrestrial tactile specialists.

MATERIALS AND METHODS
Testing facility and subject
This study was conducted in Santa Cruz, California, USA, at the University of California Santa Cruz's Long Marine Laboratory and at the California Department of Fish and Wildlife's Marine Wildlife Veterinary Care and Research Center. Testing took place in seawater-filled pools with adjacent haul-out areas. The pools received a continuous supply of fresh seawater from northern Monterey Bay. We monitored water and air temperature at 5-min intervals throughout the study with a temperature logger (TidbiT v2 Temp UTBI-001, Onset Computer Corporation, Bourne, MA, USA), and these remained similar throughout the 2-month testing period (water=15.8±0.4°C, air=15.9±1.2°C).

The subject was a healthy 4-year-old adult female sea otter [*Enhydra lutris* (Linneaus 1758)], identified as 'Selka' (USGS 6511-12R, MBA 595-12). She was trained to participate voluntarily in psychophysical procedures using operant conditioning and positive reinforcement (seafood). The sea otter received approximately 30% of her daily diet during each test session. Her daily diet was established to maintain optimal overall health and was not constrained based on session performance. Animal research was conducted under authorization from the United States Fish and Wildlife Service (research permit MA186914-2) with the approval and oversight of the Institutional Animal Care and Use Committee at the University of California Santa Cruz.

The sea otter was trained and tested to use each tactile structure (i.e. paw or vibrissae) independently in the 2AFC, in air and under water. Daily training occurred over a 17-month period prior to testing to avoid confounding her performance with practice effects and to ensure that she was an expert subject. During training, the sea otter learned to perform the task in the following order: paw in air, paw under water, vibrissae in air, vibrissae under water. Daily testing occurred over a 2-month period post-training; during testing, the sea otter performed the task in the following order: vibrissae in air, vibrissae under water, paw under water, paw in air.

Stimuli
The stimuli comprised a set of acrylic resin plates (Delrin, 20×20×2.6 cm), machined in a pattern of alternating ridges and grooves. Consistent with other published studies of tactile sensitivity (see, e.g. Dehnhardt et al., 1998; Bachteler and Dehnhardt, 1999), we used groove width as the metric of discrimination ability; groove width varied among plates but remained constant within each plate. After machining, stimuli were measured with calipers to confirm sizes and tolerances. The groove widths that defined each stimulus were 5.0, 4.0, 3.6, 3.0, 2.5, 2.4, 2.3, 2.2, 2.1 and 2.0 mm (±0.03 mm average tolerance). Ridge width (2.0 mm, ±0.03 mm average tolerance) and groove depth (5.0 mm, ±0.18 mm average tolerance) were held constant across stimuli. One stimulus per groove width was produced, except for the 2.0 mm stimulus, which served as the predetermined standard for the duration of the experiment. Two of these standard stimuli were produced, each bearing 2.0 mm grooves. As the standard was presented on every trial (simultaneously with one of many potential plates defined as the incorrect stimulus, or S−), the alternating use of two identical standards controlled for any aberrant cues the sea otter might learn after extensive practice with the same plate over hundreds of trials. Consistent with other published studies, stimuli were only presented with grooves vertically oriented; however, we rotated the stimuli 180 deg for each alternating test session to further control for any subtle physical aberrances in the plates.

We used six plates as the S− to the standard for paw testing – ranging from +1.0 mm to +0.1 mm from the standard (3.0, 2.5, 2.4, 2.3, 2.2 and 2.1 mm) – and seven plates as the S− for vibrissal testing – ranging from +1.6 mm to +0.1 mm from the standard (3.6, 3.0, 2.5, 2.4, 2.3, 2.2 and 2.1 mm). We selected these stimuli to span a gradient from easily discriminable to indiscriminable based on threshold estimation during the sea otter's extensive training period.

Test apparatus
The custom-built apparatus comprised an acrylic plastic box (55.5×15×56 cm) with an interchangeable front-facing panel to allow for two differently sized access windows: a narrow one for paw testing and a wide one for vibrissal testing (Fig. 2). The apparatus held two stimuli that fit side-by-side into mounts in the apparatus, one to the sea otter's left and the other to the sea otter's right. The mounts kept the two stimuli separated by 5.2 cm when simultaneously presented to the sea otter. Each stimulus rested against a combined clicker and mechanical switch, which were triggered when the sea otter sufficiently depressed the stimulus from its starting position to indicate her choice. The clicker served to produce an audible, salient sound for the sea otter to associate with the act of making her choice to end each trial. Each session was filmed from inside the apparatus with an overhead-mounted or lateral-mounted high-resolution camera (GoPro Hero3+, 1080, 60 frames s^{-1}) to enable *post hoc* analysis of the sea otter's behavior.

A closed door (which slid vertically into the access window) prevented the sea otter from having visual or tactile access to the stimuli between trials. When closed, the access door activated a mechanical switch mounted to the inside of the apparatus. During trials, when the door slid upwards to open the access window, the sea otter was restricted to using only tactile information. In the paw test, a horizontal slit cut into a neoprene cover for the narrow access window allowed the sea otter to only touch the stimuli with her paws and inhibited her from seeing the stimuli (Fig. 2). In the vibrissal task – during which the wide access window allowed the sea otter to freely approach the stimuli with her face – she was trained to voluntarily wear a neoprene blindfold that did not restrict her mystacial vibrissae (Fig. 2). To prevent the use of paws during the vibrissal task, she was trained to place her paws on a PVC stand attached to the front of the apparatus for the duration of each trial (Fig. 2). On the front face of the apparatus, a square target above the access door marked the fixed location for the sea otter to station (i.e. make firm contact with the target using her nose) prior to each trial (Fig. 2).
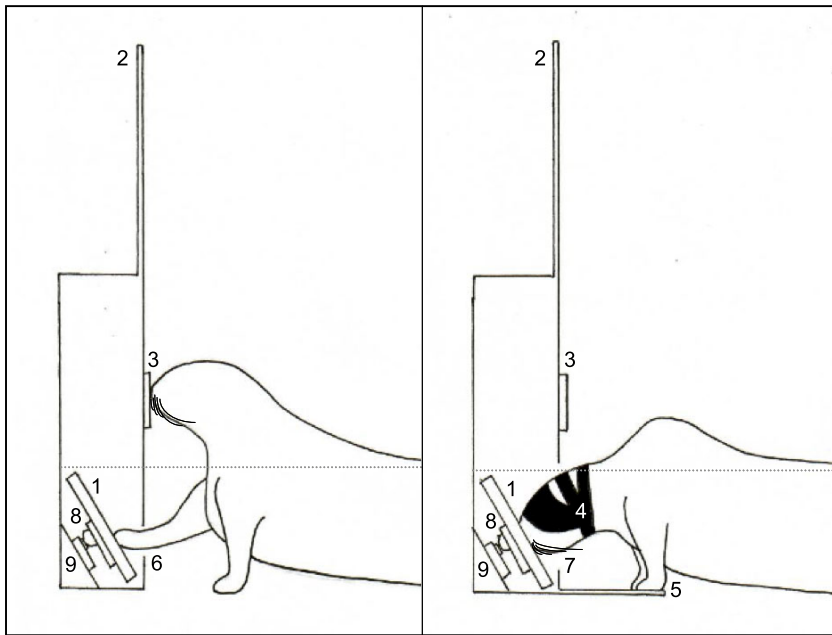
Fig. 2. Schematic drawing of experimental setup. Sea otter interacting with experimental apparatus and left stimulus (1) during paw (left panel) and vibrissal (right panel) testing. A barrier (2) prevented visual cues from the operators. To begin a trial for paw testing, the sea otter positioned her nose on a target (3) on the apparatus front. To begin a trial for vibrissal testing, the blindfolded sea otter (4) positioned her nose on the same target (3) and her paws on a PVC stand extending from the apparatus front (5). The experimenter controlled the sea otter's access to the stimuli via the paw (6) or vibrissal (7) access door. Each stimulus rested against a mechanical clicker (8) that activated an electrical switch (9) when depressed by the sea otter, signifying her choice. The horizontal dotted grey line indicates water height during underwater testing. Illustration credit: S.M.S.

The apparatus rested on a 1-m² haul-out platform in the sea otter's pool. We adjusted the height of the haul-out platform and the pool's water level to create the in-air and underwater conditions. For the in-air conditions, the water level was held just below the haul-out platform, such that the sea otter and apparatus were completely in air for each trial. For the underwater conditions, the water level was raised to completely submerge the stimuli, such that the sea otter and apparatus were partially submerged for each trial (Fig. 2). This design allowed the sea otter to retain the same stable standing position on the haul-out platform while performing the task in either medium.

A visual barrier extended vertically from the top of the apparatus to conceal two operators, sitting directly behind the apparatus on the pool deck, from the sea otter. The operators were responsible for opening and closing the access door, as well as removing and replacing the stimuli in the apparatus between trials. In a separate area that was visually and acoustically isolated from the testing enclosure, an experimenter monitored the session on a closed-circuit video system. The experimenter provided instructions to the operators via headphones during each trial. A trainer, who was seated at the side of the pool to the left of the apparatus, provided instructions and primary reinforcement (seafood) to the sea otter during each session. An Advent AV570 speaker (Audiovox Electronics Corporation, Hauppauge, NY, USA) provided conditioned, acoustic feedback to the sea otter and trainer immediately following the sea otter's choice on each trial. This feedback – previously recorded audible cues – comprised either the bridge for a correct response (bell tone) or the delta for an incorrect response (accelerated human verbal 'no').

Experimental procedure

For all conditions, the sea otter participated in a 2AFC procedure to discriminate the standard from the S−. Correct choice of the standard earned the sea otter food reinforcement (one whole, peeled shrimp), while the incorrect choice of the S− was not reinforced. The experimenter used a custom LabVIEW program (National Instruments, Austin, TX, USA) to automate data collection and provide appropriate, instantaneous auditory feedback via the speaker. The experimenter followed a predetermined sequence

order generated using a custom MATLAB script (MathWorks, Natick, MA, USA). Stimulus presentation within each session followed a predetermined, pseudorandom, modified Gellermann schedule (Gellermann, 1933) that was counterbalanced to ensure equal probability of (1) the standard appearing on the left and right stimulus positions and (2) the standard appearing in the same or alternative position from the previous trial. The overall session sequence was constrained such that neither stimulus was presented on the same side more than four times consecutively. The operators and the trainer were blind to the sequence order and the trainer was blind to individual trial conditions.

The sea otter was trained using a modified method of limits (MOL), during which the subject faced a single stimulus comparison during a session, and tested using a method of constant stimuli (MCS), during which the subject faced a fixed set of stimulus comparisons during a session (Cornsweet, 1962; Stebbins, 1970). During MOL training, the sea otter was presented with a single stimulus combination (one S− paired with the standard) in multiple trials over successive sessions. The first discrimination the sea otter learned was a smooth S− paired with the standard. The next discrimination was the S− with the largest groove width (5.0 mm) paired with the standard. Trials continued until performance met pre-determined learning criteria, defined as performance ≥75% that differed <7% across two consecutive sessions; the sea otter then continued to the next smallest S− paired with the standard. Training continued with all stimulus combinations in descending order until the sea otter had met learning criteria or reliably failed to meet learning criteria across 10 sessions.

Other than the method of stimulus presentation, the experimental procedure was identical for training and testing. A session began when the sea otter was provided access to the apparatus in the testing pool. The sea otter positioned in the water in front of the trainer, who prompted her to approach the apparatus. The sea otter initiated a trial when she made firm contact with her nose on the target; for the vibrissal conditions, the sea otter also placed her paws on the stand. One to five seconds after the sea otter positioned correctly, the access door was opened, which deactivated the mechanical door switch. The timestamp of this deactivation was automatically

recorded in the LabVIEW program to mark the start of the sea otter's access to the stimuli.

During each trial, the sea otter explored the stimuli with either her paws or her vibrissal region (depending on the test condition) and signified her choice by depressing one plate to activate simultaneously the mechanical switch and clicker located behind the plate. The activation of the stimulus mechanical switch was automatically recorded in the LabVIEW program to mark the end of the trial and trigger the acoustic feedback. After making her choice and receiving feedback, the sea otter removed her paw or face from the apparatus, and the access door was closed. The trainer delivered either primary reinforcement for a correct choice or no primary reinforcement for an incorrect choice; in either case, the trainer then directed the sea otter to a location away from the apparatus to avoid inter-trial cues that might unintentionally indicate the details of the next trial to the sea otter. To prepare the next trial, the operators removed both stimuli simultaneously, rinsed them in fresh water, and replaced the new stimulus combination concurrently in the apparatus according to the experimenter's instructions. Once the next trial was set up, the trainer provided a small food item to reinforce the sea otter's inter-trial behavior and then cued the sea otter to return to the apparatus. Inter-trial intervals generally lasted 25–30 s.

For vibrissal testing, the trainer positioned the blindfold on the sea otter at the beginning of the session. Although the sea otter was free to remove the blindfold between trials, she typically voluntarily wore the blindfold for the duration of the session. The trainer ensured the blindfold's proper positioning following each trial and prior to verbally signaling the sea otter to return to the apparatus for the next trial.

Other than the apparatus's design to restrict the sea otter to use only her paws or only her vibrissal region, the sea otter was unrestrained and free to choose her strategy (e.g. order of exploration of stimuli, duration of exploration, number of touches, manner of touching, paw preference) throughout training and testing.

Following the extensive training period with MOL, the sea otter completed 16 test sessions with MCS. One to two sessions were completed each experimental day. Each session included 28 test trials for paw testing and 24 test trials for vibrissal testing, with warm-up and cool-down phases of six to 10 trials each. The warm-up and cool-down phases were used to maintain stimulus control and assess the sea otter's motivation before and after the test phase, respectively, by presenting an S− that was easily discriminable from the standard. In the test phase of each session, the sea otter was presented with four consecutive blocks of trials. Each S− was paired with the standard once per block of trials (six-trial blocks for vibrissae, seven-trial blocks for paws). For each testing condition, the sea otter completed four sessions, which totaled 16 presentations of each S−.

Analysis and determination of discrimination thresholds

Most previous tactile discrimination studies have used linear interpolation to identify discrimination thresholds from performance data (see, e.g. Dehnhardt and Kaminski, 1995; Dehnhardt et al., 1997; Bachteler and Dehnhardt, 1999; Hille et al., 2001). However, this approach uses only a small portion of the overall data (i.e. the two stimulus levels at which performance is closest to 75%) and does not allow error estimation of the psychometric function or a quantitative comparison of psychometric functions and interpolated thresholds from different experimental conditions.

Given the limitations of the linear interpolation method, we instead used a Bayesian approach to fit a sigmoid psychometric function to the observed performance data, considering each

experimental condition separately (Wichmann and Hill, 2001). From the fitted curve, we estimated the sea otter's discrimination threshold (ΔS) – defined as the difference in groove width between the standard and the S− that the subject could reliably detect (i.e. on 75% of presentations). We also estimated the associated 95% credible interval (CI), defined as the range of difference values that includes the true value of ΔS with 95% probability.

Following previous studies (e.g. Wichmann and Hill, 2001), we used a modified two-parameter Weibull function to describe the psychometric curve:

$$\varphi(x_t; \alpha, \beta, \gamma, \lambda, \varepsilon) = \gamma + (1 - \gamma - \lambda) \cdot \left(1 - \exp\left[-\left(\frac{x_t}{\alpha \cdot \varepsilon_s}\right)^{\beta}\right]\right), \quad (1)$$

where x_t is the difference between the standard and S− in trial t ($0.1 < x < 1.6$), parameter α determines the position of the curve along the abscissa, and parameter β determines the curve's slope. Parameters γ and λ were used to adjust the function to allow for stimulus-independent errors: γ represents the maximum possible adjustment, which we fixed at 0.5 owing to the 2AFC design (that is, the poorest performance expected by chance), whereas λ represents the lapse rate – the probability of the subject's attention lapsing, resulting in incorrect responses independent of stimulus intensity. Thus $\gamma + (1 - \gamma - \lambda)$ results in a deviation of the function from the asymptotic value of 1 and sets the subject's realistic 'best' average performance. Finally, error term ε_s allowed for random effects associated with each test session s, where $\log(\varepsilon_s)$ was drawn from a normal distribution with mean 0 and standard deviation σ.

We used Markov chain Monte Carlo (MCMC) methods to fit Eqn 1 to the observed data (y_t, the subject's response to each trial), which we treated as a binomial variable with possible values 1 (correct response) or 0 (incorrect response). Specifically, for each trial, we assumed y_t was drawn from a Bernoulli distribution with probability $\varphi(x_t; \alpha, \beta, \gamma, \lambda, \varepsilon)$. We set uninformative, uniform priors for parameters α, λ and σ, and used a weakly informed prior for β (given the assumption of an increasing function), drawing from a gamma distribution with parameters shape=1.5 and rate=0.1. After a burn-in of 5000 iterations, we saved 20,000 simulations for computing posterior distributions for all parameters. We examined trace plots and Gelman–Rubin statistics to ensure model convergence (we required a Gelman–Rubin statistic of <1.01 for each parameter), and report means and CIs for all statistics. We calculated the ΔS for each psychometric curve by interpolating the estimated function value along the abscissa at the 75% correct response level, as well as the corresponding upper and lower 95% CIs.

Although our primary research aims were to assess the sea otter's performance using paws and vibrissae, in air and under water, we wanted to determine whether any observed differences in performance between structures or media were biologically relevant. This required a statistical method to compare psychometric functions. Using the same Weibull function and MCMC methods described above, we evaluated multiple models to compare the interpolated ΔS and psychometric functions across tactile structures and testing media, and we used a hierarchical model structure to account for random effects associated with different experimental sessions.

We did not set *a priori* expectations of whether tactile discrimination abilities (and, thus, psychometric curves) would differ between structures (paw versus vibrissae) or within different media (in air versus under water). Accordingly, we evaluated a nested suite of five alternative models, differing in the number of α and β

Table 1. Model comparison results for sea otter performance, including for each model the data grouping, number of α parameters (determines the curve position along the abscissa), number of β parameters (determines the curve slope), leave-one-out information criterion (LOOIC; ±s.e.m.), change in LOOIC from the best-supported model (ΔLOOIC; ±s.e.m.) and P-value associated with ΔLOOIC

Model	α	β	LOOIC	ΔLOOIC	P-value
Paw (grouped in air and under water), Vibrissae (grouped in air and under water)	**2**	**2**	**345±19.5**	**0**	**0**
Paw (in air and under water separate), Vibrissae (grouped in air and under water)	**3**	**3**	**348±19.9**	**1.73±1.42**	**0.111**
Paw (grouped in air and under water), Vibrissae (in air and under water separate)	3	3	350±19.6	2.67±0.69	0.0000553
Paw (in air and under water separate), Vibrissae (in air and under water separate)	4	4	354±19.9	4.35±1.53	0.00227
Grouped tactile structures [paw (in air and under water) and vibrissae (in air and under water)]	1	1	355±20.3	5.08±2.33	0.0147

The two best-supported models – based on the lowest LOOIC – are in bold; the ΔLOOIC and P-value associated with the top-listed model are zero, as each model's ΔLOOIC was calculated relative to this model. A model with $P<0.05$ is significantly more different than expected by chance from the top-listed model.

parameters (Table 1) to determine whether performance differed across testing conditions. In the most saturated model, the α and β parameters varied among all four experimental conditions (paw in air, paw under water, vibrissae in air, vibrissae under water), whereas in the least saturated model all experimental conditions shared a single fitted value of α and β. We then compared model fit to determine whether the data provided adequate support to consider the sea otter's performance as different between tactile structures or media. We used the leave-one-out cross-validation information criterion (LOOIC) to compare models, computing LOOIC and ΔLOOIC for each model (Vehtari et al., 2017). We identified the model with the lowest LOOIC as best supported, but also retained models with ΔLOOIC P-values >0.05 (indicating a probability greater than 0.05 that the observed ΔLOOIC was not different from 0).

All model fitting and analyses were conducted using R (https://www.r-project.org/), RStudio (RStudio, Inc., Boston, MA, USA), JAGS (Just Another Gibbs Sampler; Plummer, 2003) and the R packages rjags (http://mcmc-jags.sourceforge.net/) and runjags (Denwood, 2016).

Relative difference thresholds
We calculated the sea otter's relative difference threshold (c), or Weber fraction, as the ratio of the discrimination threshold to the standard's groove width ($c=\Delta S/2.0$). We similarly translated 95% CIs around c as the ratio of the upper and lower CIs of ΔS to the standard groove width. We used the Weber fraction to compare the sea otter's performance with published values for terrestrial and marine tactile specialists performing texture and size discrimination tasks. We were unable to compare the sea otter's performance with results from studies in which the authors either did not use discrete increments to vary the S− from the standard or measure the standard (Carvell and Simons, 1990; Kastelein and van Gaalen, 1988; Kastelein et al., 1990); in these cases, we could not calculate the Weber fraction.

After obtaining the sea otter's ΔS for each condition, we used this information to group two S− levels categorically as supra-threshold (the two stimulus levels at which the sea otter's performance was most similar to a perfect 100% mean correct response) and two S− levels categorically as near-threshold (the two stimulus levels at which the sea otter's performance was most similar to 75% mean correct response). The supra-threshold category indicated levels at which correct discrimination was likely easy for the sea otter, and the near-threshold category indicated levels at which correct discrimination was likely difficult for the sea otter. This enabled us to control for the effect of perceived difficulty when assessing the sea otter's behavioral strategy.

Behavioral strategy determination
After the conclusion of testing, a single observer reviewed the GoPro footage for each session and used frame-by-frame analysis (Adobe Premiere Pro CS6, San Jose, CA, USA) to qualitatively and quantitatively describe the sea otter's fine-scale behavioral strategy for making her decision during each trial of the test phase, including type, degree and pattern of exploration. This information was subsequently used to determine whether the sea otter altered her strategy as a function of difficulty.

To describe type of exploration, we examined lateralization in the sea otter's explorative strategy, as well as the sections of the paw (i.e. lower paw pad, upper paw pad or digits) or vibrissal region (i.e. vibrissal-only contact or a combination of vibrissal and facial skin contact) that the sea otter used to explore the stimuli. We used a chi-square test for equality of proportions to assess whether difficulty influenced the sections of the paw or vibrissal region that the sea otter used to explore the stimuli. Additionally, we used R and lme4 (Bates et al., 2015) to perform a generalized linear mixed model (GLMM) analysis that included facial skin contact as a binary categorical fixed effect to assess whether the type of contact with her vibrissal region influenced the odds of the sea otter making a correct choice. We used the outcome of a trial (i.e. correct or incorrect) as a binomial-distributed response variable and included intercepts for session as the random effect. We compared the model containing the fixed effect with a null model that only contained the random effect. We used R and MuMIn (https://CRAN.R-project.org/package=MuMIn) to assign and rank the two models based on AICc (Akaike information criterion corrected for small sample size) scores and calculate the relative importance of the fixed effect.

To describe the degree of exploration, we defined a single touch as unbroken contact of the tactile structure with a stimulus and recorded the number of touches on each stimulus before the sea otter made her choice. For the vibrissal conditions, we defined an additional variable that examined the number of directional movements the sea otter exhibited during a single touch. To describe the pattern of exploration, we recorded the order of stimulus exploration and calculated the number of stimulus comparisons the sea otter used before making her choice. We defined a single comparison as the successive exploration of two stimuli before a choice (as in Hille et al., 2001). Because of the sea otter's typical pattern of exploring only one stimulus before making her choice, comparisons occurred rarely. For example, exploration of the stimulus to the sea otter's right side followed by immediate choice of the stimulus to the sea otter's left side (R–L) was considered an exploration followed by a choice, not a comparison. Exploration of the stimulus to the sea otter's right side followed by an exploration of the stimulus to the sea otter's left side, followed by an immediate choice on the sea otter's right side (R–L–R) was considered one comparison.

Decision times
For each trial in the test phase, we initially calculated response latency as the time difference between the onset of the door's opening (which deactivated the mechanical door switch) and the full

depression of the stimulus (which activated the mechanical stimulus switch). However, this measurement was a poor indicator of decision time, because the sea otter did not always begin exploration of the stimuli immediately after gaining access to them.

To obtain a more accurate and precise measurement of decision time, a single observer reviewed the recorded video footage from each test trial and used frame-by-frame analysis to calculate the time difference (converted from frames s^{-1} to ms) between the sea otter's initial contact with the stimuli and her decision. The frame of the sea otter's initial touch was clearly distinguishable, but the point of decision depended on the sea otter's pattern of exploration. During training, the sea otter exhibited a consistent pattern of exploring the stimulus to her right side first and deciding to either choose that stimulus or move to immediately choose the stimulus to her left side without further exploration. Because this right-side-biased order of exploration created an artificial difference in latency between left and right choices, we defined the decision point in the test phase as follows: (1) for trials in which the sea otter chose the stimulus to her right side after no exploration of the stimulus to her left side, the decision point was the frame in which the sea otter began to depress the right stimulus; (2) for trials in which the sea otter chose a stimulus immediately after exploring the other stimulus, the decision point was the frame in which the sea otter broke physical contact with the stimulus she touched just prior to her choice. For the latter situation, the sea otter never explored the stimulus she chose after leaving the previous stimulus, so she effectively left one stimulus to choose the other. We report decision time as mean±s.e.m.

Our measurements of decision time focused on the time needed for the sea otter to collect and process tactile cues and then initiate a motor action to represent her decision. Thus, we excluded artifacts resulting from apparatus design or psychophysical procedure. This approach is similar to those reported for a texture discrimination task in West Indian manatees (Bauer et al., 2012) and a size discrimination task in harbor seals (Grant et al., 2013); the subjects in these studies used a strategy similar to that of the sea otter. We did not directly compare our measurements with those from tactile discrimination studies that defined decision time more broadly and, consequently, reported longer latencies (Dehnhardt and Dücker, 1996; Hille et al., 2001).

In-air texture discrimination testing with human subjects
Four human subjects used their hands in air to perform the same 2AFC discrimination task as the sea otter. Before training began, each subject received identical written instructions to choose the stimulus with smaller groove widths on each trial using any strategy (e.g. order of stimulus exploration, duration of stimulus exploration, number of touches, one or both hands, hand preference). As with the sea otter, each human was trained using a modified MOL. Upon reaching a performance plateau during training, each human was tested using MCS. During each experimental session, the humans wore a blindfold and headphones that played a broadband masker to restrict their use of visual or acoustic cues. All research with human subjects was conducted indoors (20–25°C) with written informed consent from the participants and with the approval and oversight of the University of California Santa Cruz's Institutional Review Board.

Following the training period with MOL, each subject completed four test sessions with MCS. One to two test sessions were completed each experimental day. Based on threshold estimation from published values and the subjects' training performances, we chose four plates as the S− to the standard for testing, ranging from +0.4 to +0.1 mm from the standard (2.4, 2.3, 2.2 and 2.1 mm). The session sequences were counterbalanced and constrained using

the same rules as those for the sea otter. Each test session comprised four warm-up trials, 16 test trials and four cool-down trials. In the test phase of each session, the subject was presented with four consecutive blocks of trials. Each S− was paired with the standard once per block of trials, which totaled 16 presentations of each S− over the test period.

Methods for estimating the sigmoidal function based on the observed performance data (see Eqn 1), difference thresholds, Weber fraction, strategy determination and decision times for each subject were identical to those described for the sea otter, with the exception that we evaluated over a smaller range of stimulus differences ($0.1<x<0.4$). We used the Weber fraction to compare the human subjects' performances with those of the sea otter, as well as with published values for human subjects performing texture and size discrimination tasks.

After obtaining the ΔS for each subject, we used this information to assign one S− level categorically as supra-threshold (the stimulus level at which the subject's performance was most similar to a perfect 100% mean correct response) and one S− level categorically as near-threshold (the stimulus level at which the subject's performance was most similar to 75% mean correct response) for each subject. As with the sea otter, this enabled us to test for the effect of perceived difficulty when assessing the subjects' decision times and behavioral strategies.

Effects of difficulty, structure, testing medium and species on performance
We examined whether difficulty (i.e. supra-threshold or near-threshold), tactile structure (i.e. paw or vibrissae) or testing medium (i.e. in air or under water) influenced the sea otter's explorative strategy or decision time. We used R and lme4 (Bates et al., 2015) to perform GLMM analyses that included difficulty level, tactile structure and testing medium as categorical fixed effects. We used the number of touches as a Poisson-distributed response variable, the number of comparisons before a choice as a Poisson-distributed response variable, and decision time as a log-normal-distributed response variable. We created a set of 12 models for each response variable; in the fully saturated model we allowed for an additive three-way interaction between the fixed effects and included intercepts for session as the random effect. We used R and MuMIn (https://CRAN.R-project.org/package=MuMIn) to assign and rank the models based on AICc scores and calculate the relative importance of each fixed effect.

We similarly examined whether difficulty influenced the human subjects' explorative strategy or decision time, but we used generalized linear model (GLM) analyses in addition to GLMM analyses. We assigned subject as either a random effect (for the GLMM) or as a fixed effect (for the GLM) to assess the contribution of between-subject variation to the observed data.

Additionally, we assessed the effects of species and difficulty on strategy and decision time to assess whether the humans and sea otter performed differently. Because we had multiple human subjects but only one sea otter subject, we nested (1) subject within species and (2) session within subject within species for the random effects; this maintained consistency with the inclusion of random effects in the previous analyses.

RESULTS
Sea otter discrimination thresholds
The sea otter's performance data and psychometric functions for texture discrimination using her paw and vibrissae, in air and under water, suggest differences across structure and possibly

medium (Fig. 3). The thresholds and positions of the psychometric curves along the abscissas indicate that the sea otter showed better, more consistent performance with her paw than her vibrissae and slightly better performance in air than under water for both tactile structures (paw in air: ΔS=0.24 mm, 95% CI=0.16–0.32 mm, Weber fraction=0.12; paw under water: ΔS=0.30 mm, 95% CI=0.22–0.37 mm, Weber fraction=0.15; vibrissae in air: ΔS=0.48 mm, 95% CI=0.38–0.73 mm, Weber fraction=0.24; vibrissae under water: ΔS=0.50 mm, 95% CI=0.37–0.79 mm, Weber fraction=0.25). The discrimination thresholds determined using the Bayesian approach approximated (within 0–10%) those determined with traditional linear interpolation.

We examined the model comparison results to determine whether these differences were significant given expected variation in performance, and thus how to interpret the psychophysical data in a biologically meaningful way. In general, the models used to fit the performance data agree that the sea otter's performance with her paw was superior to that with her vibrissae. The model comparison suggests that performance significantly differed between tactile structures, but not necessarily between in air and under water. Two models were identified as best supported based on LOOIC: (1) the model considering in-air and underwater data together for each structure, and (2) the model considering in-air and underwater data together for vibrissae but separately for paw (Table 1). The model considering data by experimental condition received poor support, as it ranked fourth with a significantly higher LOOIC than the

best-supported models (Table 1). We report the estimated means and CIs for each model's parameters (Table S1).

Fitting the psychometric curves to the data grouped by structure, irrespective of medium, indicated that ΔS for paw testing was 0.27 mm (95% CI=0.21–0.32 mm, Weber fraction=0.14), and ΔS for vibrissal testing was 0.47 mm (95% CI=0.40–0.59 mm, Weber fraction=0.24). Again, comparison of the two curves grouped by structure (Fig. 4) showed the sea otter's superior discrimination ability with her paw, evidenced by the left-shifted position of the psychometric curve along the abscissa and the lower calculated ΔS relative to those of her vibrissae.

Sea otter strategy
For both paw and vibrissal testing, the sea otter used a consistent strategy to explore the stimuli. She touched the stimulus presented on her right side first on all trials [100% (416/416)]. She then made her choice based on zero [95.4% (397/416)] to one sequential comparison [4.3% (18/416)]; her maximum of two sequential comparisons occurred only once [0.2% (1/416)]. Thus, the sea otter made her decision to stay (and choose the stimulus on her right) or to shift (leaving the stimulus on her right to immediately choose the stimulus on her left) based on her assessment of the similarity between the initial stimulus and her memory of the standard.

In addition to her strategy of first touching the stimulus on her right, the sea otter showed right-side-biased choice throughout testing. When the standard was presented on her right, she tended to
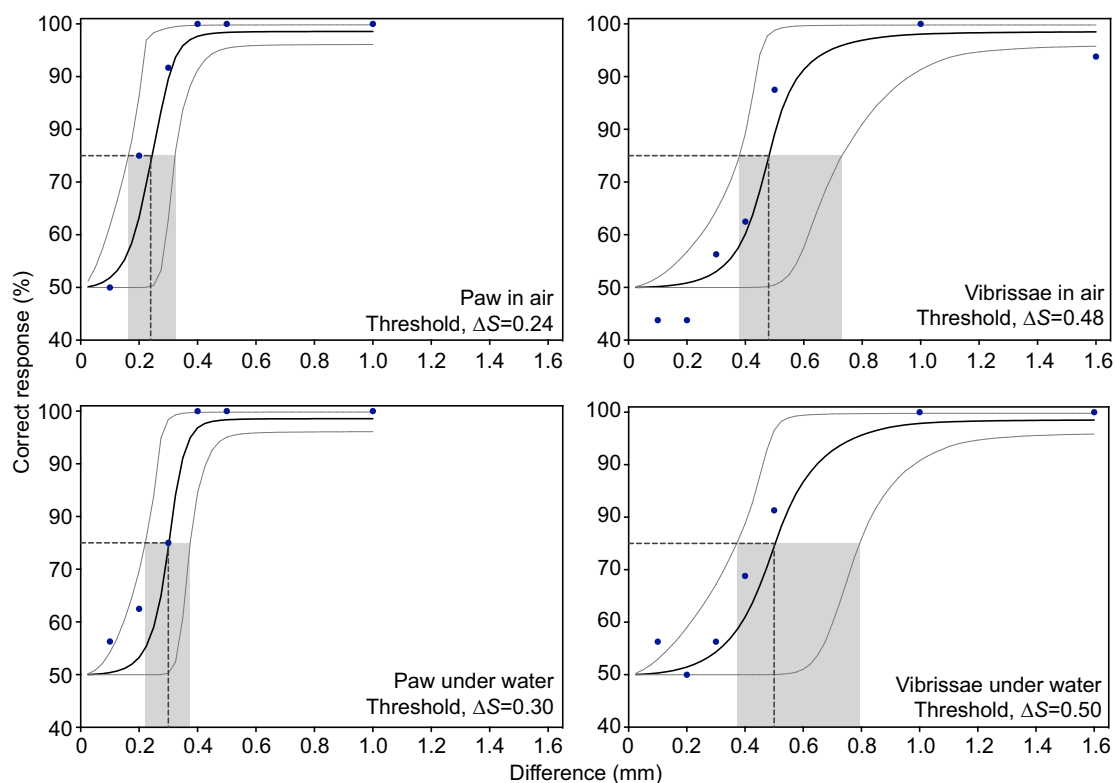

Fig. 3. Psychometric functions for sea otter paw and vibrissal tactile performance in air and under water. Correct response percentages (closed circles) are plotted against the difference between the groove widths of the incorrect stimulus (S−) and standard (2.0 mm) for each of four experimental conditions. Each data point represents the percentage of trials (n=16) for which the sea otter correctly chose the standard instead of the S−. The sea otter completed the same number of trials for each S− for paw and vibrissal testing, but she was presented with fewer S− levels in paw testing. For each experimental condition, we used a modified Weibull function and conducted Markov chain Monte Carlo (MCMC) simulations (n=35,000) to fit the psychometric function (solid black line) and 95% credible intervals (CIs; solid gray lines) to the observed data assuming that each response was generated from a Bernoulli process. Discrimination thresholds (ΔS, vertical dashed line) and 95% CIs (shaded box) at the 75% correct response level were interpolated from the fitted model along the abscissa.
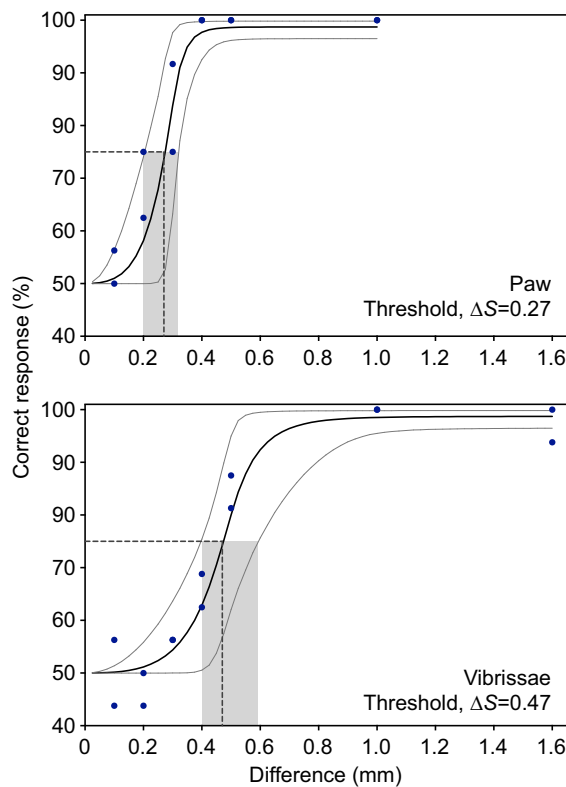
Fig. 4. Psychometric functions for sea otter paw and vibrissal tactile performance, in air and under water combined. Correct response percentages (closed circles) are plotted against the difference between the groove widths of the S− and standard (2.0 mm) for each data grouping: paw and vibrissae. Each data point represents the percentage of trials (*n*=16 each for in air and under water) for which the sea otter correctly chose the standard instead of the S−. Within a structure, two data points are plotted at each S− level (representing in air and under water separately); however, if the sea otter performed equally well, then the two data points appear to the eye as one. The sea otter completed the same number of trials for each S− for paw and vibrissal testing, but she was presented with fewer S− levels in paw testing. For each data grouping, we used a modified Weibull function and conducted MCMC simulations (*n*=35,000) to fit the psychometric function (solid black line) and 95% CIs (solid gray lines) to the observed data assuming that each response was generated from a Bernoulli process. Discrimination thresholds (ΔS, vertical dashed line) and 95% CIs (shaded box) at the 75% correct response level were interpolated from the fitted model along the abscissa.

choose correctly regardless of difficulty [supra-threshold: 98.4% (63/64); near-threshold: 89.1% (57/64)]. However, when the standard was presented on her left, she tended to choose correctly on easier trials and dropped to chance level on more difficult trials [supra-threshold: 100% (64/64); near-threshold: 46.9% (30/64)]. This suggests that the sea otter defaulted near threshold to choosing the stimulus she touched first – here, the stimulus presented on her right.

Although the sea otter was allowed to use either or both paws to explore the stimuli prior to making her choice during paw testing in air and under water, she exclusively used her right paw for all trials [100% (192/192)]. Frame-by-frame video analysis showed that she contacted the stimulus with either the entire paw [66.7% (128/192)] or exclusively with the digits (see Fig. 1a) and upper pad (see Fig. 1b) [33.3% (64/192)], but never with exclusively the lower pad (see Fig. 1c). The percentage of trials in which she used exclusively her digits and upper pad instead of her entire paw pad increased with difficulty [*P*=0.04, X_1^2=4.24; supra-threshold: 25% (16/64);

near-threshold: 42.2% (27/64)]. When using her paw, the sea otter contacted the stimulus with only subtle directional movement: she simultaneously flexed her paw, pressing her skin into the stimulus, and made quick successive lateral micro-movements resembling a vibration (Movie 1).

During vibrissal testing in air and under water, the sea otter contacted the stimulus with the midline of her nasal–oral region and did not show lateralized use of her vibrissal bed in any trial [0% (0/224)]. The sea otter did not protract her vibrissae during stimulus exploration, although capable of this controlled motion. Instead, she explored a stimulus by moving her entire head, making light contact with the surface using mystacial microvibrissae and the oral region, and sometimes mystacial macrovibrissae (Movie 1). She made larger explorative movements with her vibrissae compared with her paw, sweeping her head vertically or diagonally across the stimulus. She typically changed direction while retaining light contact with a stimulus with her vibrissae, but not her paw, and as a result explored more surface area of the stimulus and made more directional changes within a single discrete touch. This mode of exploration, the upper limit of video quality and the speed of her exploration (see 'Sea otter decision time', below) made it difficult to determine how contact with oral skin, rhinarium skin and mystacial microvibrissae contributed to her choice. However, we identified a substantial portion of trials in which the sea otter conclusively used vibrissae, without skin contact, to make her decision [48.7% (109/224)]. The percentage of trials with vibrissal-only contact was not influenced by difficulty [*P*=0.73, X_1^2=0.13; supra-threshold: 56.3% (36/64); near-threshold: 53.1% (34/64)]. Additionally, vibrissal-only contact did not affect the odds of a correct choice, because the model including vibrissal touch as a fixed effect did not differ significantly from the null model.

The sea otter's touch strategy did not differ across experimental conditions, as the best-supported model was the null model, which did not include fixed effects of difficulty, tactile structure or testing medium (Table S2). She made similar numbers of discrete explorative touches with each tactile structure in each medium at each difficulty level, and because the random effect of session accounted for a negligible degree of variance, her touch strategy was consistent across sessions. Difficulty did not influence the alternative movement pattern observed in the vibrissal conditions, in which a single discrete touch comprised multiple directional movements. Testing under water had a slight positive effect on these directional movements; however, this corresponded to an increase of less than one-half touch (Table S3). Results from model selection for the sea otter's comparison strategy similarly indicated that she maintained a consistent, low tendency to compare stimuli for all conditions (Table S2).

Sea otter decision time
The sea otter made decisions quickly with her paw (159.4±4.7 ms) and her vibrissae (346.1±10.0 ms), and for supra-threshold trials (paw: 146.1±6.4 ms; vibrissae: 306.0±18.8 ms) and near-threshold trials (paw: 179.2±9.7 ms; vibrissae: 326.3±16.3 ms) (Fig. 5, left panel). Difficulty, structure and testing medium affected the sea otter's decision time (Table S2). The coefficient estimates obtained from the model selection (Table S2) correspond to decisions that were approximately one-quarter slower when near threshold and approximately two times slower with her vibrissae. Because increased difficulty did not strongly influence the sea otter's touch or comparison strategy, her slower decisions in these conditions can be explained by increased touch duration. Testing medium had a slight effect, corresponding to approximately one-third slower decisions when under water (Table S2).
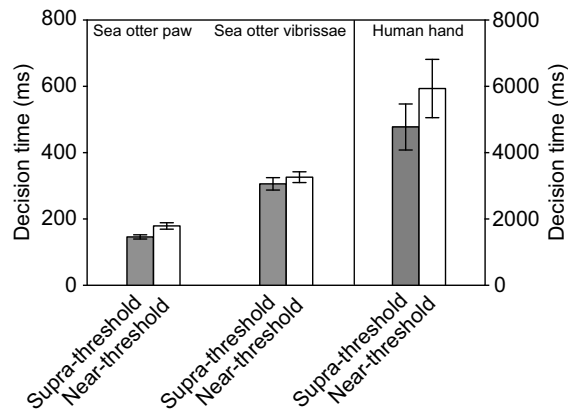
Fig. 5. Decision times for tactile discrimination with sea otter paw, sea otter vibrissae and human hand. Mean±s.e.m. decision times (ms) are plotted for supra-threshold (gray bars) and near-threshold (white bars) trials for paw (in air and under water grouped), vibrissae (in air and under water grouped) and human hands (subjects grouped). The sea otter's data correspond to the left y-axis and the humans' data correspond to the right y-axis. Note that these differ by one order of magnitude. The sea otter showed quick decision times overall (<400 ms), but quicker decisions with her paw than with her vibrissae and for supra-threshold trials. The human subjects were 15- to 30-fold slower than the sea otter using her vibrissae or paw, respectively. Although the human subjects showed quicker decision times in supra-threshold trials relative to near-threshold trials, similar to the sea otter, this effect was not significant.

Fig. 6. Psychometric functions for human hand tactile performance in air. Correct response percentages (closed circles) are plotted against the difference between the groove widths of the S− and standard (2.0 mm). Each data point represents the percentage (n=16 trials) that each human correctly chose the standard instead of the S−. Four data points are plotted at each S− level (representing performance data from each human separately); however, if the subjects performed equally well, then the two data points appear to the eye as one. Human subjects completed the same number of trials as the sea otter for each S−, but they were presented with fewer S− levels. For each subject, we used a modified Weibull function and conducted MCMC simulations (n=35,000) to fit the psychometric function (solid black line) and 95% CIs (solid gray lines) to the observed data assuming that each response was generated from a Bernoulli process. Discrimination thresholds (ΔS, vertical dashed line) and 95% CIs (shaded box) at the 75% correct response level were interpolated from the fitted model along the abscissa.

Human discrimination thresholds and strategies

The human subjects primarily used one hand to perform the discrimination task in air. One subject (KC) initially used both hands: the left hand exclusively touching the stimulus on the left and the right hand exclusively touching the stimulus on the right. This strategy differed from the other subjects, and KC showed poor, highly variable performance. To maintain consistency across subjects, we repeated testing with KC, requiring her to use only one hand; subsequent results include only her second round of testing.

Performance data from the four humans generated similar psychometric functions (Fig. 6). ΔS for the four subjects were 0.20 mm (95% CI=0.11–0.31 mm, Weber fraction=0.10), 0.21 mm (95% CI=0.12–0.31 mm, Weber fraction=0.11), 0.22 mm (95% CI=0.15–0.35 mm, Weber fraction=0.11) and 0.27 mm (95% CI=0.18–0.39 mm, Weber fraction=0.14). Human performance was comparable to that of the sea otter using her paw (Fig. 7, upper panel). Weber fractions confirm that these human data are within the range of published values (see Fig. 7, lower panel) and, thus, that the experimental paradigm generated comparable results.

Three of the four human subjects exclusively used their right hands [100% (64/64 for each subject)]. Another subject (DS) used both hands on only one trial [0.02% (1/64)], for which she chose incorrectly; other than this trial, DS exclusively used her right hand. All humans primarily used their fingertips for stimuli exploration. Inter-subject differences had a strong effect on strategy metrics, with one subject (KC) consistently increasing discrete touches, comparisons and decision time as difficulty increased relative to the other subjects (Table S4).

Significant differences were apparent between the sea otter and human subjects for strategy and decision time (Table S5). The human subjects gathered information about relative properties of the S− and the standard, instead of remembering absolute properties of the standard like the sea otter. Regardless of difficulty, the human subjects explored the stimuli with almost two times more discrete
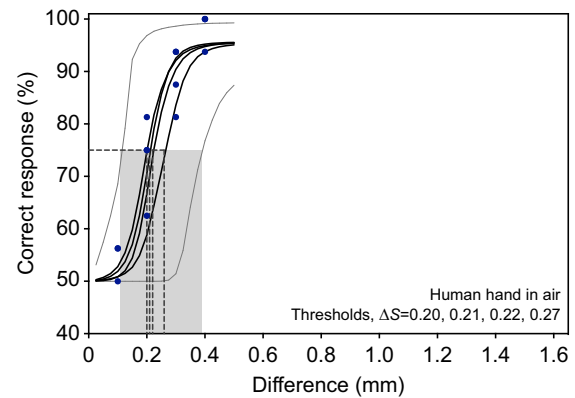
touches and one-third more stimulus comparisons than the sea otter (Table S5). Notably, the mean decision time of the human subjects was 34-fold slower (Fig. 5, right panel) than the sea otter using her paw and 15-fold slower than the sea otter using her vibrissae (Fig. 5, left panel; see Table S5). Thus, the human subjects took considerably longer to perform the same task with accuracy comparable to that of the sea otter.

DISCUSSION

This study demonstrates sensitive touch in an aquatic top predator. The sea otter learned to discriminate textured stimuli in all four testing conditions in the absence of sensory cues other than taction. She showed more sensitive and rapid abilities with her paw than with her vibrissae, and similar performance in air and under water. The sea otter's performance can be generally compared with those obtained from tactile specialists in texture and size discrimination studies (Fig. 7, lower panel). These include terrestrial animals in air (Dehnhardt et al., 1997; Hille et al., 2001; Lamb, 1983; Morley et al., 1983), amphibious animals in air and under water (Dehnhardt, 1994; Dehnhardt and Dücker, 1996; Dehnhardt et al., 1998), and aquatic animals under water (Bachteler and Dehnhardt, 1999; Bauer et al., 2012).

Temperature can influence mammalian tactile performance, because blood perfusion to peripheral sensory structures – which may be reduced in cold temperatures – is critical for maintaining neural sensitivity. However, the constant and moderate temperatures in this study likely minimized the effects of temperature on measured differences in tactile sensitivity between tactile structures or media.

Psychophysical methods can also influence sensitivity measurements. Fixed-level (e.g. MCS) procedures can overestimate thresholds (and, thus, underestimate sensory ability) relative to adaptive (e.g. MOL) procedures (Kollmeier et al., 1988; Stillman,
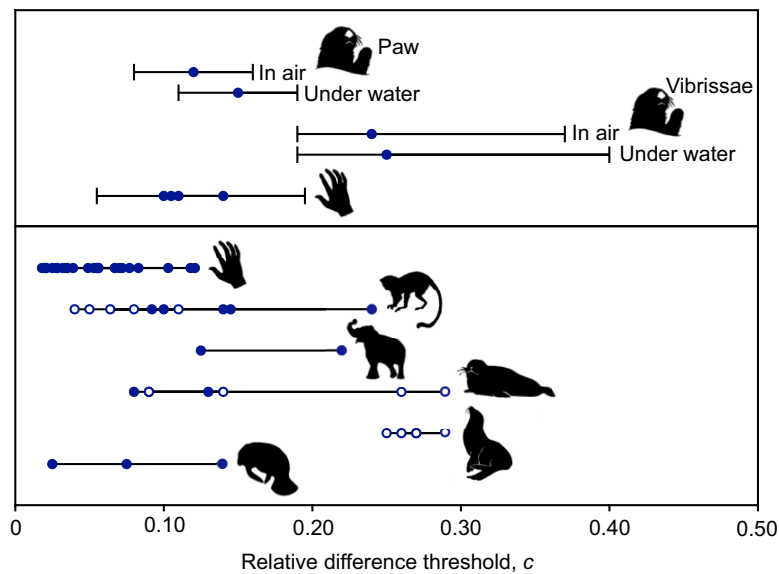
Fig. 7. Tactile sensitivity of sea otter paw and vibrissae compared with terrestrial and aquatic specialists: humans, squirrel monkey, Asian elephant, harbor seal, California sea lion and West Indian manatee. Upper panel (present study): the relative difference threshold (c) and 95% CIs of the sea otter paw, sea otter vibrissae and human hands in air. c is the ratio of the difference threshold, ΔS, to the standard's groove width ($c=\Delta S/2.0$). Each closed circle represents c from a subject (sea otter, $n=1$; human, $n=4$). Lower panel: the relative difference threshold (c) of terrestrial tactile specialists [human hands in air (Lamb, 1983; Morley et al., 1983), squirrel monkey hands in air (Hille et al., 2001), elephant trunk in air (Dehnhardt et al., 1997)], amphibious tactile specialists [harbor seal vibrissae under water (Dehnhardt et al., 1998) and California sea lion vibrissae in air (Dehnhardt, 1994; Dehnhardt and Dücker, 1996)] and an aquatic tactile specialist [West Indian manatee vibrissae under water (Bachteler and Dehnhardt, 1999; Bauer et al., 2012)]. c is calculated from the standard's groove width or size used in the corresponding study. Each closed circle represents c from a subject performing a texture discrimination task (human, $n=18$; squirrel monkey, $n=4$; elephant, $n=2$; harbor seal, $n=2$; manatee, $n=3$). Each open circle represents c from a subject performing a size discrimination task (squirrel monkey, $n=6$; harbor seal, $n=6$; California sea lion, $n=5$). If subjects showed equal c, then the data points appear to the eye as one, even though they are plotted separately. For studies in which subjects performed the same discrimination task with multiple sets of standards (Dehnhardt, 1994; Dehnhardt and Kaminski, 1995; Hille et al., 2001; Lamb, 1983; Morley et al., 1983), the reported sample size reflects the discrimination tasks – plotted separately – even if the subject was the same. Illustration credit: K. Finch.

1989; Taylor et al., 1983). We found preliminary support for this methodological artifact with the sea otter: thresholds calculated via linear interpolation (see, e.g. Dehnhardt et al., 1998) during MOL training were slightly lower than calculated thresholds during MCS testing. Because the thresholds from other studies were obtained with MOL (Bachteler and Dehnhardt, 1999; Dehnhardt et al., 1997, 1998; Hille et al., 2001), the sea otter's slightly elevated thresholds relative to these species may reflect methodological differences, not true differences in tactile sensitivity.

We base our comparisons in this study on the stable, repeatable performance of a highly trained individual. Other studies describe small inter-subject differences in threshold measurements and attribute these to differences in strategy (see, e.g. Bauer et al., 2012; Dehnhardt and Kaminski, 1995; Dehnhardt et al., 1997). We report similar findings for the human subjects tested in this study. Although we certainly expect to find variation in sea otter tactile sensitivity at the population level, assessing this variation requires research focused on collecting lower resolution data than those we report here.

The sensitive sea otter tactile system likely enables high foraging efficiency for processing hard-shelled prey at the water's surface and for hunting visually cryptic prey in low light conditions under water (Bodkin et al., 2004, 2007; Estes et al., 2003). Additionally, the quick exploration and decision-making demonstrated by the sea otter in this study are consistent with energy-rate-maximizing behavior documented for wild foraging sea otters (Ostfeld, 1982; Thometz et al., 2016a). Thometz et al. (2016a) report that sea otters spend half of their 46–72 s foraging dives traveling to and from prey patches; thus, search time equates to 23–36 s for each foraging dive

(Thometz et al., 2016a). In this short time frame, a sea otter must find and capture prey to offset substantial energetic costs of foraging (Yeates et al., 2007), high baseline metabolic demands (Costa and Kooyman, 1982) and additional energetic costs of reproduction, such as providing for a pup (Thometz et al., 2016a,b).

The few documented descriptions of underwater foraging behavior in this species suggest the importance of paws and vibrissae for capture of prey (Hines and Loughlin, 1980; Shimek, 1977), which take shelter infaunally or in high-refuge habitats to avoid detection (Lowry and Pearse, 1973; Raimondi et al., 2015). These prey can show active defense to avoid capture if detected by predators, such as burrowing deeper into the sediment or affixing more tightly to the substrate (e.g. Watanabe, 1983). The combination of sensitive tactile structures in sea otters likely enables quick and accurate abilities to detect prey and interpret whether that prey is worth pursuing. Paws may be especially critical to reach into crevices that a sea otter vibrissal complex is too large to exploit.

Translating these experimental results into predictions of sea otter tactile space is difficult, as artificial stimuli differ from typical prey texture and shape. Sedimentation, vegetation and relief likely make prey discrimination more difficult than in our controlled experimental setting. Notably, however, the thresholds measured in this study correspond to discrimination of objects that differ by the width of standard mechanical pencil lead or less (≤0.5 mm). Prey differ from their micro-habitats by more than this amount, in both size and texture. Additionally, the size difference between prey at which biomass increases is larger than this amount. Thus, both discrimination of prey identity and size should be within tactile discrimination range of foraging sea otters.

The specialized tactile sensitivity in sea otters and the increased paw sensitivity relative to vibrissal sensitivity – both measured behaviorally in this study – coincide with predictions based on brain (Radinsky, 1968) and vibrissal morphology (Marshall et al., 2014). In addition, the measured difference in sensitivity between tactile structures agrees with behavioral observations: wild sea otters use their paws to manipulate and eat prey items at the water's surface, and captive sea otters preferentially use their paws to grasp food and objects (S.M.S., unpublished observations). This pattern is consistent with the sea otter's different decision time between tactile structures: she made quicker decisions with her paw than with her vibrissae. This may result from differences in mechanoreceptor structure, innervation and distribution, or simply from the sea otter's ability to move her paw across the stimuli with more coordination than her entire head.

We can also consider fine-scale aspects of behavioral performance – speed of decision-making and explorative strategy – in the context of patterns demonstrated by other known tactile specialists. These are important when considering the link between structure and function in the sea otter tactile system and interpreting observed foraging patterns in this species.

Decision time and the speed–accuracy trade-off

The sea otter's supra-threshold decision times for either paw or vibrissal discrimination were comparable to those for auditory signal detection in phocids (Sills et al., 2014, 2015), visual discrimination in humans (Kirchner and Thorpe, 2006) and size discrimination in harbor seals (Grant et al., 2013). However, the sea otter's near-threshold decision times were 1.5- to 3-fold faster (Kirchner and Thorpe, 2006; Sills et al., 2014, 2015). At the extreme, the sea otter performed at least 15-fold faster than manatees in a comparable texture discrimination task across all tested levels (Bauer et al., 2012). This means that the sea otter achieved similar accuracy more quickly than these other species when using either her paw or her vibrissae near threshold, and more quickly than the manatees for the task in general.

Even when directly comparing the sea otter with the human subjects in this study, the sea otter maintained quicker decisions with her paw or her vibrissae than the human subjects with their fingertips. Notably, the sea otter's slowest decision time with her paw (500 ms) was still faster than the quickest decision time for humans (767 ms).

Unlike the sea otter, the human subjects typically compared the stimuli before making a choice. Because we did not restrict the trial length for either species, their similar reported sensitivities do not control for obvious differences in stimulus exploration. If the human subjects were restricted to the same explorative time chosen by the sea otter, we would expect a substantial decrease in performance. Lamb (1983) reported a 60% decrease in mean performance when human subjects were restricted to 300 ms stimulus contact time, similar to or greater than the sea otter's mean contact time in this study, instead of 1200 ms. This restricted time is still faster than the human subjects' mean contact times in this study. We found support for the influence of explorative time on sensitivity measurements, because the human subject with the slowest mean decision time (KC; 13,572 ms) had the lowest calculated threshold (i.e. better sensitivity), and the human subject with the fastest mean decision time (JY; 1007 ms) had the highest calculated threshold (i.e. poorer sensitivity).

Sensory perception is a trade-off between speed and accuracy (see, e.g. Fitts, 1966; Wickelgren, 1977). Star-nosed moles represent the mammalian threshold for processing tactile information, making

decisions to attack prey in 25 ms, but they must correct erroneous directional movements one-third of the time (Catania and Remple, 2005). In psychophysical tests, improved accuracy with increased explorative time or successive comparisons has been demonstrated in harbor seals performing size discriminations (Dehnhardt and Kaminski, 1995) and humans performing texture discriminations (Sinclair and Burton, 1991). As difficulty increases, subjects require longer decision times (Bachteler and Dehnhardt, 1999; Bauer et al., 2012; Dehnhardt and Dücker, 1996); however, the presence or intensity of this response can vary by individual even on the same task (Dehnhardt and Kaminski, 1995; Hille et al., 2001).

Explorative strategy

In this study, the sea otter consistently employed a quick and decisive strategy, in which she relied on memory of the standard's absolute properties instead of relative properties of the standard and S−. This strategy reduced the 2AFC discrimination paradigm into a less-sensitive go/no-go procedure. This tendency has been documented in harbor seals (Dehnhardt and Kaminski, 1995; Grant et al., 2013), manatees (Bachteler and Dehnhardt, 1999; Bauer et al., 2012) and squirrel monkeys (Hille et al., 2001) on similar tactile discrimination tasks.

The sea otter's propensity to contact the stimuli with her shorter, rostrally oriented microvibrissae instead of her longer macrovibrissae is similar to vibrissal use in pinnipeds during the identification stage of tactile discrimination tasks (Dehnhardt, 1990, 1994; Grant et al., 2013; Kastelein and van Gaalen, 1988). However, the sea otter's lack of lateral movements differed from other species. Lateral movements have been reported as optimal for feeling texture (Lederman and Klatzky, 1990, 1993; Morley et al., 1983) and were used frequently by the humans in this study and by squirrel monkeys, manatees and rats performing texture discrimination in other studies (Bachteler and Dehnhardt, 1999; Carvell and Simons, 1990; Hille et al., 2001). The explorative strategy used by the sea otter in this study provides an interesting case study; however, because inter-individual differences in strategy have been documented in other species, further generalizations should be avoided.

Future directions

This study highlights how a behavioral approach can address questions about tactile cues relevant for prey capture in the wild. For example, this study focused on active touch, yet sea otters may use hydrodynamic information while foraging for burrowed invertebrates, similar to harbor seals' ability to detect simulated benthic flatfish breathing currents (Niesterok et al., 2017). Although sea otter vibrissae seem morphologically adapted to active touch rather than passive touch required for hydrodynamic detection, this may not preclude sea otters from detecting water currents emitted by prey as a byproduct of respiration. Further behavioral experiments should assess whether sea otter hydrodynamic detection thresholds fall within these typical flow rates.

With respect to temperature, sea otters must retain sensory function in cold habitats – sea surface temperatures reach −3°C in their Alaskan range (NOAA National Data Buoy Center, https://www.ndbc.noaa.gov/). Similar to other marine mammals (Hyvärinen, 1989; Hyvärinen et al., 2009; Ling, 1966; Marshall et al., 2006; McGovern et al., 2015), sea otter vibrissae have an elongated upper cavernous sinus, which may serve as thermal protection (Marshall et al., 2014) to retain heat in these peripheral sensory structures (Dehnhardt et al., 1998, 2003; Erdsack et al., 2014).

We are currently investigating thermal adaptations in sea otter paws, and we predict that substantial blood flow is directed to the mechanoreceptors. Notably, thermographic images of wild otters collected in California and Alaska show considerable heat loss from both the vibrissal pads and the paws in air. Investigations of neural and thermoregulatory structures in sea otter paws will assist in interpreting structure–function relationships in this species and in other otter species that differ in diet preferences and primary mode of prey capture. This research is presently ongoing in our laboratory.

Conclusions

This behavioral study describes how a sea otter interacts with textured stimuli using touch. Our results indicate that sea otter paws and vibrissae can be used to discern the fine details of textured surfaces. Tactile sensitivity is generally comparable to that of terrestrial and marine specialists, including humans performing the same experimental task. Paws showed heightened sensitivity relative to vibrissae, but each structure showed similar performance whether in air or under water.

Our interpretations of the sea otter's sensitivity measurements are likely conservative when considering her consistent tendency to choose without comparing stimuli and different psychophysical methods used to evaluate other tactile specialists. Thus, these results may underestimate the true capabilities of the sea otter tactile system relative to other species. Additionally, determining the extent to which these abilities may be derived in sea otters is difficult given the present lack of information about tactile sensitivity in species not traditionally viewed as tactile specialists, as well as the need to consider other stimuli that are important to aquatic animals.

The significance of this research lies beyond the measurement and comparison of sensory thresholds. Our findings improve the understanding of sensory biology in sea otters and build a mechanistic framework to interpret observed behavior in wild sea otters – such as dive patterns and activity expenditure – especially during foraging for visually cryptic prey species and in low light periods. More broadly, this study contributes to our knowledge of sensory ecology and foraging behavior in air-breathing aquatic vertebrates, including the importance of touch for these top predators.

Author contributions
Conceptualization: S.M.S., C.J.R.; Methodology: S.M.S., J.M.S., C.J.R.; Software: S.M.S., M.T.T.; Validation: S.M.S., C.J.R.; Formal analysis: S.M.S., M.T.T.; Investigation: S.M.S., J.M.S., C.J.R.; Data curation: S.M.S.; Writing - original draft: S.M.S.; Writing - review & editing: S.M.S., J.M.S., M.T.T., C.J.R.; Visualization: S.M.S.; Supervision: C.J.R.; Project administration: S.M.S., C.J.R.; Funding acquisition: S.M.S., C.J.R.

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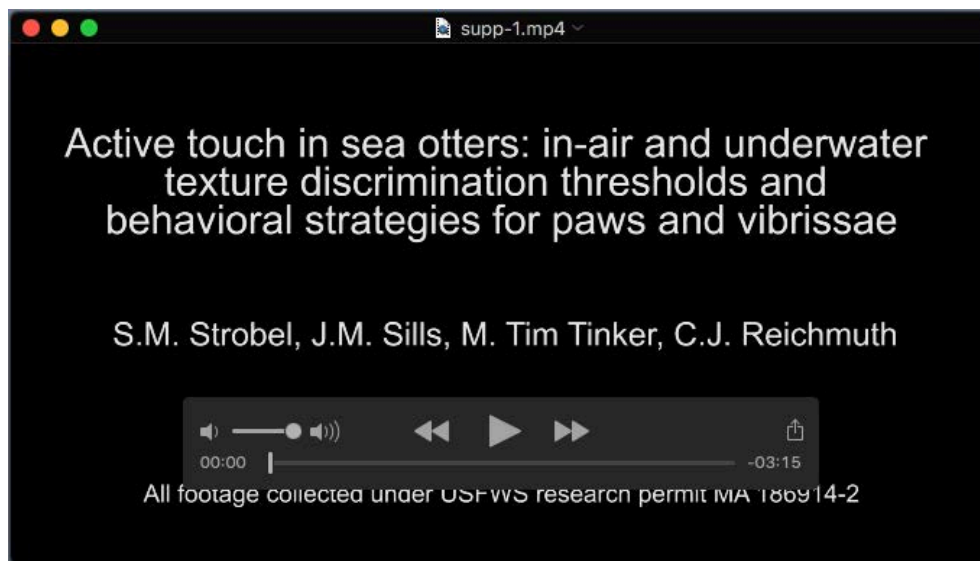
Movie 1. Sea otter's behavioral strategy for paw and vibrissal texture discrimination in air and under water. Video footage of the sea otter interacting with stimulus combinations. For each experimental condition, two trials are shown at full speed and ¼-speed. The sea otter chooses correctly each trial. These trials are representative of her tendencies to explore the right stimulus first and not compare stimuli before making a choice. Video collection authorized under USFWS research permit MA186914-2.

Table S1. Means and 95% credible intervals for parameter estimates of Bayesian models.

Model	Parameter	Mean(s)	CI(s)
Paw (grouped air and water)	α_{paw}	*0.29*	*0.23 - 0.34*
Vibrissae (grouped air and water)	$\alpha_{vibrissae}$	*0.51*	*0.42 - 0.63*
	β_{paw}	*7.50*	*1.35 - 20.63*
	$\beta_{vibrissae}$	*6.29*	*1.46 - 14.44*
	λ	*0.013*	*0.00047 - 0.030*
	σ	*0.097*	*0.000078 - 0.23*
Paw (air and water separate)	$\alpha_{paw, air}$	*0.26*	*0.19 - 0.34*
Vibrissae (grouped air and water)	$\alpha_{paw, water}$	*0.31*	*0.24 - 0.38*
	$\alpha_{vibrissae}$	*0.51*	*0.42 - 0.63*
	$\beta_{paw, air}$	*8.07*	*0.82 - 24.1*
	$\beta_{paw, water}$	*13.05*	*1.29 - 34.1*
	$\beta_{vibrissae}$	*6.29*	*1.39 - 14.47*
	λ	*0.014*	*0.0003 - 0.032*
	σ	*0.102*	*0.00066 - 0.24*
Paw (grouped air and water)	α_{paw}	0.29	0.23 - 0.34
Vibrissae (air and water separate)	$\alpha_{vibrissae, air}$	0.52	0.37 - 0.73
	$\alpha_{vibrissae, water}$	0.55	0.39 - 0.78
	β_{paw}	7.63	1.40 - 21.08
	$\beta_{vibrissae, air}$	10.09	0.83 - 27.72
	$\beta_{vibrissae, water}$	7.53	0.92 - 21.72
	λ	0.013	0.0002 - 0.031
	σ	0.11	0.00032 - 0.25

Paw (air and water separate)	$\alpha_{paw,\ air}$	0.26	0.18 - 0.33
Vibrissae (air and water separate)	$\alpha_{paw,\ water}$	0.31	0.24 - 0.39
	$\alpha_{vibrissae,\ air}$	0.53	0.39 - 0.74
	$\alpha_{vibrissae,\ water}$	0.56	0.39 - 0.79
	$\beta_{paw,\ air}$	8.26	0.98 - 24.94
	$\beta_{paw,\ water}$	13.21	1.13 - 34.12
	$\beta_{vibrissae,\ air}$	10.23	0.87 - 28.04
	$\beta_{vibrissae,\ water}$	7.71	0.81 - 22.43
	λ	0.014	0.00022 - 0.033
	σ	0.12	0.00048 - 0.27
Grouped tactile structures	α	0.39	0.31 - 0.47
[paw (in air and under water) and	β	4.89	1.88 - 9.27
vibrissae (in air and under water)]	λ	0.015	0.00044 - 0.035
	σ	0.31	0.11 - 0.54

The two best-supported models are in bolded italics.

Table S2. Results from GLMM model selection for sea otter strategy: number of discrete exploratory touches, number of stimulus comparisons, and decision time (ms).

Model No.	Intercept	Str_v	Med_{uw}	Str_v x Med_{uw}	$Diff_{nt}$	$Diff_{nt}$ x Str_v	$Diff_{nt}$ x Med_{uw}	AICc	ΔAICc	AIC weight
Number of discrete exploratory touches										
1	*1.05*	*n.i.*	*n.i.*	*n.i.*	*n.i.*	*n.i.*	*n.i.*	*534.23*	*0.00*	*0.78*
2	1.06	0.96	0.96	1.14	n.i.	n.i.	n.i.	540.06	5.83	0.04
3	1.02	1.08	n.i.	n.i.	1.05	0.90	n.i.	540.20	5.97	0.04
4	1.03	1.03	1.02	n.i.	0.99	n.i.	n.i.	540.35	6.12	0.04
5	1.03	n.i.	1.05	n.i.	1.02	n.i.	0.96	540.35	6.12	0.04
6	1.07	0.96	0.96	1.14	0.99	n.i.	n.i.	542.15	7.92	0.01
7	1.004	1.08	1.02	n.i.	1.05	0.90	n.i.	542.27	8.04	0.01
8	1.02	1.02	1.05	n.i.	1.02	n.i.	0.96	542.42	8.19	0.01
9	1.04	1.01	0.96	1.14	1.05	0.90	n.i.	544.08	9.85	0.01
10	1.05	0.96	0.98	1.14	1.02	n.i.	0.96	544.23	10.00	0.01
11	0.99	1.08	1.05	n.i.	1.07	0.90	0.96	544.35	10.12	0.00
12	1.03	1.01	0.98	1.14	1.07	0.90	0.96	546.19	11.96	0.00
Importance		**0.18**	**0.18**	**0.07**	**0.17**	**0.07**	**0.06**			
Number of stimulus comparisons										
1	0.06	0.25	0.25	28	n.i.	n.i.	n.i.	107.4	0.00	0.21
2	0.04	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	107.6	0.18	0.19
3	0.03	0.94	0.25	28	4.00	0.08	n.i.	107.6	0.19	0.19
4	0.03	~1	~0	7.17e8	3.00	0	4.78e7	108.6	1.20	0.12
5	0.01	6.19	n.i.	n.i.	4.00	0.08	n.i.	109.3	1.85	0.08
6	0.07	0.25	0.25	28	0.86	n.i.	n.i.	109.4	2.02	0.08
7	0.05	0.25	0.39	28	1.50	n.i.	0.4	110.9	3.50	0.04
8	0.01	5.81	1.55	n.i.	4.00	0.08	n.i.	111.0	3.56	0.04
9	0.02	n.i.	2.58	n.i.	1.50	n.i.	0.4	112.6	5.16	0.02
10	0.03	1.55	1.55	n.i.	0.86	n.i.	n.i.	112.8	5.41	0.01
11	0.01	5.58	2.09	n.i.	5.50	0.09	0.55	112.9	5.46	0.01
12	0.02	1.55	2.42	n.i.	1.50	n.i.	0.4	114.3	6.88	0.01
Importance		**0.79**	**0.72**	**0.64**	**0.59**	**0.44**	**0.19**			
Decision time										

1	130.5	1.22	1.95	1.37	0.83	n.i.	n.i.	3127.7	0.00	0.22
2	121.5	1.38	2.13	1.37	0.83	0.85	n.i.	3128.3	0.64	0.16
3	139.2	1.09	1.95	1.23	n.i.	n.i.	n.i.	3128.6	0.89	0.14
4	137.9	1.22	1.82	1.25	0.83	n.i.	1.13	3129.0	1.31	0.12
5	130.1	1.23	2.12	1.24	n.i.	0.86	n.i.	3129.3	1.63	0.10
6	128.3	1.36	2.00	1.26	0.83	0.86	1.11	3130.0	2.21	0.07
7	146.9	1.09	1.82	1.13	n.i.	n.i.	1.12	3130.0	2.26	0.07
8	152.9	n.i.	1.82	1.13	n.i.	n.i.	1.13	3130.3	2.62	0.06
9	137.3	1.23	1.98	1.13	n.i.	0.86	1.12	3130.7	2.99	0.05
10	146.1	1.23	2.09	n.i.	n.i.	0.87	n.i.	3142.7	15.0	1.21e-04
11	184.7	1.23	n.i.	1.33	0.81	n.i.	n.i.	3295.7	168.1	7.18e-38
12	224.0	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	3297.0	169.3	3.85e-38
Importance		**0.94**	**1.0**	**1.0**	**0.58**	**0.38**	**0.37**			

Fixed ($Diff_{nt}$ = difficulty, near-threshold; Str_v = tactile structure, vibrissae; Med_{uw} = testing medium, under water) and interactive effects between the fixed effects were systematically removed to create the suite of models. Models are ranked according to the corrected Akaike information criterion (AICc). The AIC weight of each model and the relative importance of each variable (*i.e.*, the summed AIC weights of each model in which the variable is included) are listed as proportions. All model coefficients have been exponentiated for ease of interpretation. The intercept, therefore, represents the number of touches, stimulus comparisons, or decision time (ms) under the default values of the fixed effects (structure = paw, medium = in air, difficulty = supra-threshold). Other coefficients represent multipliers relative to the default values; "n.i." indicates that the variable was not included in the model. Note that because the expected values are so close to 0, it is possible for the multipliers to be very large or very small. The best supported model for number of discrete exploratory touches, the null model, is bolded and italicized.

Table S3. Results from GLMM model selection for sea otter strategy using her vibrissae: directional explorative touches.

Model No.	Intercept	Med_{uw}	$Diff_{nt}$	$Diff_{nt}$ x Med_{uw}	AICc	ΔAICc	AIC weight
1	1.60	1.40	n.i.	n.i.	373.90	0.00	0.48
2	1.66	1.40	0.93	n.i.	375.71	1.80	0.20
3	1.90	n.i.	n.i.	n.i.	376.13	2.23	0.16
4	1.56	1.56	1.06	0.80	377.11	3.21	0.10
5	1.97	n.i.	0.93	n.i.	377.90	4.00	0.07
Importance		**0.78**	**0.36**	**0.10**			

Fixed ($Diff_{nt}$ = difficulty, near-threshold; Med_{uw} = testing medium, under water) and interactive effects between the fixed effects were systematically removed to create the suite of models. Models are ranked according to the corrected Akaike information criterion (AICc). The AIC weight of each model and the relative importance of each variable (*i.e.*, the summed AIC weights of each model in which the variable is included) are listed as proportions. All model coefficients have been exponentiated for ease of interpretation. The intercept, therefore, represents the number of directional touches under the default values of the fixed effects (medium = in air, difficulty = supra-threshold). Other coefficients represent multipliers relative to the default values; "n.i." indicates that the variable was not included in the model.

Table S4. Results from GLMM and GLM model comparison for human strategy: number of discrete exploratory touches, number of stimulus comparisons, and decision time (ms).

Model No.	Model Type	Intercept	$Diff_{nt}$	$Subj_{DS}$	$Subj_{JY}$	$Subj_{KC}$	$Diff_{nt}$ x $Subj_{DS}$	$Diff_{nt}$ x $Subj_{JY}$	$Diff_{nt}$ x $Subj_{KC}$	AICc	ΔAICc	AIC weight
Number of discrete exploratory touches												
1	*GLM*	*2.33*	*1.18*	*0.74*	*0.77*	*1.74*	*n.i.*	*n.i.*	*n.i.*	*428.97*	*0.00*	*0.87*
2	GLM	2.5	1.03	0.70	0.80	1.45	1.12	0.91	1.40	433.17	4.20	0.11
3	GLMM	2.33	1.18	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	437.79	8.82	0.11
4	GLMM	2.53	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	437.97	9.00	0.0097
5	GLMM	2.39	1.12	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	442.41	13.43	0.0011
6	GLM	2.47	1.18	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	468.52	39.55	2.25e-09
Importance			**0.99**		**0.98**			**0.11**				
Number of stimulus comparisons												
1	*GLM*	*0.77*	*1.36*	*0.83*	*1.03*	*3.41*	*n.i.*	*n.i.*	*n.i.*	*366.91*	*0.00*	*0.90*
2	GLM	0.81	1.23	0.77	1.23	2.92	1.14	0.71	1.30	371.44	4.54	0.09
3	GLMM	1.01	1.36	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	376.73	9.83	0.007
4	GLMM	1.19	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	378.96	12.05	0.002
5	GLMM	1.06	1.24	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	382.04	15.14	0.0005
6	GLM	1.20	1.36	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	432.62	65.71	4.83e-15
Importance			**1.0**		**0.99**			**0.09**				
Decision time												
1	*GLM*	*2391.6*	*1.38*	*1.27*	*0.33*	*4.85*	*n.i.*	*n.i.*	*n.i.*	*2480.3*	*0.00*	*0.86*
2	GLM	2668.3	1.17	1.60	0.36	4.20	0.66	0.88	1.25	2483.9	3.64	0.14
3	GLMM	2857.3	1.38	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	2560.6	80.3	3.14e-18
4	GLMM	3471.9	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	2570.6	90.3	2.09e-20
5	GLM	4776.6	1.24	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	2608.5	128.2	1.25e-28

6	GLMM	3319.7	1.08	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	2628.4	148.1	6.01e-33
Importance			**1.0**		**1.0**			**0.14**				

The fixed effects ($Diff_{nt}$ = difficulty, near-threshold, $Subj_{DS}$ = subject (DS); $Subj_{JY}$ = subject (JY); $Subj_{KC}$ = subject (KC)) were systematically removed to create the suite of models. Models are ranked according to the corrected Akaike information criterion (AICc). The AIC weight of each model and the relative importance of each variable (*i.e.*, the summed AIC weights of each model in which the variable is included) are listed as proportions. All model coefficients have been exponentiated for ease of interpretation. The intercept, therefore, represents the number of touches, number of stimulus comparisons, or decision time (ms) under the default values of the fixed effects (difficulty = supra-threshold, subject = CM). Other coefficients represent multipliers relative to the default values; "n.i." indicates that the variable was not included in the model. Model 3 and Model 5 differed with respect to the random effect—in Model 3, subject was included as a random effect, without an interaction with difficulty; in Model #3, the slope and intercept of each subject's response to difficulty was allowed to vary. The best-supported model for each response variable is in bolded italics.

Table S5. Results from GLMM and LMM model comparisons for sea otter and human: discrete exploratory touches, number of stimulus comparisons, and decision time (ms).

Model No.	Intercept	Species$_{so}$	Diff$_{nt}$	Diff$_{nt}$ x Species$_{so}$	AICc	ΔAICc	AIC weight
Number of discrete exploratory touches (GLMM)							
1	2.54	0.41	n.i.	n.i.	975.46	0.00	0.49
2	2.43	0.41	1.09	n.i.	976.32	0.86	0.32
3	2.34	0.45	1.18	0.84	977.29	1.83	0.20
4	1.61	n.i.	n.i.	n.i.	1031.16	55.70	3.93e-13
5	1.54	n.i.	1.09	n.i.	1032.00	56.50	2.58e-13
Importance		**1.0**	**0.51**	**0.20**			
Number of stimulus comparisons (GLMM)							
1	1.03	1.32	0.04	n.i.	487.68	0.00	0.52
2	1.01	1.36	0.05	0.63	489.09	1.41	0.26
3	1.20	n.i.	0.04	n.i.	489.38	1.70	0.22
4	0.18	1.32	n.i.	n.i.	549.52	61.84	1.94e-14
5	0.21	n.i.	n.i.	n.i.	551.24	63.56	8.21e-15
Importance		**0.78**	**1.0**	**0.26**			
Decision time (LMM)							
1	*2891.33*	*1.35*	*0.0006*	*98.37*	*7439.8*	*0.00*	*0.97*
2	2795.32	1.41	0.066	n.i.	7447.0	7.23	0.026
3	3431.33	n.i.	0.065	n.i.	7487.6	47.82	4.03e-11
4	720.11	1.39	n.i.	n.i.	7529.8	89.97	2.84e-20
5	876.76	n.i.	n.i.	n.i.	7569.3	129.46	7.51e-29
Importance		**1.0**	**1.0**	**0.97**			

The fixed effects (Diff$_{nt}$ = difficulty, near-threshold; Species$_{so}$, sea otter) and interactive effects between the fixed effects were systematically removed to create the suite of models. Models are ranked according to the corrected Akaike information criterion (AICc). The AIC weight of each model and the relative importance of each variable (*i.e.*, the summed AIC weights of each model in which the variable is included) are listed as proportions. All model coefficients have been exponentiated for ease of interpretation. The intercept, therefore, represents the number of touches, stimulus comparisons, or the decision time (ms) under the default values of the fixed effects (species = human, difficulty = supra-threshold). Other coefficients represent multipliers relative to the default values; "n.i." indicates that the variable was not included in the model. Note that because the expected value for sea otter is much smaller than that for human, the multipliers can be very large or very small. The best supported model for decision time, the saturated model, is bolded and italicized.