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Implications of tactile enrichment on the behaviour and whisker movements of four species of carnivorans

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ABSTRACT

Caniformia include a range of aquatic, semi-aquatic and terrestrial species, which reveal diversity in their whisker arrangements and shape. Whisker movements play a crucial role in the perception of tactile information, allowing whiskered mammals to distinguish between shapes, sizes, and textures. Despite the significance of whisker movements in sensory perception, few studies have focussed on measuring whisker movements during tactile sensing. Whisker enrichment tasks have the potential to expand behavioural repertoires of animals in captivity and reduce stereotypical behaviours. However, despite whiskers being essential in guiding foraging and exploration in many mammalian species, tactile whisker enrichment tasks are rare. Here, we utilised a novel tactile enrichment device to investigate the whisker movements in four Caniform species in captivity, including two pinnipeds- South African fur seals (*Arctocephalus pussilus*) and harbour seals (*Phoca vitulina*), a mustelid – Eurasian otter (*Lutra lutra*), and a canid – red fox (*Vulpes vulpes*) during a texture discrimination task. This study is the first to explore the impact of tactile enrichment on the behavioural repertoire of caniforms in captivity and provides the first insight of whisker movements in South African fur seals. The introduction of the tactile enrichment device did not increase the behavioural repertoire, nor did it lead to an increase in stereotypical behaviours or aggression in any of the species. However, it did successfully encourage natural whisker movements in the pinnipeds and otter. The whisker amplitude measure was especially high in the South African fur seals. We suggest that such a complex, discrimination-based enrichment task might only be feasible for more trainable caniforms, such as pinnipeds, rather than more neophobic species, such as the red fox, which did not interact with the enrichment device throughout the study. Therefore, while our enrichment device increased natural whisker movements, an even simpler foraging task might encourage tactile sensing without the requirement for training, making tactile whisker enrichment available to a wider group of species.

1. Introduction

Caniformia is the "dog-like" suborder of Carnivora, including dogs, bears, raccoons, mustelids and pinnipeds. Within the Caniformia, an aquatic lifestyle has evolved a number of times, including in the pinnipeds, as well as in semi-aquatic mustelids (Botton-Divet et al., 2017) and ursids (Slater et al., 2010). An aquatic lifestyle has important implications for feeding, locomotion and sensing (Van Valkenburgh, 2007; Botton-Divet et al., 2017) that have led to diverse morphological adaptations, especially revealed in sensory structures, such as the whiskers, which are vibrotactile sensors used to guide locomotion and foraging (Dougill et al., 2020; 2023; Grant and Goss, 2022). Aquatic carnivorans, such as pinnipeds, have more sensitive whiskers, compared to terrestrial mammals (Stephens et al., 1973; Hyvärinen, 1989; Reep et al., 2001; Marshall et al., 2006; Mattson and Marshall, 2016). A recent paper (Dougill et al., 2023) found that aquatic Carnivora species have thicker, shorter whiskers than those of terrestrial species with semi-aquatic species being somewhat intermediary between the two. The authors suggest that the thicker whiskers of the aquatic carnivora may be stiffer and more able to maintain their shape and position during underwater sensing. Indeed, whisker positioning is important for sensing. In object identification tasks, alterations in the positioning and

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movement of whiskers are thought to enhance the quality of tactile information gained from touch, for example, by increasing the number of contacts, and controlling the force of the whiskers against a surface (Mitchinson et al., 2007; Grant et al., 2009; Grant and Goss, 2022). California sea lions have even been found to make task-specific movements with their whiskers, showing precise control over movement and perception, that has only ever before been described in humans (Milne et al., 2020). Harbour seals can use their whiskers to distinguish between different textured grooves with widths as small as 0.2 mm (Dehnhardt et al., 1998), and can rapidly assess size differences in objects in less than half a second (Grant et al., 2013). However, despite whisker movements being an important sensory manifestation, few studies have specifically focussed on measuring whisker movements (Milne and Grant., 2014; Milne et al., 2020; Milne et al., 2021).

Animals in captivity, such as those in zoos, can have reduced expressions of natural behaviours (Mason, 1991; Shyne, 2006; Mason et al., 2007) and enrichment tasks are employed to encourage species-typical behaviours (Markowitz., 1982). Most enrichment tasks encourage feeding or foraging behaviours (Foster-Turley and Markowitz., 1982; Lindburg, 1998; Ross, 2002; Kistler et al., 2009; Hocking et al., 2015), and can be paired with sensory tasks, such as by using additional auditory or olfactory cues (Kastelein and Wiepkema, 1989; Grindrod and Cleaver, 2001; Hunter et al., 2002; Hocking et al., 2014; Samuelson et al., 2017; Wegman and DeLong, 2023). Introducing enrichment tasks can cause an expansion of an animal's behavioural repertoire and a reduction in stereotypical behaviours (Lindburg, 1988; Kastelein and Wiepkema, 1989; Aday, 1993; Hunter et al., 2002; Swaisgood, Shepherdson., 2005; Nelson., 2010; Hocking et al., 2014; 2015). However, despite whiskers playing a key role in guiding exploration, hunting, and foraging in many mammalian species (Hyvärinen, 1989; Anjum et al., 2006; Adachi et al., 2022), it is rare for tactile whisker enrichment tasks to be adopted. A previous study measured whisker movements during novel object exploration in sixteen mammalian species (including five Caniform species, *Mustela furo, Mustela nivalis, Lutra lutra, Vulpes vulpes and Phoca vitulina*) (Grant et al., 2023), and found prominent whisker movements in all species tested, and aspects of whisker control (such as asymmetric whisker movements) present in all species of caniformia tested, suggesting that whisker enrichment can promote whisker movements. Other studies have developed whisker enrichment tasks for pinnipeds only, including active feeding (Milne et al., 2020); ball-balancing (Milne et al., 2014) and object discrimination (Grant et al., 2013; Milne et al., 2022). The focus of studies on pinnipeds is probably due to their prevalence in captivity, alongside their ease of training. Many of these studies have primarily focussed on tasks of discrimination of object shapes and sizes, although these can take a long time to train (Grant et al., 2013; Milne et al., 2022). Moreover, since many other species also actively employ their whiskers, it is important to encourage variable whisker movements in other species, especially in other aquatic species.

This study presents a novel tactile enrichment device for a textural discrimination task, and measures resulting whisker movements in four caniform species. These include two aquatic pinniped species: South African fur seals and harbour seals, one semi-aquatic mustelid: Eurasian otter, and one terrestrial canid: red fox. The device was entirely novel and designed to mimic a domestic pet puzzle board, with the hope that food will provide a motivator for learning the task, without needing the specific training that is usual for discrimination tasks. Texture was selected as the focus for the task, since this is likely to promote large whisker movements as the animal will sweep their whiskers over the surface, which has previously been observed in California sea lions (*Zalophus californianus*) (Dehnhardt and Dücker, 1996; Milne et al., 2022) and sea otters (*Enhydra lutris*) (Strobel et al., 2018). This study marks the first investigation into the effectiveness of tactile enrichment in enhancing the behavioural repertoire of caniforms in captivity and provides the first description of South African fur seal whisker movements.

2. Methods

2.1. Animals

Four caniform species were selected across three families – two pinnipeds: South African fur seals (*Arctocephalus pussilus*) and harbour seals (*Phoca vitulina*), one mustelid: Eurasian otter (*Lutra lutra*), and one canid: red fox (*Vulpes vulpes*) – representing aquatic, semi-aquatic and terrestrial species, respectively. The pinnipeds used in this study were all female adults, and housed at Rhyl SeaQuarium, UK. The South African fur seals included Bubbles (5 years old), Gina (5 years old), and Flo (5 years old); and the harbour seals were Ina (20 years old) and Pamina (18 years old). The Eurasian otter, Loki, was a 7-year old male, and the red fox, Ariel, was a 5-year-old female, and both were housed at the Wildwood Trust, UK. Two additional red foxes and one South African fur seal were also present for the study but did not choose to interact with the enrichment; therefore, they were not included further in the study. All the animals used in this study have previously been exposed to enrichment tasks, however these were variable between the collections and species (as is usual, i.e. see Grant et al., 2023). The red fox was only trained for hand-feeding and had not been exposed to any other forms of training. The Eurasian otter completed target training regularly, and all the pinnipeds undertook daily husbandry training as well as some aspects of public display work and have previously been exposed to a whisker object discrimination task (similar to Milne et al., 2020). Following the procedures outlined by Milne and Grant (2014), the animals in this study were not blindfolded. This decision was made to ensure that the whisker movements were ethologically relevant to the naturalistic behaviours observed in the wild, since their whisker movements would always occur naturally in conjunction with sight. Blindfolding the individuals could also potentially lead to an increased reliance on whisker contact resulting in atypical whisker movements (Arkley et al., 2014; Grant et al., 2018). All experiments were approved by the Manchester Metropolitan University ethical committee (ID:6009), as well as local committees at Rhyl SeaQuarium and the Wildwood Trust. The introduction of enrichment aligns with standard zoo husbandry practices.

2.2. Experimental Apparatus

The enrichment device was modelled on a domestic pet puzzle board, with the hope that the food would provide a motivator for learning the task, without needing any specific training. It consisted of a metal frame and acrylic sheet containing six square slots (Fig. 1a). Each slot has a moveable door with tactile stimuli, including two doors with a smooth surface without any grooves, two doors with fine grooves spaced 5 mm apart (2 mm depth), and two doors with wider grooves spaced 10 mm apart (2 mm depth). The 10 mm textured doors were the target doors (S+), and the others were distractors (S-) (Fig. 1a). This means that the animal has the chance to find two target doors per session, an improvement to usual discrimination tasks, that need to be reset after only one trial (Grant et al., 2014; Milne et al., 2022). Each door was 3D printed in Nylon (Fuse One printer) to ensure accurately positioned ridges and vapor-smoothed to give a smooth surface between the textured ridges. The slots behind the target texture were filled with food (see Fig. 1b) (such as pieces of herring and mackerel for the harbour seals and South African fur seals, and pieces of chick, rat, ox heart or fish for the red fox and Eurasian otter). This provided a reward to the animals to help them recognise the target texture. A GoPro camera recording at 120 frames per second (fps) was secured in a waterproof case and mounted on top of the apparatus. This allowed the whiskers to be viewed from above when interacting with the enrichment device, which is a standard approach to tracking whisker movements (Voigts et al., 2008; Grant et al., 2009, 2012; 2023; Mitchinson et al., 2011). The apparatus was set up to conduct the experiment on the ground within the animal enclosures (Fig. 1c, g, i) or held underwater for the harbour seals by a

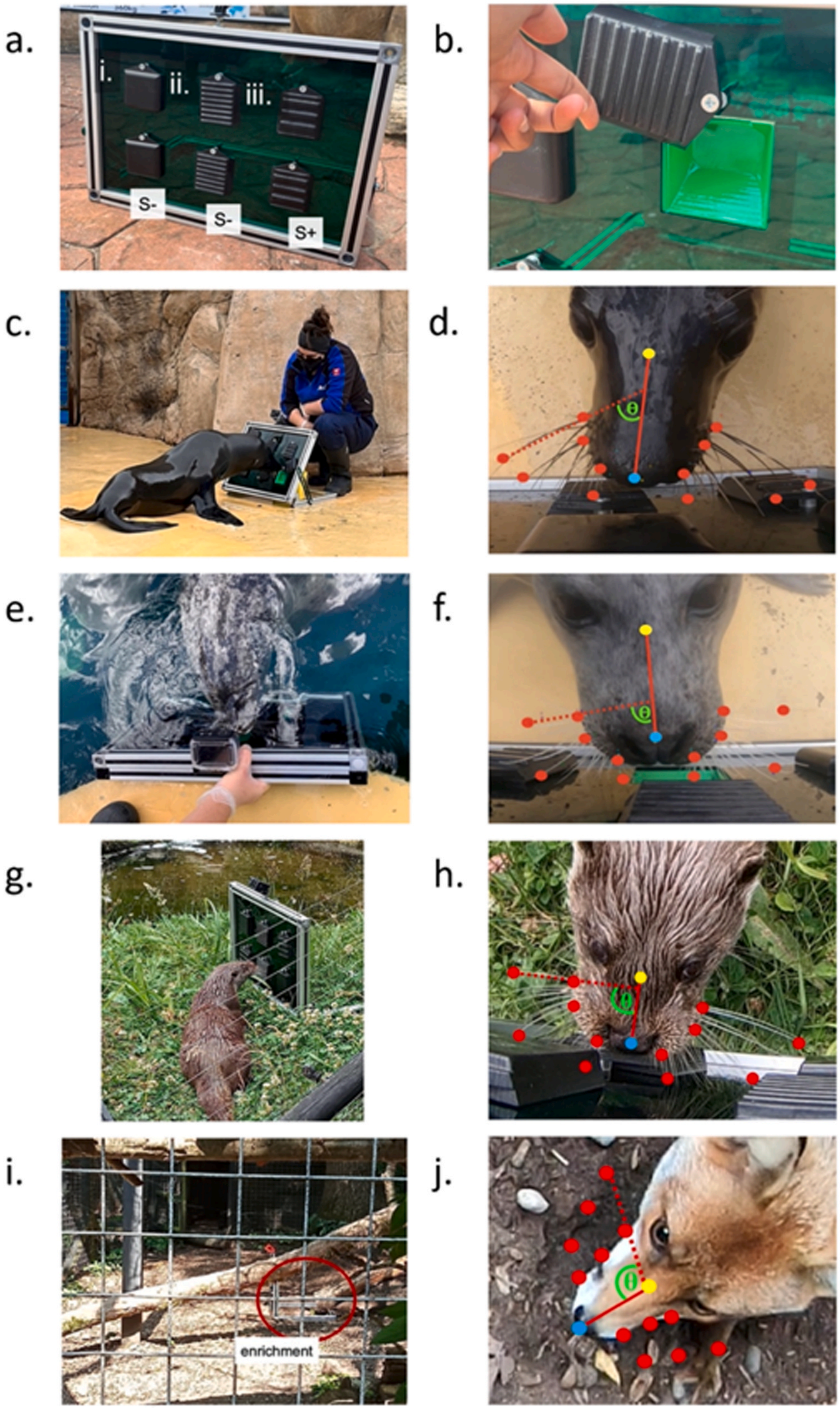

Fig. 1. Enrichment device set up (left panels) and whisker tracking using the Manual whisker annotator (right panels). **a)** Enrichment device with different texture doors, wherein (**i**) distractor (S-) texture with a smooth surface, lacking grooves, (**ii**) distractor (S-) texture with 5 mm grooves, and (**iii**) target (S+) texture with 10 mm grooves, **b)** Parallel swing opening of door with slot, **c)** experimental setup on land for South African fur seals*;* **d)** South African fur seal tracking frame; **e)** enrichment device was held underwater by trainer for harbour seals; **f)** harbour seal tracking frame; **g)** setup for Eurasian otter; **h)** Eurasian otter tracking frame; **i)** setup for red fox inside enclosure; **j)** red fox tracking frame. *Red dots* = points tracked along whiskers; *yellow dots* = nose point; *blue dots* = orientation point; θ = measured whisker angle through which the whisker angular position, amplitude and asymmetry is derived.

trainer (Fig. 1e), who was positioned on the beach area behind the enrichment device.

2.3. Ethograms

Ethograms were created for all four species based on available behavioural literature (Smith and Litchfield, 2010; Hocking et al., 2015; Azevedo et al., 2015) and modified to fit behaviours displayed *ad libitum* (Table1; see Supplementary material Table. S1 and S2 for individual species ethograms). Behavioural observations were conducted over three weeks, wherein 20 minutes (1200 seconds) of continuous focal sampling was carried out twice a day per individual, at a time when the animals were not engaging in training, feeding, enrichment, or shows. Individual behaviours were further categorised and grouped into the following categories: random locomotion, maintenance, interactions, stereotypic, out of sight, other.

Table 1.
General ethogram for behaviours with operational definitions.

Behaviour Type	*Behaviour*	*Description*
Locomotion	Land Locomotion	Walking or running, to travel from one area to another on land.
	Random Swimming	Non-repetitive swimming around the pool without any specific pattern.
	Rafting	Floating on the surface of the water with one of the front flippers and hind flipper out of the water
	Surfacing	Popping head at the surface of the water, without using front limbs to swim around; presumably to breathe and collect air.
	Surface swimming	Swimming on the surface of the water with head over the surface.
	Deep-dive	Descending to deeper parts of the pool from the surface in a single swim.
Maintenance	Resting	Inactive on land with entire body lying on the ground with eyes either closed or open
	Defecating	Excreting faeces and/or urine
	Grooming	Scratching, licking, or biting at itself, or rubbing body against a hard surface
	Feeding/ chewing	The animal is biting, chewing, handling or ingesting food
	Drinking	Ingesting water
	Digging	Using paws of front limbs and clawing at the ground to dig a hole or scuff the ground
	Nesting	Moving and arranging bedding material before lying down
	Rolling	Laying down on the ground and rolling body horizontally
Exploration	Exploration	Exploring the enclosure by sniffing with visual scanning of surroundings
Vigilance	Vigilance	On land or head out of water while swimming, visually scanning surroundings
Interactions	Play	Play behaviour directed at itself, conspecifics, keepers or visitors; may be using other enrichment objects
	Vocalising	Making a noise, calling
	Conspecific interaction	Any physical interaction between conspecifics
	Keeper Interaction	Following/ interacting with keeper, usually as keeper is walking around enclosure boundaries
	Aggression	Biting/ clawing/ slapping front limbs at conspecific in an intentionally harmful manner.
Stereotypic	Patterned Locomotion	Travelling in 'laps' in a continuous repetitive pattern of revolutions at constant speed. Not necessarily stereotypic, may just indicate limited or common locomotion routes
Other	Other	Any other un-remarkable behaviours observed other than the ones above.
Out of Sight	Out of Sight	Animal is outside field of view of observer.

2.4. Experimental Protocol

The data collection occurred in three phases. Phase 1 consisted of five days of behavioural observations **before** introduction of the enrichment device. However, upon discussions with the animal keepers, for the harbour seals and red foxes who are quite shy and neophobic, the enrichment device was put in their enclosures to get them habituated to its presence. During this time, it was ignored and not interacted with by the keepers, and no food was put in or near it. Species-specific protocols and flexibility are often part of comparative behaviour work in agreement with the recommendations of Grant et al. (2023). Phase 2 comprised of **training** sessions during which the enrichment device was set with food and introduced to the animals (either individually, in pairs, or to the whole group). The purpose of these sessions was to get the animals accustomed to correctly selecting the 10 mm texture door as the target by rewarding them with the food behind the door each time they made the correct choice and opened it. It was realised during the beginning of this phase that the animals required guidance by the keepers in order to associate the presence of food with the target texture, and could not complete the task without keeper input. This was done in different ways depending on the species (as per recommendations of Grant et al., 2023). For the harbour seals and South African fur seals, progressive stages included: (i) one day with all doors absent and only fish present in the slots; (ii) two days with one door of each texture present with fish behind them. This stage was crucial for the harbour seals that took longer to move the doors and get to the food due to their larger muzzles; and (iii) three days with all doors present and the only target texture doors with fish behind them. For the red foxes, the enrichment device was loaded with food daily and placed in their enclosure, then removed after one hour. For the Eurasian otter, progressive stages included: i) two days with enrichment device in enclosure with food behind target door, and all doors slightly open, although the otter did not approach the device after the first contact on the first day; ii) therefore, we then did five days with a target stick to help find target door, and all doors slightly open; iii) four days with all doors present and the only target texture doors with food behind them. Behavioural observations were made during this period for each animal. Phase 3 was the **post-training** phase, wherein the animal did the full task, with minimal guidance, including freely exploring and choosing the door with the target texture, then opening it to be rewarded with food. Each animal was filmed interacting with the enrichment for a duration of approximately 10–50 mins, with one to two sessions per day for a week. Additional food was given throughout each session to reward participation. The position of the doors was changed every day, to avoid the habituation of the animals to the positions of the target doors. Behavioural observations were also conducted for five days of this phase for each animal.

2.5. Video analysis

All the video clips were collected from the enrichment sessions, and individual trials were identified for further analysis. A trial was defined as an approach and whisker touch with a target door, distractor door or additional food item. Trials were included based on the following criteria: (i) the camera had a clear view of the nose and at least one side of the muzzle, including a full whisker field, and (ii) the animal did not exhibit significant rolling or pitching of its head. In total, we selected 54 trials for the harbour seals (20 during training of enrichment and 34 post-training), 76 trials for the South African fur seals (8 during training and 68 post-training), 45 trials for the Eurasian otter (9 during training and 36 post-training), and four trials for the red fox (all during training since the fox did not learn the task). In each trial the nose tip point and orientation point, in between the eyes, were manually tracked, along with three whiskers on both sides of the face (see Fig. 1d, f, h, j), where possible, as sometimes only three whiskers on one side of the face that were in field of view could be tracked (for 9 trials in harbour seal, 35 in

South African fur seals, 13 trials in the Eurasian otter and 3 in the Red fox). This tracking was performed for every frame of the video clip using an open-source tracking tool, the 'Manual Whisker Annotator' (MWA) (Hewitt et al., 2016). For each whisker, two points were tracked: the base of the whisker and the shaft - a point two-thirds along its length. Whisker variables were then calculated, including whisker angular position (mean whisker angle determined by averaging all the tracked whisker angular positions over all frames), whisker maximum amplitude (difference between the maximum and minimum whisker angular positions), and whisker asymmetry (difference between the mean left whisker angular positions and the mean right angular position, when data for both sides were available) (Milne and Grant, 2014).

2.6. Statistical Considerations

The normality of all data was assessed using Shapiro-Wilks. The behavioural data did not follow the assumption of normality, and Kruskal-Wallis tests were adopted to compare the mean time spent doing the behaviours i) before enrichment, ii) during training of enrichment, and iii) post-training of enrichment. For the red fox, which did not directly engage with the enrichment, a Paired Wilcoxon test was conducted to compare i) before enrichment and ii) during training of enrichment. The whisker measurement data was compared between trials for when the animal was i) eating food, ii) contacting the target texture, and iii) contacting the distractor textures on the enrichment. These comparisons were conducted on individuals (Supplementary material), as well as grouped per-species. Whisker angular position and amplitude data was not normally distributed for most animals, therefore a non-parametric Kruskal Wallis comparison of means was carried out, followed by a Dunn's Post-hoc Test (Derek et al., 2023). For whisker asymmetry, analysis of variance (ANOVA) was performed, followed by a Mann-Whitney U pairwise comparison which was also followed to compare behaviours i) during training of enrichment, and ii) post-training of enrichment.

Throughout all tests, the critical value of α was set at $p < 0.05$. Mean values are presented as mean ± standard deviation in the text. All statistical analyses were conducted in R (R version 2023.09.1+494, R Development Core Team.., 2022). We use statistics here to purely describe the behaviours we see in our sample, comparing individuals pre, during and post learning of the enrichment. Due to our low sample numbers, there is not independence between our sampling units, therefore, we will not make any inferences about how this enrichment task might affect the population, as we would need more animals for this.

3. Results

3.1. Effect of tactile enrichment on overall behaviours

For the fur seals (Fig. 2a), behavioural observations showed no significant differences in behaviours in response to the enrichment when looking at all individuals in the grouped data, except in patterned swimming (H= 7.41; p = 0.025), which increased slightly during the post-training stage (19.79± 44.14), compared to before enrichment (2.33± 12.78). (Z= −2.29; p = 0.04). There were some significant behavioural effects in response to the enrichment when individuals were analysed separately (see Supplementary material Fig. S1). For Bubbles, self-grooming (H= 6.00; p= 0.04; df=2) and random swimming (H= 6.32; p = 0.042; df=2) were affected. For Flo, patterned swimming (H= 6.35; p = 0.041; df=2) and vocalising (H= 5.99; p = 0.04) were affected, and for Gina, it was only aggression towards conspecifics which was affected (H= 6.34; p = 0.041; df=2). However, while the main effect was significant in these behaviours, post-hoc comparisons revealed no significant differences within the three enrichment periods for any of these examples (p >0.05 for all).

For harbour seals (Fig. 2b), grouped analysis of both individuals showed no statistical significance in differences for any behaviours in response to the enrichment (p>0.05). Individual analysis revealed Pamina showing significant differences in mean times spent patterned swimming ($F_{2,18}$= 3.58; p = 0.04) and surface swimming ($F_{2,18}$= 3.62; p = 0.04); but of these, post-hoc results only showed significant effects in surface swimming during the training period (118.88±27.45), which was higher than before enrichment (67.25±55.25; p= 0.045; Z= 0.95); no significant difference was seen with the post-training period. With Ina, surfacing was the only behaviour that showed significant differences (H= 6.70; p = 0.03; df= 2), where she spent no time doing this in the post-training period (0), compared to before the training (90.37 ±103.90; p= 0.03, Z=2.57) (see Supplementary material Fig. S1).

For the Eurasian otter (Fig. 2c), the time spent being vigilant (H= 6.08; p= 0.047) and resting (H= 6.12; p= 0.046), were the only two behaviours that were statistically significant in response to the enrichment. However, these differences in means were reflected as non-significant in the post-hoc pairwise comparisons for the three periods (all p> 0.05). For the red fox (Fig. 2d), there was no significant difference in the mean time spent doing any particular behaviour in the two periods (p > 0.05).

3.2. Effect of tactile enrichment on whisker positions and movements

The tactile enrichment device promoted whisker movements in all species, although these varied between species (see Supplementary Material Video 1). The South African fur seals showed significantly different whisker amplitudes overall, between the conditions of eating, touching target texture and distractors (Fig. 3a-c and Fig. 4; Kruskal-Wallis results: p< 0.001; df=2; Supplementary Material Table S.3). The whisker amplitudes were higher when eating the fish directly (66.59 ±27.74), compared to interacting with the target texture (46.73±27.14; p<0.001, Z= 3.97) and distractor textures (44.73±23.91; p<0.001, Z= 4.22). There was no significant difference between the mean amplitude when interacting with the target and distractor textures (p=0.66, Z= −0.43; Supplementary Material Table S.3). Similar results could be seen when the individuals were analysed separately (see Supplementary Material Fig. S2), for both Bubbles (Kruskal-Wallis results: p= 0.02, df= 2) and Gina (Kruskal-Wallis results: p= 0.002, df=2), where mean whisker amplitude values were significantly higher when eating the fish directly (Bubbles = 54.93±24.49; Gina= 73.53±28.26) compared to interacting with the target texture (Bubbles = 54.93±24.48; p=0.02, Z= 2.61; Gina = 52.16±32.23; p=0.01, Z= 2.75) or distractor textures (Bubbles= 34.32±19.57; p=0.02, Z= 2.67; Gina= 44.21±23.43; p=0.001, Z= 3.53). No significant difference was present between whisker amplitudes for the target and distractor textures of both animals (p > 0.05; see Supplementary Material Fig. S2). With Flo, the mean amplitude between the three textures did not differ significantly (p > 0.05). The mean whisker angular position was not statistically significant for the fur seals overall (Kruskal-Wallis results: p= 0.32 df= 2) and neither individually (p> 0.05 for all animals; (Supplementary material Fig. S2). Similarly, there was no significant effect on the mean whisker asymmetry when investigating with the different textures or when feeding overall for all fur seals (Kruskal-Wallis results: p= 0.27, df=2; Supplementary Material Table S.3) and neither individually (p> 0.05 for all animals).

The results of the ANOVA and Kruskal-Wallis for harbour seals (grouped (Fig. 3. d-f) and individual (see Supplementary Material Fig. S2) and the Eurasian otter (Fig. 3. g-i) showed that their whisker variables did not significantly alter when the animal was eating food directly or when interacting with either of the target or distractor textures on the enrichment (all ps > 0.05, for mean angular position, mean amplitude, and mean asymmetry; Supplementary Material Table S.2) (See also Fig. 4). As the red fox did not interact with the enrichment during any of the trials, no comparative test results could be obtained; however, some whisker metrics were obtained for when Ariel the fox was eating directly, for mean whisker angular position (79.38±20.29),

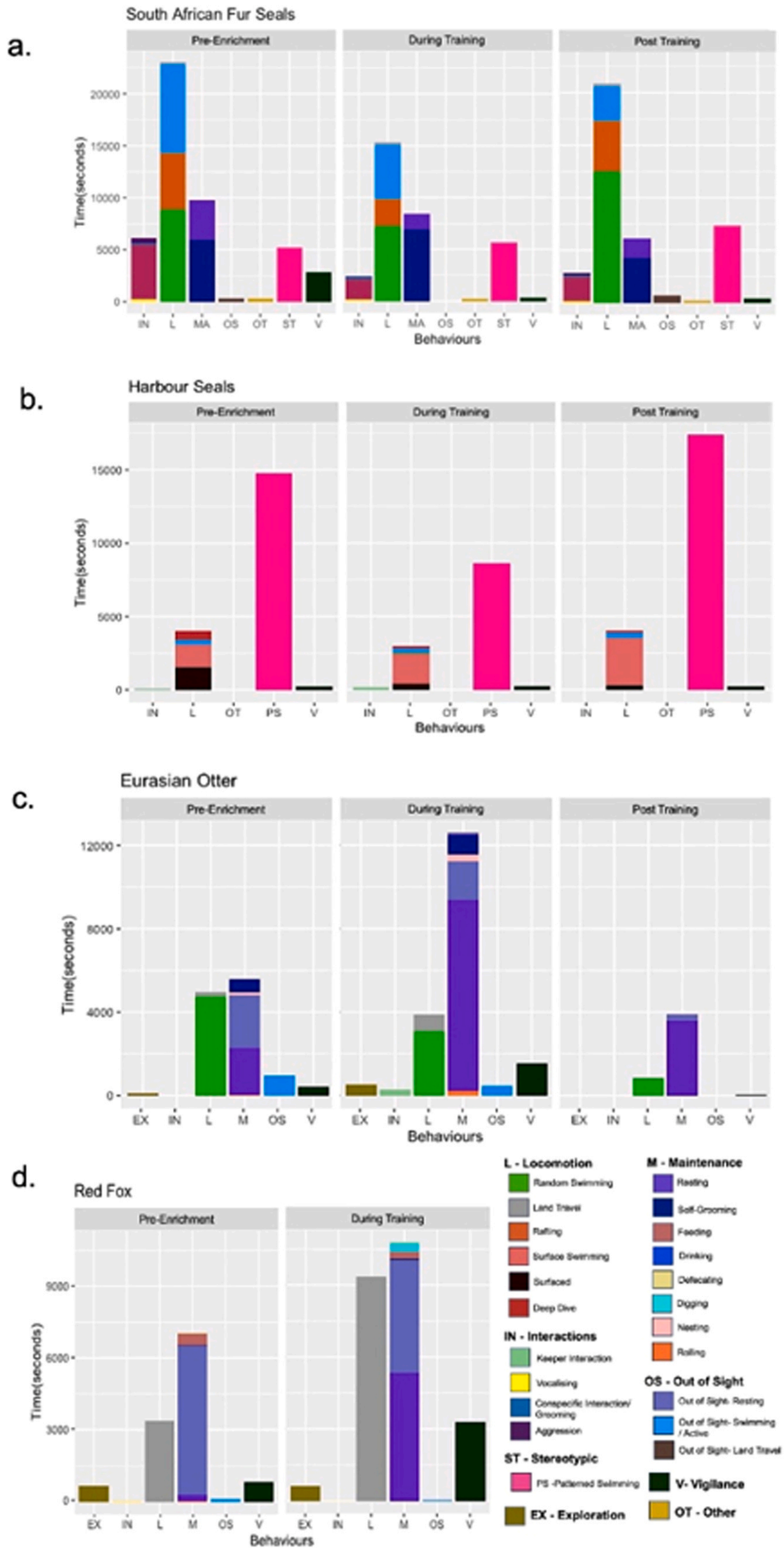

Fig. 2. Total time spent doing each behaviour grouped into behavioural categories for all individuals for **a.** South African Fur seals (3 individuals); **b.** Harbour seals (2 individuals); **c.** Eurasian Otter (1 individual); **d.** Red Fox (1 individual). Each figure is divided into columns showing 'Pre-Enrichment': time spent doing the behaviours before using the enrichment device (Phase. 1); 'During Training': time spend doing the behaviours while being trained (Phase. 2); 'Post-Training': time spent doing the behaviours after-training during enrichment experimental period (Phase. 3).

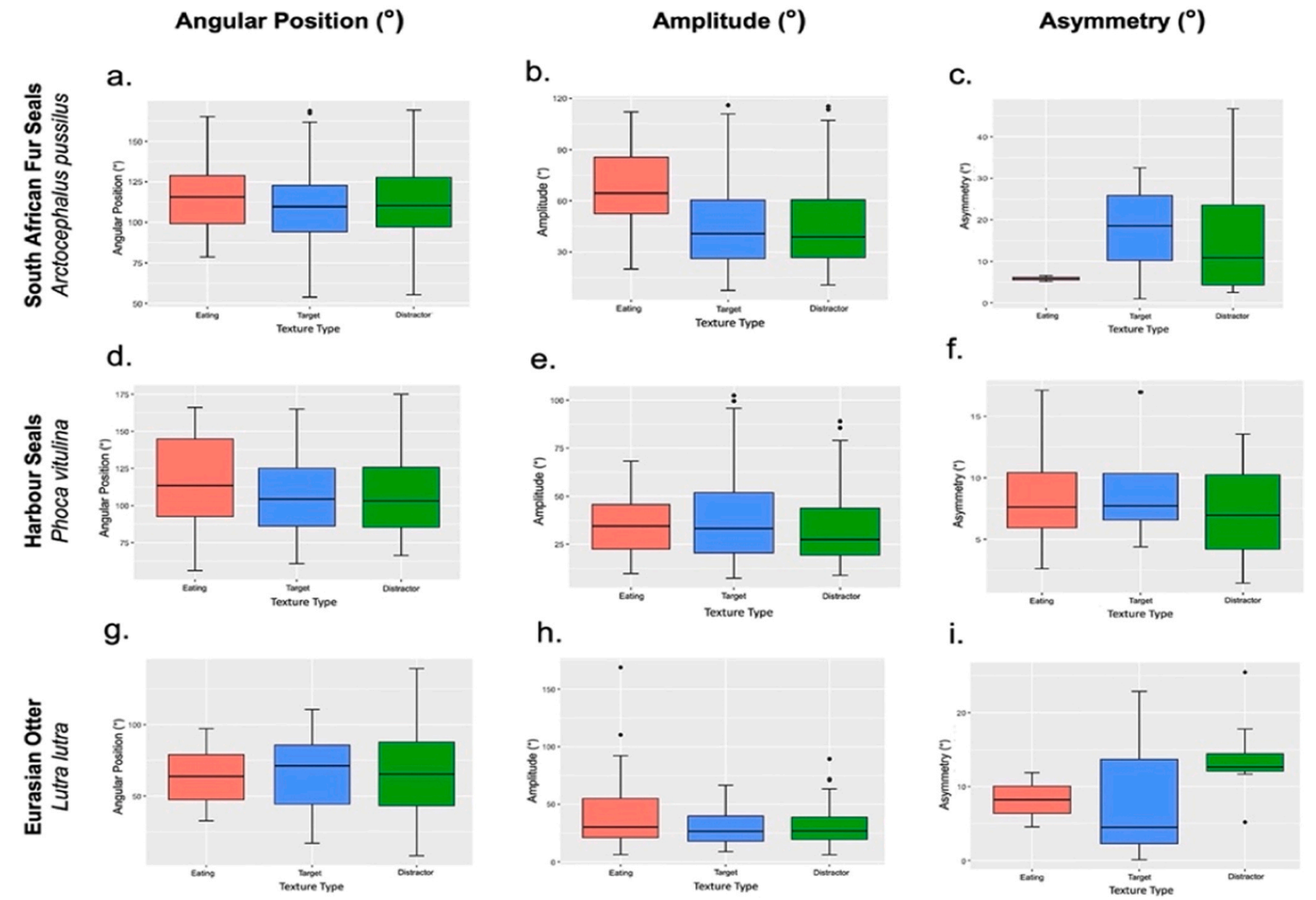

Fig. 3. Whisker movements when eating food (red), interacting with target texture (blue) and distractor textures (green). Figures **a-c** show whisker measurements for South African fur seals, **d-f** show those for harbour seals and figures **g-i** show those of the Eurasian otter. Plots for red fox were not available since the animal never interacted with the enrichment.

maximum amplitude (24.18±9.84), and asymmetry (5.05±2.87) (Fig. 4; Supplementary Material Table S.3).

3.3. Comparing whisker movements during and post-enrichment training

Additional comparative statistical tests were conducted using data wherever available to study the difference in whisker measurements during enrichment training and post-training periods. Results of paired Wilcoxon tests revealed that the overall mean whisker angular position was observed to be significantly higher ($W = 6786$, $p = 0.047$) in the South African fur seals in the during-training period (117.83± 22.68), compared to post training (108.66± 24.75) (see Fig. 5a-c). On individual analyses, it was observed that Bubbles had significantly higher whisker amplitudes ($W = 249$, $p = 0.034$) post-training of enrichment (39.53± 21.88), compared to during (24.69± 10.23), while other whisker variables were non-significant ($p > 0.05$). Gina showed significantly higher whisker angular positions ($W = 1910$, $p = 0.039$) during the training of enrichment (117.83± 22.68) compared to post training (108.66± 24.75). Otherwise, there was no statistically significant difference found in the whisker angular positions, amplitudes and asymmetry for the harbour seals or Eurasian otter in the during training and post-training of enrichment periods ($p > 0.05$) (Fig. 5d-i). The post-training data was absent for the red fox.

4. Discussion

This study is the first to explore the impact of tactile enrichment on enhancing the behavioural repertoire of captive caniform species. It is the first step in understanding the importance and effects of textured tactile enrichment in a captive setting. A novel tactile enrichment device was used to examine the resulting whisker movements adopted to differentiate textures in four caniform species, including two pinnipeds-South African fur seals (*Arctocephalus pussilus*) & harbour seals (*Phoca vitulina*), a mustelid – Eurasian otter (*Lutra lutra*), and a canid – red fox (*Vulpes vulpes*). While we had hoped that the animals would all naturally explore the device to learn the task, we found that all species that successfully learned the task needed keeper input, especially to target to the correct texture. We observed that overall, the enrichment did not lead to any significant changes in the species behaviours, including no increase in stereotypy or aggression in any individual involved in the study (Fig. 2). Whilst introduction of the enrichment did not increase the behavioural repertoire of the individuals, their use of the enrichment did successfully encourage whisker movements in all animals that engaged with the texture discrimination task. The presence of whisker movements and whisker asymmetry in all species also suggests some control strategies being used by the animals during object investigation (Fig. 3c, f, i).

Assessment of the effects of the enrichment on behaviour repertoires showed significant differences in some specific behaviours (such as random swimming, self-grooming, patterned swimming, and vocalising in some South African fur seals; surface swimming and patterned swimming in harbour seals; vigilance and resting in the Eurasian otter; and no significant differences in red fox behaviour). No significant changes in levels of stereotypical behaviours or aggression were

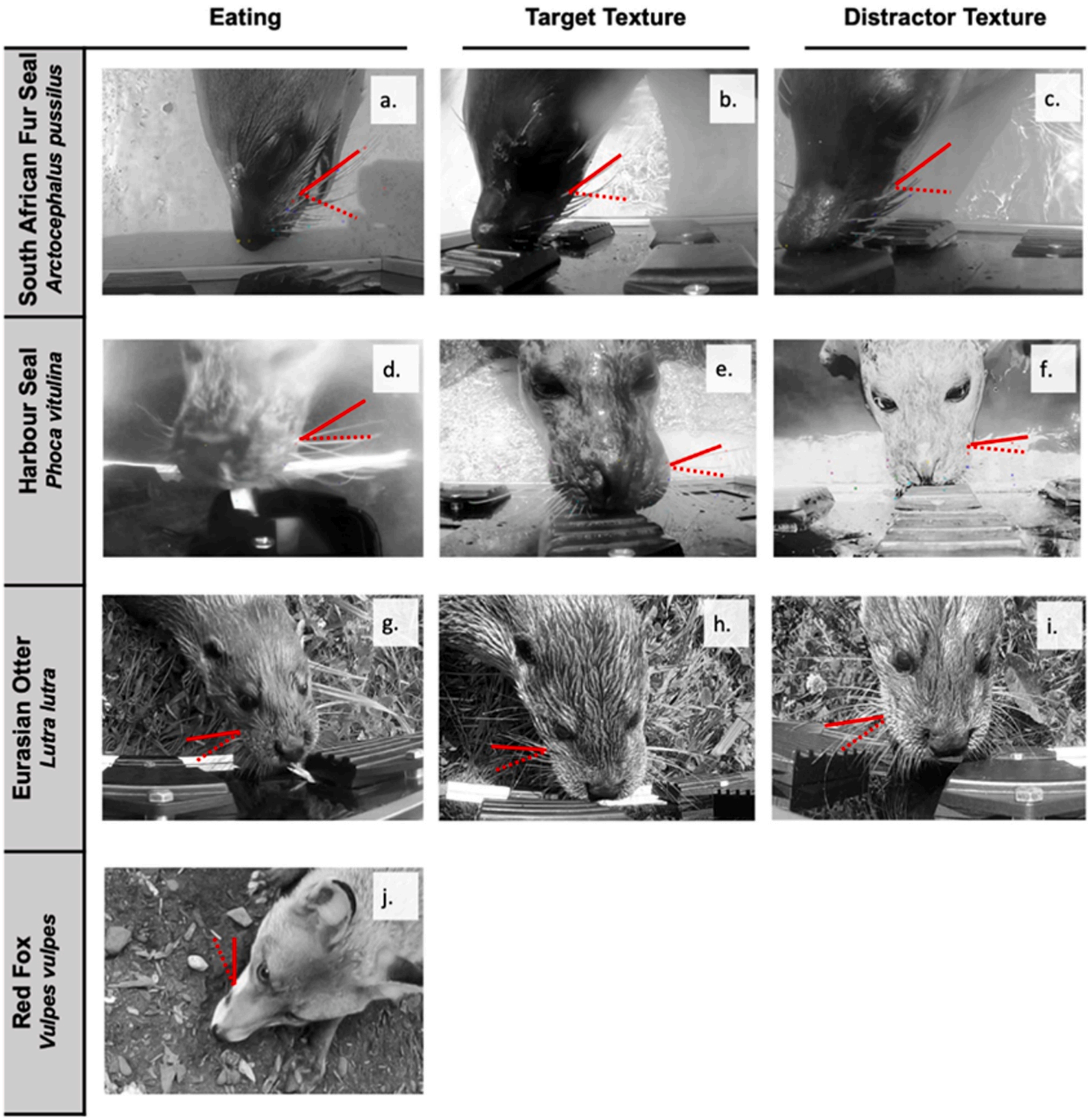

Fig. 4. Video frames showing range of whisker movements observed during enrichment tasks. In **a.)** South African fur seals range of whiskers amplitude is seen to be larger when eating fish, compared to target (**b.)**) and distractor textures (**c.)**) which appear to be similar to one another. Whisker amplitudes are relatively smaller and do not appear significantly different in each task for the harbour seal (**d-f.)**), Eurasian otter (**g-i.)**), and red fox (**j.)**).

observed in any species. A marginal increase in patterned swimming in the South African fur seals and harbour seals in the post-training enrichment period was noticed (Fig. 2a. & b). This cannot be presumed to be because of the enrichment, since towards the end of the post-training period, construction work took place near to both the seal enclosures just beyond the aquarium boundaries and may have contributed to this change in behaviour. For the Eurasian otter, the overall behaviour repertoire was much smaller in the post enrichment training period (see Fig. 2c), although this was not statistically significant. Behaviours in categories such as exploration, interactions and some from maintenance occurred rarely during post-training and the animal spent most of its time resting. On discussion with the keepers, they interpreted this finding as the animal working hard through the post-training period, eating lots of food, and taking time to rest and digest following a successful enrichment session – concluding that this was a positive finding. This increase in resting was similarly observed for the red fox, although again it was not significant (Fig. 2d). A similar observation was also made by Kistler et al., (2009), where a feeding treatment led to higher resting times in foxes. In our study, the foxes were provided with food in and around the enrichment device due to their reluctance of interacting with it, and this additional food probably led to a subsequent resting period.

There were varying responses by the four species to the enrichment device. While the pinnipeds and otter, which are easily trained and regularly exposed to various kinds of enrichment, did manage to learn the texture discrimination task, the red fox showed signs of neophobia, never interacting with the textures during the entire study. It is worth noting that the otter was also nervous of the enrichment device in the

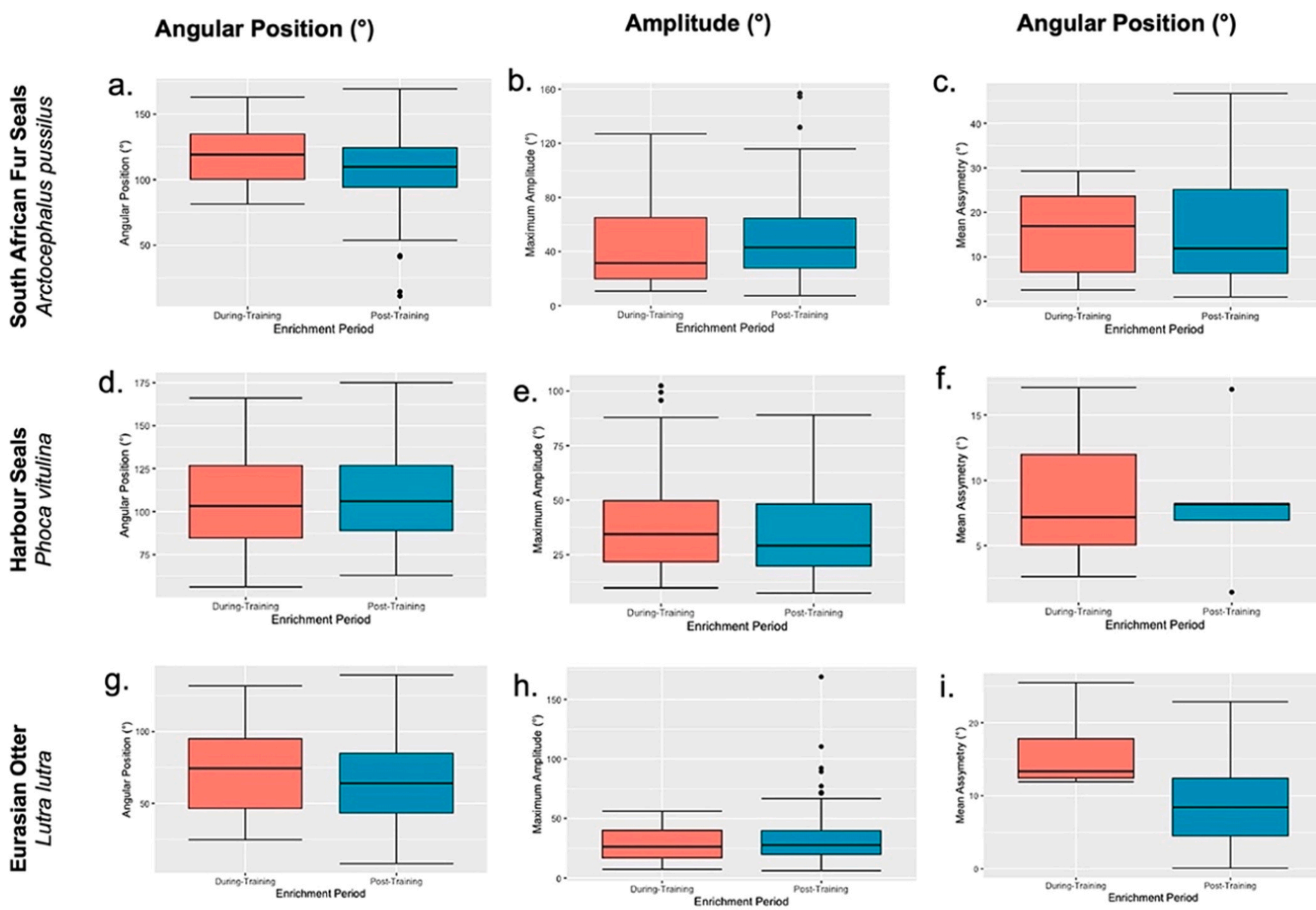

Fig. 5. Whisker angular position, maximum amplitude, and asymmetry compared for periods of during training and post-training of enrichment for South African fur seals (a-c.), harbour seals (d-f.), and Eurasian otter (g-i).

first two sessions and rarely approached it. It was only with the encouragement of a target stick that the individual started to engage and learn the task. This showcases the useful effect of training in zoos (Fernandez, 2022; Brando and Norman, 2023). In addition, it reveals the complexities of enrichment engagement. While the device looks very much like a domestic dog enrichment toy, that will be naturally explored by domestic pets, captive caniform species may be more neophobic and less motivated to explore complex enrichment devices without the aid of training and additional food rewards.

The enrichment device encouraged whisker movements in all the species that interacted with it (South African fur seals, harbour seals and Eurasian otter) (see Supplementary Material Video.1). Of the three whisker variables that were measured, whisker amplitude was the only one which was found to be significantly higher in South African fur seals when eating fish compared to when interacting with any of the textured doors on the enrichment device (Fig. 4.; Supplementary Material Table S.3). However, these differences were not found in the other three species (Fig. 4; Supplementary Material Table S.3). Despite the South African fur seals having larger whisker amplitudes when eating fish, they do also have very large whisker amplitudes when exploring the enrichment device. Milne et al. (2021) also found that textured objects promoted whisker movements with larger amplitudes in California sea lions. The results here thus add to the evidence that, like human fingertip movements, whisker movements play a role in texture discrimination in Otariids. The perception of texture is known to depend on the movement of biological tactile sensors (Diamond, 2010), and is thought to enhance tactile signals. When investigating textures, both pinniped species and the Eurasian otter in this study were observed making lateral head movements and sweeping their whisker along the texture doors, before directing their nose towards the doors (see Supplementary Material Video.1). This combination of head and whisker movements have also been observed in California sea lions (Dehnhardt and Dücker, 1996; Milne et al., 2021), and similar stroking or rubbing movements to assess texture has also been documented in human fingertips (Gibson, 1962; Lamb, 1983; Lederman, 1983) and the hands of squirrel monkeys (Hille et al., 2001) and sea otters (Strobel et al., 2018). Therefore, providing textured objects to whiskered animals may increase these important perceptual whisker movements.

When we compare whisker position and movement variables across different tasks from previous caniform whisker studies, it can be seen that the median amplitude of harbour seal, Eurasian otter and red fox whiskers exhibited in the current study closely resembles those of another object exploration study carried out by Grant et al. (2023) (see Table 2). This suggests that object-related whisker positions and movements may be relatively similar within the same species, even if the exact task is different. South African fur seals have not had their whisker movements described before, although when we look at their whisker movements in comparison to another widely studied Otariid, the California Sea lion (Milne et al., 2020; Milne et al., 2021), both species have similarly high values of whisker angular positions and amplitudes, which are larger than those of the harbour seals (see Table 2). This may indicate within-family similarities in pinniped whisker movements; however, studies need to be conducted in more pinniped species to confirm this.

Being the first to investigate textured enrichment stimuli provides us with insights into understanding the varied abilities of caniform species to respond to tactile stimuli, beyond the usual training and feeding enrichment that is typically provided to them in zoos. While the animals

Table 2
Comparative summary of median whisker measurements (angular position and amplitude) with results observed from other previously conducted whisker movement studies.

Species	*Common Name*	*Task*	*Ang. Pos.*	*Amp.*	*Reference*
Phoca vitulina	Harbour Seal	Eating	113.47 ±32.02	34.51 ±15.78	Current Study
		Touching target texture	104.35 ±28.09	33.25 ±22.72	
		Touching distractor	103.03 ±26.89	27.48 ±18.11	
Phoca vitulina	Harbour Seal	Object exploration	119.59 ±7.00	27.74 ±8.56	Grant et al. (2023)
Phoca vitulina	Harbour Seal	Fish sweeping	-	17.00	Milne et al. (2020)
Acrtocephalus pussilus	South African Fur Seal	Eating	116.30 ±21.93	64.56 ±27.74	Current Study
		Touching target texture	108.32 ±26.14	41.94 ±23.90	
		Touching distractor	110.17 ±23.73	38.81 ±27.13	
Zalophus californianus	California Sea Lion	Discrimination task- Small texture (non-target)	59.94 ±13.13	35.56 ±10.77	Milne et al. (2021)
		Discrimination task- Medium texture (target)	58.02 ±14.28	35.44 ±17.17	
		Discrimination task- Large texture (non-target)	61.01 ±17.32	31.82 ±17.07	
Zalophus californianus	California Sea Lion	Fish sweeping	-	19.00	Milne et al. (2020)
Lutra lutra	Eurasian Otter	Eating	64.06 ±20.55	43.56 ±37.86	Current Study
		Touching target texture	66.05 ±25.26	29.78 ±15.11	
		Touching distractor	66.73 ±30.30	29.45 ± 14.85	
Lutra lutra	Eurasian Otter	Object exploration	102.06±10.91	43.04 ±9.98	Grant et al. (2023)
Vulpes vulpes	Red Fox	Eating	79.37 ±20.29	24.18±9.84	Current Study
Vulpes vulpes	Red Fox	Object exploration	83.19 ±17.08	39.65 ±11.00	Grant et al. (2023)

required training to interact successfully with the enrichment device, from observing these interactions, we can now make recommendations for future whisker enrichment trials. Pinnipeds and otters are known to be inquisitive, preferring to seek a challenge when foraging in captivity (Foster-Turley, Markowitz., 1982; Roberts et al., 2023), and we observed them easily engaging with our enrichment device under the guidance of trainers. However, the foxes in our study were relatively neophobic. Previous studies on red foxes have shown them successfully engaging with feeding enrichment, including electronic feeders, self-service food boxes and scatter-feeding (Kistler, 2009), and these can lead to an increase in exploratory foraging behaviours (Macdonald, 1988; Kistler, 2009). Therefore, perhaps a simpler feeding enrichment device might make the task more accessible to shyer animals, and not require additional training and support from keepers. On the whole, a texture discrimination task was successful in promoting whisker movements here, so we would suggest that a textured food board, with visible and accessible food rewards may be more ideal at stimulating the whiskers while also delivering food. An element of texture discrimination could still be included in the task by having the food only in certain areas or textures on the board. Such a device might be more inclusive for a larger range of caniform species in captivity.

CRediT authorship contribution statement

Lewis Chambers: Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Alyx Elder:** Writing – review & editing, Investigation, Data curation. **Emma McLoughlin:** Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Sarah Roberts:** Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Katherine Todd:** Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Robyn A Grant:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Amisha A Nakhwa:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Vicki Breakell:** Writing – review & editing, Supervision, Project administration, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2024.106261.

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