Characterisation of whisker control in the California sea lion (*Zalophus californianus*) during a complex, dynamic sensorimotor task.

Alyx O. Milne[1,2] and Robyn A. Grant[1*]

1. Conservation, Evolution and Behaviour Research Group, Division of Biology and Conservation Ecology, Manchester Metropolitan University, Manchester, UK
2. Blackpool Zoo, Blackpool, UK

* Corresponding Author: robyn.grant@mmu.ac.uk, Tel: +44 (0)161 2476210

Keywords: active touch, vibrissal, pinniped, sensing, haptics

Abstract

Studies in pinniped whisker-use have shown that their whiskers are extremely sensitive to tactile and hydrodynamic signals. While pinnipeds position their whiskers on to objects and have some control over their whisker protractions, it has always been thought that head movements are more responsible for whisker positioning than the movement of the whiskers themselves. This study uses ball-balancing, a dynamic sensorimotor skill that is often used in human and robotic coordination studies, to promote sea lion whisker movements during the task. For the first time, using tracked video footage, we show that sea lion whisker movements respond quickly (26.70 milliseconds) and mirror the movement of the ball, much more so than the head. We show that whisker asymmetry and spread are both altered to help sense and control the ball during balancing. We believe that by designing more dynamic sensorimotor tasks we can start to characterise the active nature of this specialised sensory system in pinnipeds.

Introduction

Active sensing is based on sensory feedback and movements that are task specific (Prescott et al. 2011); for instance, in humans, fingertips make lateral movements to judge object texture and vertical movements to judge object softness (Gibson 1962). Active touch is the control of the movement of touch sensors to maximise information from the environment (Prescott et al. 2011; Grant et al. 2014). Studies in the field of *haptics* incorporate both sensation and movements to measure touch capabilities during texture, shape and size differentiation tasks. The most popular experimental tasks in humans and control engineering experiments involve balancing sticks (Fleishman et al. 1961; Cabrera and Milton 2004; Stepan 2009), balls (Fleishman et al. 1961), balls-on-beams (Iqbal et al. 2005) or balls-on-plates (Awter et al. 2002; Van Waelvelde 2004; Lee et al. 2008). These balancing tasks challenge both movement control and sensory feedback abilities. These tasks have also been used in diagnosing coordination disorders (Jongmans et al. 2003) and testing robotic control abilities (Awter et al. 2002; Iqbal et al. 2005; Lee et al. 2008).

Active touch sensing studies in animals focus on vibrissal touch sensing, with rodents, insectivores and pinnipeds labelled as *whisker specialists*. Pinnipeds, in particular, have been used in active touch sensing studies, due to the prominence of their facial vibrissae and their ability to move them using a network of voluntary muscles (Berta et al. 2005). Indeed, vibrissal touch is thought to be more efficient in pinnipeds, than in terrestrial mammals, due to the whiskers being more sensitive (having ten times more nerve fibers) (Rice et al. 1986; Hyvärinen, 1989) and unaffected by temperature changes (Dehnhardt et al. 1998; Mauck et al. 2000). The California sea lion (*Zalophus californianus*) has 38 vibrissal hairs on each side of their face, which can grow up to 20 cm (Dehnhardt, 1994), and play a primary role in active touch sensing (Dykes 1975; Hyvärinen 1989; Dehnhardt 1994; Dehnhardt et al. 2001; Leinwand 2003; Mitchinson et al. 2007) and hydrodynamic trail following (Gläser et al. 2011; Hanke et al. 2013). California sea lions can use their whiskers to discriminate between different shapes (Dehnhardt 1990) and sizes, down to surface area differences as small as 0.5 cm (Dehnhardt 1994; Dehnhardt and Dücker, 1996). While vibrissal touch is often thought of as an active sensory system (Prescott et al. 2011; Grant et al. 2014) there has been little evidence of whisker control in pinnipeds. Dehnhardt (1994) conducted a size differentiation task, and found that although California sea lions protracted their whiskers and positioned their most rostral whiskers on to the stimuli, there were no significant differences between whisker movements on different sized objects. Dehnhardt (1994) rather observed that the sea lions used small head movements to position their whiskers during the task, rather than whisker movements per se.

Active touch sensing tasks in pinnipeds have, therefore, focussed on discrimination thresholds thus far, rather than on their ability to control whisker movements. These discrimination studies have indicated that head positioning, rather than whisker control, drives the placement of whisker positions on sensory stimuli (Dehnhardt 1994; Grant et al. 2013). To explore this further, perhaps a more complex, dynamic sensorimotor task is needed to promote whisker movements. Even though sea lions are sometimes considered synonymous with the ability to ball-balance, this complex sensorimotor task has yet to be explored in these animals. Therefore, this study will draw inspiration from human haptic studies to explore how California sea lions use their whiskers during a ball-balancing task. This study will investigate whether whisker control, between the left and right sides, coordinates ball positioning. This study will then go on to characterise whisker positions and movements as the sea lions balance three differently sized balls.

Materials and Methods

Animals

The study was conducted at the Active Oceans Arena in Blackpool Zoo that houses a total of nine individual California sea lions (*Zalophus californianus*). Three California sea lions were used in this study: Gina (female, ten-years old), Anya (female, six-years old) and Elmo (male, four-years old). All three were born at Blackpool Zoo; Gina and Anya were full sisters, whereas Elmo was not related. The sea lions had all performed the ball balancing behaviour numerous times prior to this investigation, in public displays and in training sessions; therefore they were not trained any new behaviours for this study. The sea lions were not blindfolded for this task; this was in part due to limiting undue stress on the animals as they had not been blindfolded before, and also to keep the experiment as ethologically relevant as possible. Indeed, exploring whisker use in the absence of vision might have rather limited applications in sea lions. All experiments were approved by local ethics committees.

Apparatus

Three different sized footballs were used for the ball-balancing task, consisting of a small (Ø38 cm), medium (Ø56 cm) and large (Ø71 cm) ball. The balls weighed 140g, 310g and 426g, respectively. While the weight difference might have affected the sea lions' behaviour, the balls were selected to keep texture and material constant between the balls, rather than the weight. The experiments were carried out in a sheltered arena, to prevent the lighter balls from being affected by the wind, and it was noted that the larger ball was easier for the sea lions to balance, which was likely to be an effect of its size, rather than weight (see the Discussion section). Experiments were carried out in a dry training arena behind the main enclosure. A black tarpaulin sheet was draped and secured over the perimeter fence of the sea lions training area (Fig. 1a), to enable the whiskers to be seen more clearly against the light coloured fence (Fig. 1b and c). A sea lion station was positioned so that the animals could elevate their forelimbs easily during the task (Fig. 1a). A tripod was set up behind the sea lions station and a camera positioned to film the top half of the sea lion during the task (Fig. 1b and c). This allowed the positions of the whiskers to be viewed, from behind the subject. The camera used was a waterproof GE DV1 Pocket Digital Camcorder (HD 1080p), recording at 60 frames per second to eliminate blurring during fast whisker movements.

Experimental Procedures

Sampling took place over five weeks, throughout May and June 2013, including a training week without data collection. This training week was to make sure the sea lions were fully desensitised to the recording apparatus and to check the positioning of the camera. Sessions were conducted at the same time every day (around 4pm), taking care that the sea lions were not involved in any public displays directly prior to undertaking the task. During the task, each sea lion was taken into the training area (Fig. 1a) alone. The same two trainers were present each time. Trainer 1 would collect the sea lion, bring it to the station and then stand ready to record the footage directly behind the animal. Trainer 2 would conduct the experiment, including rewarding, training and monitoring the sea lion throughout. During a session each animal received approximately 20-40% of its daily food amount. This was freshly thawed cut mackerel, cut herring or whole sprats.

Each sea lion was thrown a ball to catch and balance using ball-balancing commands that they already knew. The duration of balancing varied between 10-50 seconds this gives variable duration reinforcement, which the trainers have found to increase attention and maintain performance in multiple consecutive trails in the sea lions (Milne 2013, Pers Comms). Once the designated balancing duration had been reached, trainer 2 would clap their hands once and whistle and the sea lion would return the ball to them. The sea lion was then rewarded with fish. Each of the three balls was given to the sea lions three times in a pseudo-random order (Gellermann, 1933), totalling nine balancing trials in each training session. Once the session was complete, the sea lions were returned to the rest of the group in the main pool. The three sea lions were used for one session per day, in no particular order, allowing a total of 20 days of footage, with 9 trials a day, giving a total of 540 individual trials. The sea lions were trained using positive reinforcement, therefore if the sea lion was to perform an incorrect behaviour, for example dropping the ball, that trial would be repeated. If this happened more than three times in one session the sea lion would be returned to their pen and the session terminated until all other sea lions had completed the task. The sea lion would then be given another chance to attempt the session.

Video Selection and Analysis

All video clips were examined for analysis. This was to ensure videos selected showed the following: (i) all whiskers were visible by the camera throughout the entire clip, (ii) the head was accurately lined up with the camera, (iii) there was enough lighting to see all the whiskers against the black background, and (iv) the sea lion did the correct behaviour. In total, after viewing all video clips, ninety were selected for analyses (ten video clips per sea lion for each of the three different balls, giving thirty clips per animal). Each video was tracked manually using the open source video tracking toolbox ‘Tracker’ (Tracker 4.80, Douglas Brown 2013, www.cabrillo.edu). Two whiskers on each side of the face were tracked along with the mid-point of the head (between the eyes), the centre of the ball and the tip of the nose. The whiskers selected for tracking were the second from the front and second from the back on each side of the muzzle (Fig. 1b and c). Two points were tracked on each whisker: the base and the shaft (a point around two thirds along the whisker shaft) (Fig. 1c). This made eleven tracked points in total. The tracking was conducted over a three second period in every three frames; tracking started once the sea lion had steadied itself after receiving the ball from Trainer 2. A small sample of videos was tracked three times by two researchers to measure the accuracy of manual tracking the footage. Findings showed that 95% of the tracked points fell within 1.1 cm of each other when they were repeated. This is a high level of accuracy for a zoomed-out video with manual tracking.

From the tracked points, head orientation, ball orientation and whisker variables could then be calculated. *Head orientation* and *ball orientation* were calculated as the angle from each point to the nose tip, from the horizontal (Fig. 1b). Whisker angular position was calculated as the angle between the whisker and the midline of the head, such that forward moving whisker positions (protractions) gave larger whisker angular positions. Due to observed relationships between whisker asymmetry and head rotations in other animals (Towal and Hartmann 2006; Mitchinson et al. 2011), head orientation was chosen as the measure of head movement in this paper; however, the same analyses were run on lateral head movements in Supplement 1 and showed a similar pattern of results with the timings. Whisker *offset* is the mean whisker angle and was calculated by averaging all the whisker angular positions per side. Whisker *amplitude* was calculated as the difference between the maximum and minimum whisker angular positions (averaged over whiskers and sides). Whisker *spread* was the difference between the rostral and caudal whisker angular positions (averaged over sides). Whisker *asymmetry* was calculated as the difference between the left whisker angular positions and the right (left whisker angles, minus right whisker angles, averaged over front and back whisker). These measures were only calculated in two-dimensions, while 3-dimensional measures of movement would be really interesting, this study only examines the 2-dimensional movements when the head is lined up with the camera (point ii above).

Statistical considerations

As the movements of the head, ball and whiskers were periodic, per-frame measures of head orientation, ball orientation and whisker asymmetry were cross-correlated to get a measure of correlation and delay (lag) between the de-meaned signals in each clip, of: i) ball orientation and whisker asymmetry, ii) ball orientation and head orientation, and iii) whisker asymmetry and head orientation. These analyses were also run for all sea lions individually (Supplement 2), as the results were robust over all three sea lions only pooled data is presented here (in Fig. 2). To compare differences between the sea lions and the different ball sizes, per clip (mean) measures of lags, whisker offset, amplitude, spread and asymmetry were compared using between-ANOVAs. All the data was normally distributed. Where means are reported in the text, they are reported as mean ± standard deviation.

Results

Sea lions use their whiskers quickly and accurately during ball balancing

All three sea lions moved their whiskers during ball balancing. Whisker movements responded quicker to changes in ball position than head movements, indicated by smaller time lags between the ball orientation and whisker asymmetry (Fig. 2a), compared to ball movement and head orientation (Fig. 2c). Indeed the mean and standard deviation of the lags was 26.70±52.08 milliseconds for the ball and whiskers, and 129.03±57.35 milliseconds for the ball and head orientation, averaged over all sea lions. In addition, ball orientation was better correlated to whisker asymmetry ($r=0.53$, $p<0.05$) than head orientation ($r=0.45$, $p<0.05$), which can be seen in Fig. 2b and d. The same analyses were run on just the caudal whisker data and gave the same pattern of findings, which was to make sure the ball was not significantly affecting the contacted rostral whiskers (Supplement 3).

An example clip to illustrate the quick, accurate response of the whiskers to changing ball orientation can be seen in Fig. 3. Fig. 3b shows the ball orientation, whisker asymmetry and head orientation for the same example. The whisker asymmetry follows the ball orientation closely with maximums coinciding simultaneously. Indeed, in 70% of clips, whisker asymmetry had zero lag (coincided simultaneously) with ball orientation, compared to 0% of the clips for head orientation (refer to the red and black solid lines in Fig. 3b). The head orientation tracks the ball orientation with slightly less accuracy and with a clear delay in this example (Fig. 3b, dashed lines). This is shown using the coloured arrows in Fig. 3b. The red arrow and black arrows indicate minima in the traces for whisker asymmetry and ball orientation, respectively, which coincide together; whereas the dashed arrow shows the corresponding head orientation minima with a delay of a quarter of a second. Whisker asymmetry and head orientation were also reasonably correlated ($r=0.37$, $p<0.05$), with whisker movements being ahead of head movements, with an overall mean of 103.83±57.17

milliseconds. This pattern can also be seen in the series of video stills in Fig. 3c. At T=0.85 seconds (Fig. 3c, i) the ball starts to move to the right and the right whiskers protract forward. At T=1.15 seconds (Fig. 3c, ii), the head moves to the right with the right whiskers still protracted. Everything comes to centre and stabilises at T=1.7 seconds (Fig. 3c, iii). The whole video can be seen in Supplementary movie 1.

Sea lion whisker positions and movements depend on object size

Sea lions showed a certain amount of control over their whisker movements and positions depending on the ball size. Sea lion whisker movements were more delayed on the large balls (Fig. 2a), and quicker on the small balls (F(2,80)=5.340, p=0.007). Indeed, Elmo had zero whisker lags for all small ball trials (Fig 2a). On larger balls, their whiskers were less spread out (Fig. 4c, F(2,80)=3.279, p=0.043) and also positioned further back, with lower offset values (Fig. 4a, F(2,80)=7.760, p<0.001). This shows a certain degree of whisker control in response to ball size, as it is the opposite of the simple pattern observed in Fig. 2a, where more forward whisker movements resulted in reduced whisker spread (more bunched up whiskers).

Whisker movements and positions can vary between individuals

Whisker positions and movements varied slightly between individuals, even though the overall patterns in time lag and positions still hold. In particular, Anya had slower head reactions in response to changing ball orientations (longer time lags, Fig. 2c, F(2,80)=14.395, p<0.001), she also exhibited less whisker asymmetry (Fig. 5d, F(2,80)=18.598, p<0.001) and larger whisker amplitudes (Fig. 4b, F(2,80)=31.977, p<0.001), than Gina or Elmo.

Discussion

This is the first study to identify that pinnipeds move their whiskers significantly during a sensorimotor task, rather than just their head. Indeed, results from this study show that whisker positions are quicker and more correlated to ball movements than those of the head. This was not simply as a result of the ball contacting the whiskers as the same, if not stronger, patterns in the data were observed when using values from only the caudal whiskers that tended not to contact the ball at all (Supplement 3). While it is clear that the whiskers are moving, it is unclear whether the whiskers themselves can act to stabilise the ball. It could be that the whisker movements are sensing where to direct the motion of the head. Indeed, in rodents, whisker asymmetry precedes head rotations (Towal and Hartmann 2006; Mitchinson et al. 2011; Grant et al. 2012) and serves to scan the area that the head is moving in to. While whisker movements precede head movements here, they are better correlated to ball movements (Fig. 3b), which suggest they might not be simply directing the head.

The mean position (offset) of the whiskers and the whisker spread are both altered on different sized balls. Whiskers are positioned with smaller offset values (are less protracted) on larger balls. Larger balls also have more bunched up whiskers (reduced spread). This firstly shows that the sea lions have the capacity to decouple the normal pattern of spread and offset. In Fig. 2a, it can be seen that as whiskers move forward they usually get more bunched up, this is probably a result of the muscle architecture and can be seen in many example whisker traces. On the large ball, however, the reverse is true; that the whiskers are positioned further backward and are more bunched up. De-coupling between usual patterns in whisker spread and offset can be seen during object contact in rodents (Grant et al. 2009), and shows that whisker spread can be actively controlled during object exploration. It might be that more whiskers are recruited to balance a larger ball, and are thus more bunched up, perhaps showing some evidence for whisker-driven ball control. While the whiskers, in isolation, are probably not able to entirely stabilise the ball, they seem to be recruited to control the ball at early stages of movement, while the head is used for later, larger-scale stabilisations.

Whisker lags are also altered on the different sized balls. Whiskers respond slower to movements of the large ball, than movements of the small ball. Fig. 5 shows that the same degree of ball orientation causes a larger surface rolling movement of the medium ball (m) compared to the small ball (s) (indicated by the pink circle). Smaller balls thus require quicker reactions to changes in ball orientation to prevent them from rolling, which agrees with our data here. It is easier to balance larger balls, therefore, as larger surface rotations are likely to be easier to detect and reactions can be slower. Indeed, Elmo, the younger seal, struggled with balancing the smallest ball during the training week as it required faster and more accurate whisker movements. Studies with balancing sticks in humans have also found that longer sticks are easier to balance, because the same degree of orientation causes a larger displacement of the stick’s tip, which is easier to detect (Cabrera and Milton 2004).

While the overall data patterns hold true over the three sea lions, there were some differences, with Anya having slower head movements, higher amplitude whisker movements and less whisker asymmetry. Lags in response to balancing tasks can be related to age or coordination deficits (Jongmans 2003), however, Anya is not the oldest and did not have any larger latencies in whisker responses. Rather, the sea lions balanced the balls differently between them. Gina tended to keep her head very still laterally, and bounced the balls on her nose, Anya made large lateral head movements and Elmo was somewhere in the middle of the two (See Supplement 2). Observed differences between animals in this study flags up the difficulties with conducting experiments on a limited number of animals, which is very common in studies of this type. While it is very difficult to access large numbers of marine mammals, care must be taken when reviewing work from studies that only have one or two subjects (Dehnhard and Dücker 1996; Wieskotten 2010a, 2010b; Grant et al. 2013).

Using a dynamic task in this way has encouraged more whisker movements, and identified the importance of whisker positions during active touch tasks. While more static discrimination tasks give detailed and accurate information about tactile capabilities, they are not able to encourage suitable whisker movements, and often head movements appear to be more responsible for whisker positioning, than the movement of the whiskers themselves (Dehnhardt, 1994, Grant et al. 2013). While this ball-balancing task is not a naturalistic behaviour that sea lions perform in the wild, it has been used in this study as a complex sensorimotor task that has encouraged whisker movement and control. Perhaps similar whisker movements might be used in other dynamic tactile tasks. For instance, Fig. 6 shows that sea lions might use similar strategies to guide moving fish towards their mouths. In Fig. 6 the sea lion whiskers are bunched up and protracted forward, and asymmetries can be observed in the whisker fields as the sea lions orient their whiskers towards the travelling fish. Indeed, it would be interesting to further explore the role of whisker movements in hunting and prey capture in the future. We see this study as an initial investigation in to dynamic sensing tasks in pinnipeds, and hope that experiments of this type might help us to better understand the active nature of this tactile sensory system.

Acknowledgements

The authors would like to thank all the staff at Blackpool Zoo for their full co-operation and assistance, especially Alex Kidd (sea lion Trainer), who was the secondary trainer throughout the project. We are also grateful for the support from the Division of Biology and Conservation Ecology at Manchester Metropolitan University throughout the study.

Ethical Standards

All experiments comply with UK regulations and were approved by ethics committees at both Manchester Metropolitan University and Blackpool Zoo.

References

Awter S, Bernard C, Boklund N, Master A, Ueda D, Craig K (2002) Mechatronic design of a ball-on-plate balancing system. Mechatronics 12(2):217-228

Berta A, Sumich JL, Kovacs KM. (2005) Marine Mammals: Evolutionary Biology, Academic Press, San Diego

Brown D, Wolfgang C (2013) Tracker 4.8 xs. Cabrillo College. www.cabrillo.edu/~dbrown/tracker/ Accessed 1st June 2013

Cabrera JL, Milton JG (2004) Human stick balancing: Tuning Lèvy flights to improve balance control. Chaos 14:691

Dehnhardt G (1990) Preliminary results from psychophysical studies on the tactile sensitivity in marine mammals. In: Thomas JA, Kastelein RA (eds) Sensory abilities of cetaceans, Plenum, New York, p 435-446

Dehnhardt G (1994). Tactile size discrimination by a California sea lion (*Zalophus californianus*), using mystacial vibrissae. J Comp Physiol *A* 175:791-800

Dehnhardt G, Dücker G (1996) Tactual discrimination of size and shape by a California sea lion *(Zalophus californianus*). Animal Learning & Behavior 24(4):366-374

Dehnhardt G, Mauck B (2008) Mechanoreception in secondarily aquatic vertebrates. In: Thewissen JGM, Nummela S (Eds) Sensory evolution on the threshold–adaptations in secondarily aquatic vertebrates, University of California Press, Berkely, p 295-314

Dehnhardt G, Mauck B, Hyvärinen H (1998) Ambient temperature does not affect the tactile sensitivity of mystacial vibrissae in harbor seals. J Exp Biol 201: 3023-3029

Dehnhardt G, Mauck B, Hanke W, Bleckmann H (2001). Hydrodynamic trial following in harbor seals (*Phoca vitulina*). Science 293: 102-104

Dykes RW (1975) Afferent fibres from mystacial vibrissae of cats and seals. J Neurophysiol 38: 650-662

Fleishman EA, Thomas P, Munroe P (1961) The Dimensions of Physical Fitness- A Factor Analysis of Speed, Flexibility, Balance, and Coordination Tests. Handbook, Yale University. DTIC Document

Gibson JJ (1962) Observation on active touch. Psychological Review 69(6): 477-472

Gellermann LW (1933) Chance orders of alternating stimuli in visual discrimination experiments. J Genet Psychol 42:206-208

Gläser N, Wieskotten S, Otter C, Dehnhardt G, Hanke W (2011) Hydrodynamic trial following in a California sea lion (*Zalophus californianus).* J Comp Physiol *A* 197:141-151

Grant RA, Itskov PM, Towal B, Prescott TJ (2014) Active touch sensing: finger tips, whiskers and antennae. Frontiers in Behavioral Neuroscience 8:50

Grant R, Mitchinson B, Fox C, Prescott TJ. (2009) Active touch sensing in the rat, Anticipatory and regulatory control of whisker movements during surface exploration. Journal of Neurophysiology 101: 862-874

Grant RA, Mitchinson B, Prescott TJ (2012) The development of whisker control in rats in relation to locomotion. Dev Psychobio 54(2):151-168

Grant R, Wieskotten S, Wengst N, Prescott T, Dehnhardt G, (2013). Vibrissal touch sensing in the harbor seal (*Phoca vitulina*): how do seals judge size? J Comp Physiol A 199(6):521-533

Hanke W, Wieskotten S, Marshall C, Dehnhardt G (2011) Hydrodynamic perception in true seals (*Phocidae*) and eared seals (*Otariidae*). J Comp Physiol A 199(6):421-440

Hyvärinen H (1989) Diving in Darkness: Whiskers as sense organs of the Ringed seal (*Phoca hispida*). Journal of Zoology 238: 663-678

Iqbal J, Khan MA, Tarar S, Khan M, Sabahat Z (2005) Implementing ball balancing beam using digital image processing and fuzzy logic. Canadian conference on Electrical and Computer Engineering 2241-2244

Jongmans MJ, Smits-Engelsman BCM, Schoemaker MM (2003) Consequences of Comorbidity of Developmental Coordination Disorders and Learning Disabilities for Severity and Pattern of Perceptual-Motor Dysfunction. J Learn Disabil 36(6): 528-537

Lee K, Achhammer S, Drexler S, Wollherr D (2008) Basketball Robot: Ball-on-Plate System without Visual Information. Proceedings of the 17th World Congress The International Federation of Automatic Control 1606.10.3182/20080706-5-KR-1001.1606

Mauck B, Eysel U, Dehnhardt G (2000) Selective heating of vibrissal follicles in seals *(Phoca vitulina*) and dolphins (*Sotalia fluviatilis guianensis*). J Exp Biol 203:2125-2131

Mitchinson B, Grant RA, Arkley KP, Perkon I, Prescott TJ (2011) Active vibrissal sensing in rodents and marsupials. Philosophical Transactions B. 366(1581): 3037-3048

Prescott TJ, Diamond ME, Wing AM (2011) Active touch sensing. Philosophical Transactions B 366(1581):2989-2995

Rice FL, Mance A, Munger BL (1986) A comparative light microscopical analysis of the sensory innervation of the mysticial pad. 1. Innervation of vibrissal follicle-sinus complexes. J Comp Neurol 252:154-174

Stepan G (2009) Delay effects in the human sensory system during balancing. Phil Trans R Soc A 367: 1195-1212

Towal RB, Hartmann M J (2006). Right-left asymmetries in the whisking behavior of rats anticipate head movements. J Neurosci 26(34), 8838-8846

Van Warelvelde H, De Weerdt Q, De Cock P, Smits-Engelsman BCM (2004) Aspects of the validity of the Movement Assessment Battery for Children. Human Movement Science 23(1):49-60

Wieskotten S, Dehnhardt G, Mauck B, Miersch L, Hanke W (2010a) Hydrodynamic determination of the moving direction of an artificial fin by a harbor seal (*Phoca vitulina*). J Exp Biol 213: 2194-2200

Wieskotten S, Dehnhardt G, Mauck B, Miersch L, Hanke W (2010b) The impact of glide phases on the trackability of hydrodynamic trials in harbor seals (*Phoca vitulina*). J Exp Biol 213:3734-3740

FIGURE CAPTIONS

Figure 1, Test set-up and tracking during the ball-balancing task. a) the dry training arena, including the sea lion station and black sheet; b) an example video still, including the tracked points (red points) and an indication of the ball orientation (Øball) and head orientation (Øhead); c)) an example video still, including the tracked points (red points) and an indication of the right, caudal tracked whisker angle.

Figure 2, Whisker and head responses to ball-balancing. a. The lag, in seconds, between changes in ball orientation and changes in whisker asymmetry. The graph shows larger balls have slower whisker lags. Anya has zero lags for all trials on the small ball. b. A scatter graph of whisker asymmetry and ball orientation, showing values from all tracked frames. c. The lag, in seconds, between changes in ball orientation and changes in head orientation. The graph shows Anya having larger lags, compared to the other sea lions. d. A scatter graph of head orientation and ball orientation, showing values from all tracked frames. e. The lag, in seconds, between changes in whisker asymmetry and changes in head orientation. f. A scatter graph of whisker asymmetry and head orientation, showing values from all tracked frames. Graphs on the left hand side show mean values with standard error bars. Asterisks (*) show significant results and differences ($p<0.05$).

Figure 3, an example clip showing whisker, head and ball orientations on a medium ball by Elmo. a. left (blue) and right (red) whisker mean angular positions throughout a tracked clip. Angular spread is also shown (dotted line) and tends to decrease as whiskers move forward, such that more forward whiskers are more bunched up. b. Angular ball orientation, whisker asymmetry and head orientation. Ball orientation and whisker asymmetry peak at similar times and are well correlated. There is a slight delay in head orientation. c. Series of video stills of one cycle of ball movements. i. The ball moves right (decreases ball orientation) and whiskers on the right protract forward (decrease in whisker asymmetry); ii. The head and nose rotates right (decrease in head orientation), until the ball stabilises in iii. Some of the tracked points on the seal can be seen by the red dots. Pink arrows refer to the movement of the ball, and the brown arrow to the movement of the head.

Figure 4, whisker positions and movements. a. Whisker offset values (mean whisker positions), show that whiskers have lower offset values on large balls compared to small balls. b. Whisker amplitude, which is largest for the sea lion Anya. c. Angular whisker spread, which is smallest on large balls overall, and can be seen to be true for both Anya and Elmo. d. Whisker asymmetry, which is lowest in Anya. All graphs show mean values with standard error bars. Asterisks (*) show significant differences ($p<0.05$).

Figure 5, surface displacement on medium and small balls, following a change in ball orientation. a. The ball is in line with the head. b. the ball rotates and rolls on the nose. There is a surface displacement on the medium ball (m), which is larger here than if the ball was smaller (s). The small ball is indicated by the smaller pink circle. The dashed line in b corresponds to the original position in a. This example shows Elmo balancing the medium ball.

Figure 6, whisker protractions and asymmetries during feeding in two sea lions. Images courtesy of Stephen Birtwistle, Blackpool Zoo.

Figure 1

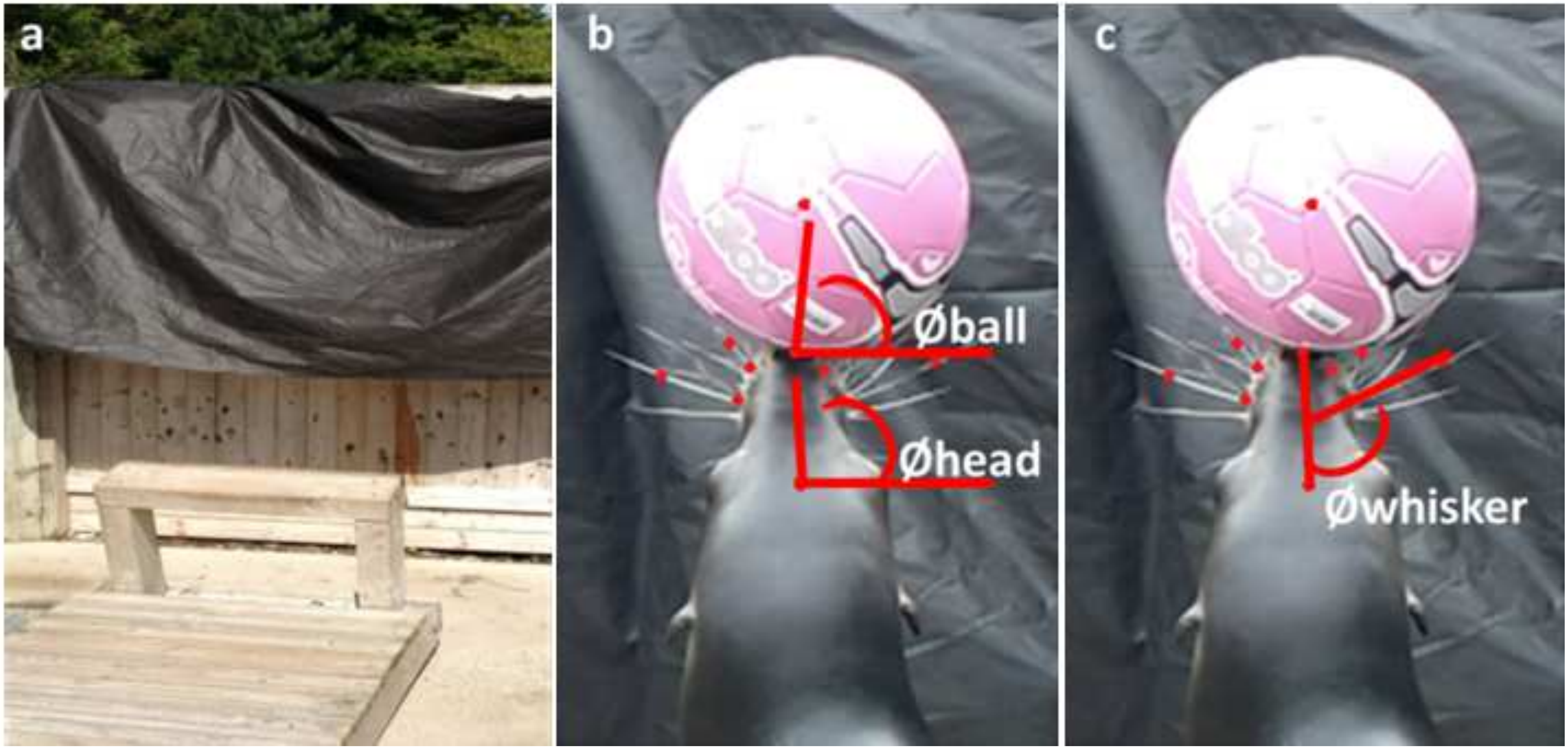


Figure 2

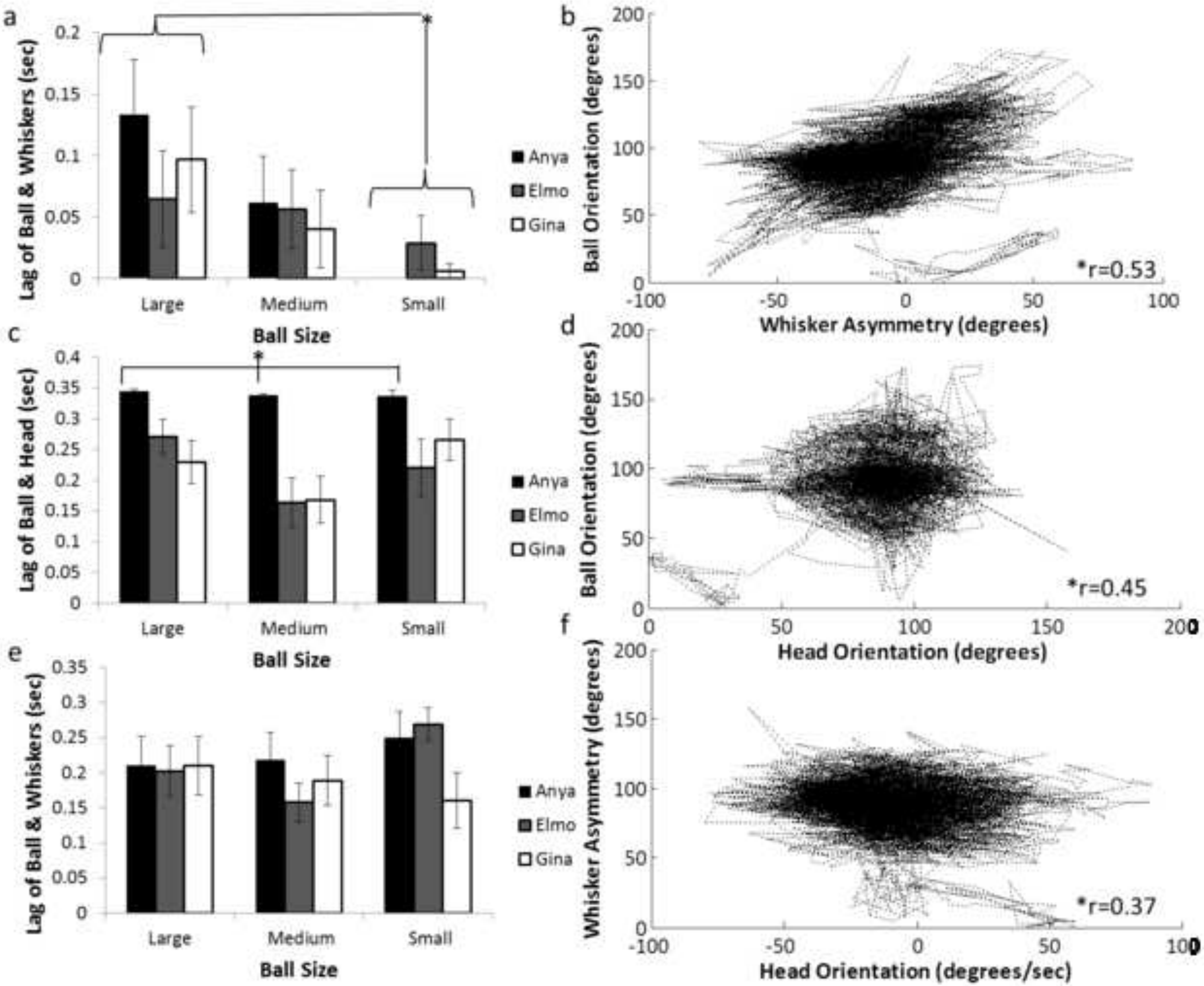
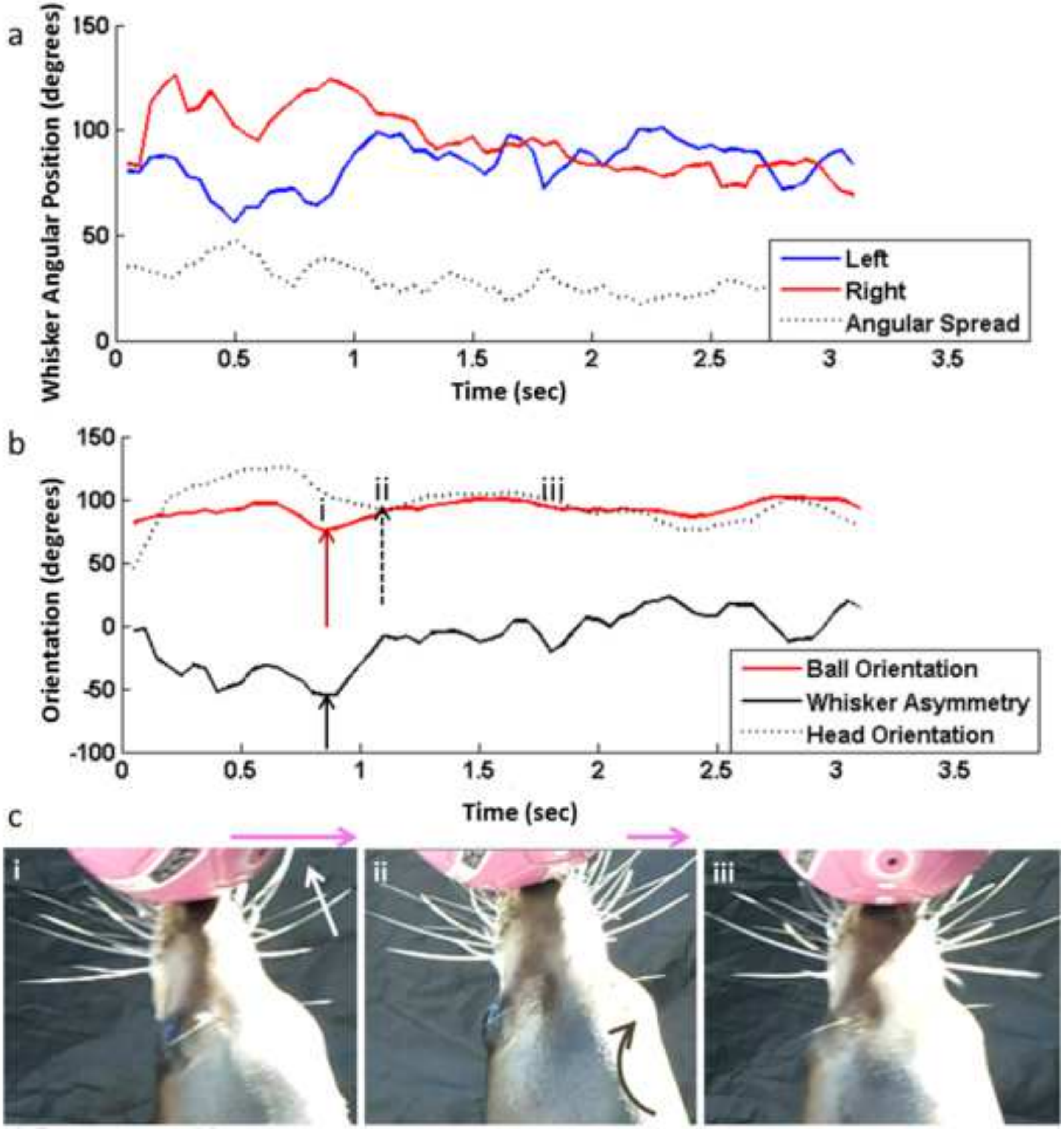

a
Lag of Ball & Whiskers (sec)
0.2
0.15
0.1
0.05
0
*
Large
Medium
Small
Ball Size
■ Anya
■ Elmo
☐ Gina
b
Ball Orientation (degrees)
200
150
100
50
0
-100
-50
0
50
100
Whisker Asymmetry (degrees)
*r=0.53
c
Lag of Ball & Head (sec)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
*
Large
Medium
Small
Ball Size
■ Anya
■ Elmo
☐ Gina
d
Ball Orientation (degrees)
200
150
100
50
0
0
50
100
150
200
Head Orientation (degrees)
*r=0.45
e
Lag of Ball & Whiskers (sec)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Large
Medium
Small
Ball Size
■ Anya
■ Elmo
☐ Gina
f
Whisker Asymmetry (degrees)
200
150
100
50
0
-100
-50
0
50
100
Head Orientation (degrees/sec)
*r=0.37

Figure 3



Ball starts to move right
Whiskers on right protract forward
Head does not respond yet.

Ball starts to slow
Whiskers still protracted on the right, head also rotates right

Ball stops moving
Whiskers and head become central and symmetric

Figure 4

Click here to download high resolution image

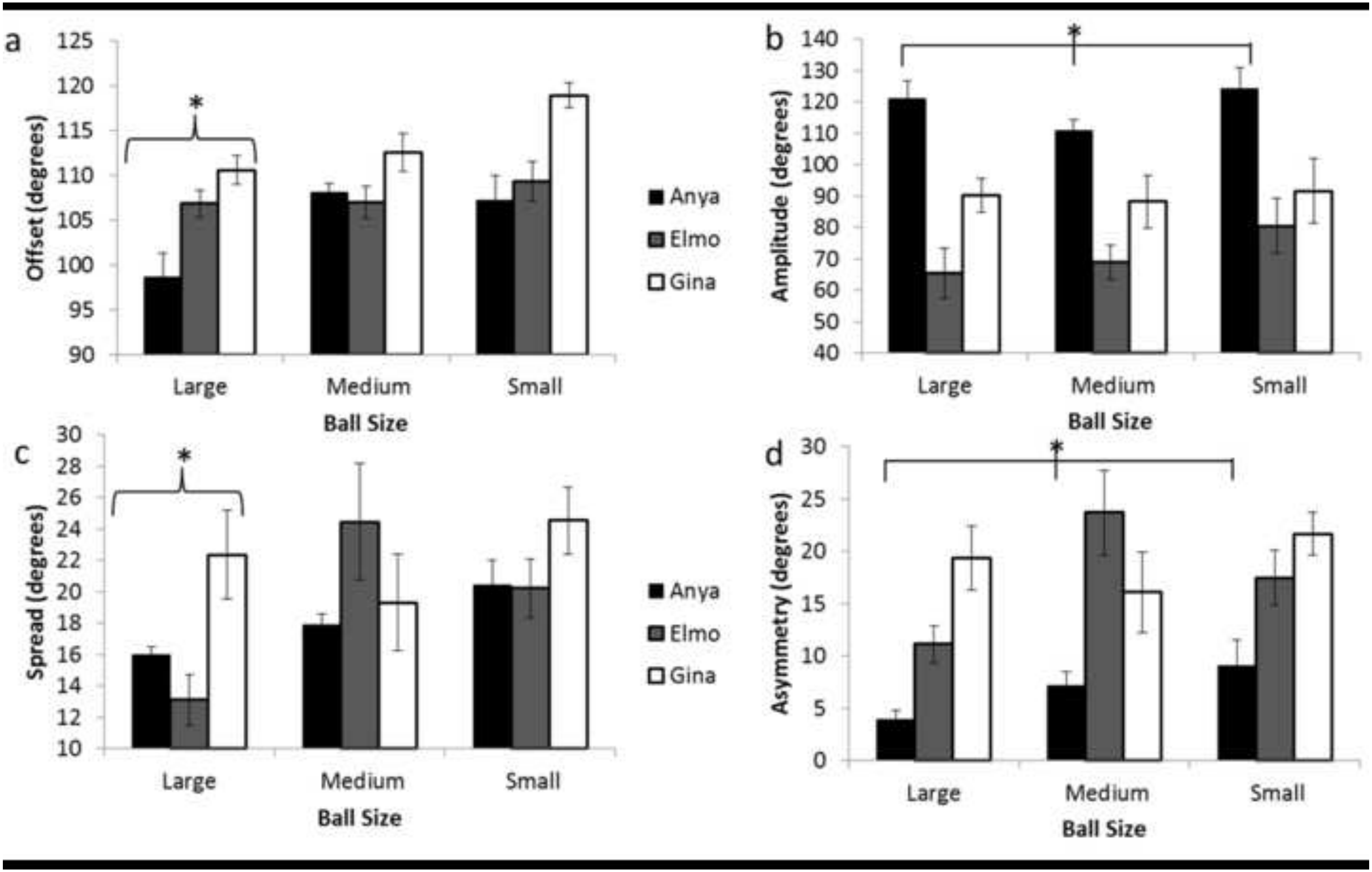


Figure 5

Click here to download high resolution image

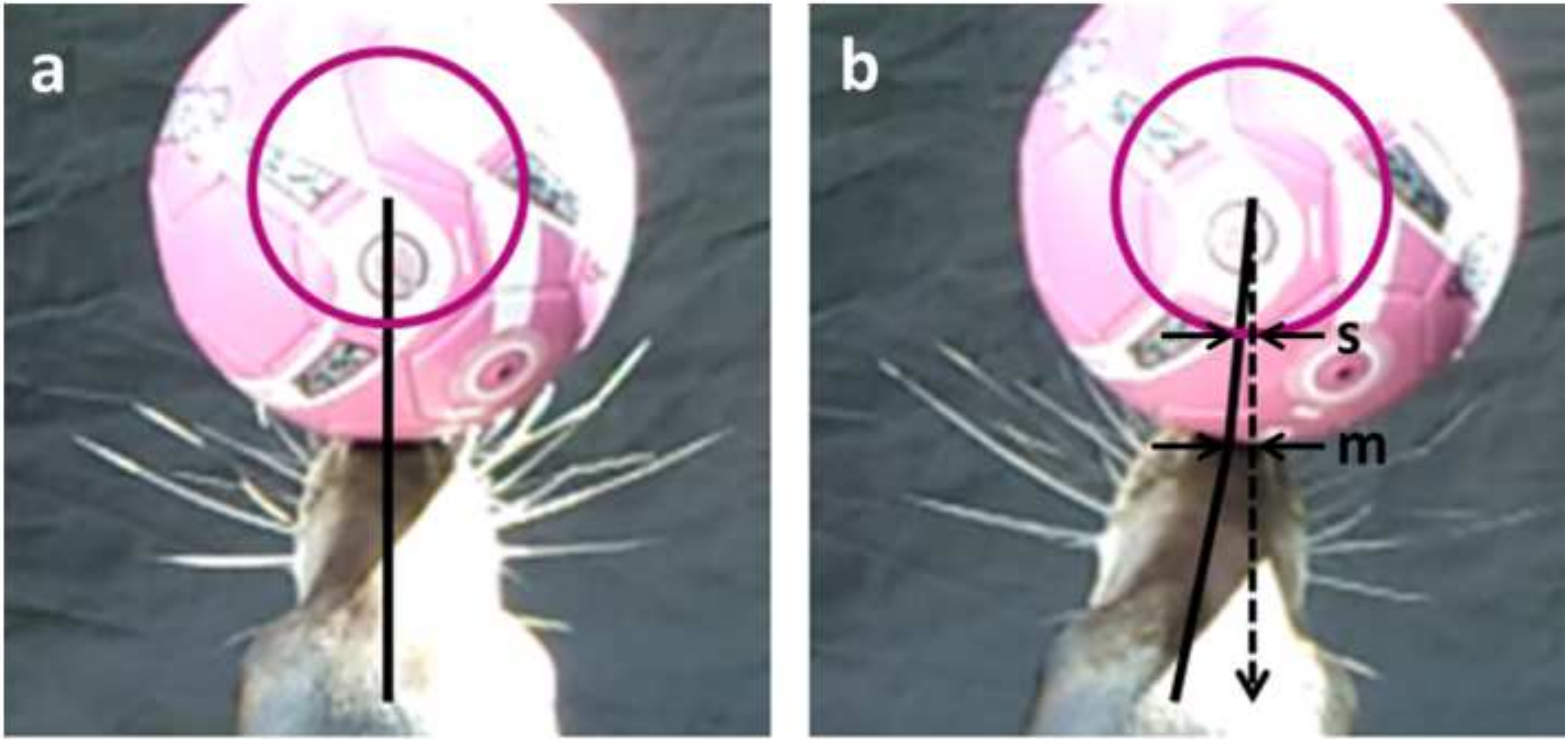


Figure 6

Click here to download high resolution image

Supplementary Material 1, 2, 3

Supplementary Movie 1