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

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## 12 **Abstract**

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

## 25 **Introduction**

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

39 Active touch sensing studies in animals focus on vibrissal touch sensing, with rodents,  
40 insectivores and pinnipeds labelled as *whisker specialists*. Pinnipeds, in particular, have been  
41 used in active touch sensing studies, due to the prominence of their facial vibrissae and their  
42 ability to move them using a network of voluntary muscles (Berta et al. 2005). Indeed,  
43 vibrissal touch is thought to be more efficient in pinnipeds, than in terrestrial mammals, due

44 to the whiskers being more sensitive (having ten times more nerve fibers) (Rice et al. 1986;  
45 Hyvärinen, 1989) and unaffected by temperature changes (Dehnhardt et al. 1998; Mauck et  
46 al. 2000). The California sea lion (*Zalophus californianus*) has 38 vibrissal hairs on each side  
47 of their face, which can grow up to 20 cm (Dehnhardt, 1994), and play a primary role in  
48 active touch sensing (Dykes 1975; Hyvärinen 1989; Dehnhardt 1994; Dehnhardt et al. 2001;  
49 Leinwand 2003; Mitchinson et al. 2007) and hydrodynamic trail following (Gläser et al.  
50 2011; Hanke et al. 2013). California sea lions can use their whiskers to discriminate between  
51 different shapes (Dehnhardt 1990) and sizes, down to surface area differences as small as 0.5  
52 cm (Dehnhardt 1994; Dehnhardt and Dücker, 1996). While vibrissal touch is often thought of  
53 as an active sensory system (Prescott et al. 2011; Grant et al. 2014) there has been little  
54 evidence of whisker control in pinnipeds. Dehnhardt (1994) conducted a size differentiation  
55 task, and found that although California sea lions protracted their whiskers and positioned  
56 their most rostral whiskers on to the stimuli, there were no significant differences between  
57 whisker movements on different sized objects. Dehnhardt (1994) rather observed that the sea  
58 lions used small head movements to position their whiskers during the task, rather than  
59 whisker movements per se.

60 Active touch sensing tasks in pinnipeds have, therefore, focussed on discrimination  
61 thresholds thus far, rather than on their ability to control whisker movements. These  
62 discrimination studies have indicated that head positioning, rather than whisker control,  
63 drives the placement of whisker positions on sensory stimuli (Dehnhardt 1994; Grant et al.  
64 2013). To explore this further, perhaps a more complex, dynamic sensorimotor task is needed  
65 to promote whisker movements. Even though sea lions are sometimes considered  
66 synonymous with the ability to ball-balance, this complex sensorimotor task has yet to be  
67 explored in these animals. Therefore, this study will draw inspiration from human haptic  
68 studies to explore how California sea lions use their whiskers during a ball-balancing task.  
69 This study will investigate whether whisker control, between the left and right sides,  
70 coordinates ball positioning. This study will then go on to characterise whisker positions and  
71 movements as the sea lions balance three differently sized balls.

## 72 **Materials and Methods**

### 73 *Animals*

74 The study was conducted at the Active Oceans Arena in Blackpool Zoo that houses a  
75 total of nine individual California sea lions (*Zalophus californianus*). Three California sea

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

### 10 *Apparatus*

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

### 27 *Experimental Procedures*

28 Sampling took place over five weeks, throughout May and June 2013, including a  
29 training week without data collection. This training week was to make sure the sea lions were  
30 fully desensitised to the recording apparatus and to check the positioning of the camera.  
31 Sessions were conducted at the same time every day (around 4pm), taking care that the sea  
32 lions were not involved in any public displays directly prior to undertaking the task. During

108 the task, each sea lion was taken into the training area (Fig. 1a) alone. The same two trainers  
109 were present each time. Trainer 1 would collect the sea lion, bring it to the station and then  
110 stand ready to record the footage directly behind the animal. Trainer 2 would conduct the  
111 experiment, including rewarding, training and monitoring the sea lion throughout. During a  
112 session each animal received approximately 20-40% of its daily food amount. This was  
113 freshly thawed cut mackerel, cut herring or whole sprats.

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

### 130 *Video Selection and Analysis*

131 All video clips were examined for analysis. This was to ensure videos selected  
132 showed the following: (i) all whiskers were visible by the camera throughout the entire clip,  
133 (ii) the head was accurately lined up with the camera, (iii) there was enough lighting to see all  
134 the whiskers against the black background, and (iv) the sea lion did the correct behaviour. In  
135 total, after viewing all video clips, ninety were selected for analyses (ten video clips per sea  
136 lion for each of the three different balls, giving thirty clips per animal). Each video was  
137 tracked manually using the open source video tracking toolbox 'Tracker' (Tracker 4.80,  
138 Douglas Brown 2013, www.cabrillo.edu). Two whiskers on each side of the face were  
139 tracked along with the mid-point of the head (between the eyes), the centre of the ball and the

140 tip of the nose. The whiskers selected for tracking were the second from the front and second  
141 from the back on each side of the muzzle (Fig. 1b and c). Two points were tracked on each  
142 whisker: the base and the shaft (a point around two thirds along the whisker shaft) (Fig. 1c).  
143 This made eleven tracked points in total. The tracking was conducted over a three second  
144 period in every three frames; tracking started once the sea lion had steadied itself after  
145 receiving the ball from Trainer 2. A small sample of videos was tracked three times by two  
146 researchers to measure the accuracy of manual tracking the footage. Findings showed that  
147 95% of the tracked points fell within 1.1 cm of each other when they were repeated. This is a  
148 high level of accuracy for a zoomed-out video with manual tracking.

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

### 168 *Statistical considerations*

169 As the movements of the head, ball and whiskers were periodic, per-frame measures  
170 of head orientation, ball orientation and whisker asymmetry were cross-correlated to get a  
171 measure of correlation and delay (lag) between the de-meaned signals in each clip, of: i) ball

172 orientation and whisker asymmetry, ii) ball orientation and head orientation, and iii) whisker  
173 asymmetry and head orientation. These analyses were also run for all sea lions individually  
174 (Supplement 2), as the results were robust over all three sea lions only pooled data is  
175 presented here (in Fig. 2). To compare differences between the sea lions and the different ball  
176 sizes, per clip (mean) measures of lags, whisker offset, amplitude, spread and asymmetry  
177 were compared using between-ANOVAs. All the data was normally distributed. Where  
178 means are reported in the text, they are reported as mean  $\pm$  standard deviation.

## 179 **Results**

### 180 *Sea lions use their whiskers quickly and accurately during ball balancing*

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

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

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

### 209 *Sea lion whisker positions and movements depend on object size*

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

### 219 *Whisker movements and positions can vary between individuals*

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

## 225 **Discussion**

226 This is the first study to identify that pinnipeds move their whiskers significantly  
227 during a sensorimotor task, rather than just their head. Indeed, results from this study show  
228 that whisker positions are quicker and more correlated to ball movements than those of the  
229 head. This was not simply as a result of the ball contacting the whiskers as the same, if not  
230 stronger, patterns in the data were observed when using values from only the caudal whiskers  
231 that tended not to contact the ball at all (Supplement 3). While it is clear that the whiskers are  
232 moving, it is unclear whether the whiskers themselves can act to stabilise the ball. It could be  
233 that the whisker movements are sensing where to direct the motion of the head. Indeed, in  
234 rodents, whisker asymmetry precedes head rotations (Towal and Hartmann 2006; Mitchinson



235 et al. 2011; Grant et al. 2012) and serves to scan the area that the head is moving in to. While  
236 whisker movements precede head movements here, they are better correlated to ball  
237 movements (Fig. 3b), which suggest they might not be simply directing the head.

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

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

264 While the overall data patterns hold true over the three sea lions, there were some  
265 differences, with Anya having slower head movements, higher amplitude whisker movements  
266 and less whisker asymmetry. Lags in response to balancing tasks can be related to age or

267 coordination deficits (Jongmans 2003), however, Anya is not the oldest and did not have any  
1 268 larger latencies in whisker responses. Rather, the sea lions balanced the balls differently  
2 269 between them. Gina tended to keep her head very still laterally, and bounced the balls on her  
3 270 nose, Anya made large lateral head movements and Elmo was somewhere in the middle of  
4 271 the two (See Supplement 2). Observed differences between animals in this study flags up the  
5 272 difficulties with conducting experiments on a limited number of animals, which is very  
6 273 common in studies of this type. While it is very difficult to access large numbers of marine  
7 274 mammals, care must be taken when reviewing work from studies that only have one or two  
8 275 subjects (Dehnhard and Dücker 1996; Wieskotten 2010a, 2010b; Grant et al. 2013).

17 276 Using a dynamic task in this way has encouraged more whisker movements, and  
18 277 identified the importance of whisker positions during active touch tasks. While more static  
19 278 discrimination tasks give detailed and accurate information about tactile capabilities, they are  
20 279 not able to encourage suitable whisker movements, and often head movements appear to be  
21 280 more responsible for whisker positioning, than the movement of the whiskers themselves  
22 281 (Dehnhardt, 1994, Grant et al. 2013). While this ball-balancing task is not a naturalistic  
23 282 behaviour that sea lions perform in the wild, it has been used in this study as a complex  
24 283 sensorimotor task that has encouraged whisker movement and control. Perhaps similar  
25 284 whisker movements might be used in other dynamic tactile tasks. For instance, Fig. 6 shows  
26 285 that sea lions might use similar strategies to guide moving fish towards their mouths. In Fig. 6  
27 286 the sea lion whiskers are bunched up and protracted forward, and asymmetries can be  
28 287 observed in the whisker fields as the sea lions orient their whiskers towards the travelling  
29 288 fish. Indeed, it would be interesting to further explore the role of whisker movements in  
30 289 hunting and prey capture in the future. We see this study as an initial investigation in to  
31 290 dynamic sensing tasks in pinnipeds, and hope that experiments of this type might help us to  
32 291 better understand the active nature of this tactile sensory system.

47 292

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299 **Ethical Standards**

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

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54 380 FIGURE CAPTIONS

55  
 56 381 **Figure 1, Test set-up and tracking during the ball-balancing task.** a) the dry training arena,  
 57 382 including the sea lion station and black sheet; b) an example video still, including the tracked points  
 58 383 (red points) and an indication of the ball orientation ( $\emptyset$ ball) and head orientation ( $\emptyset$ head); c) an

384 example video still, including the tracked points (red points) and an indication of the right, caudal  
385 tracked whisker angle.

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

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

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

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

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

Figure 1  
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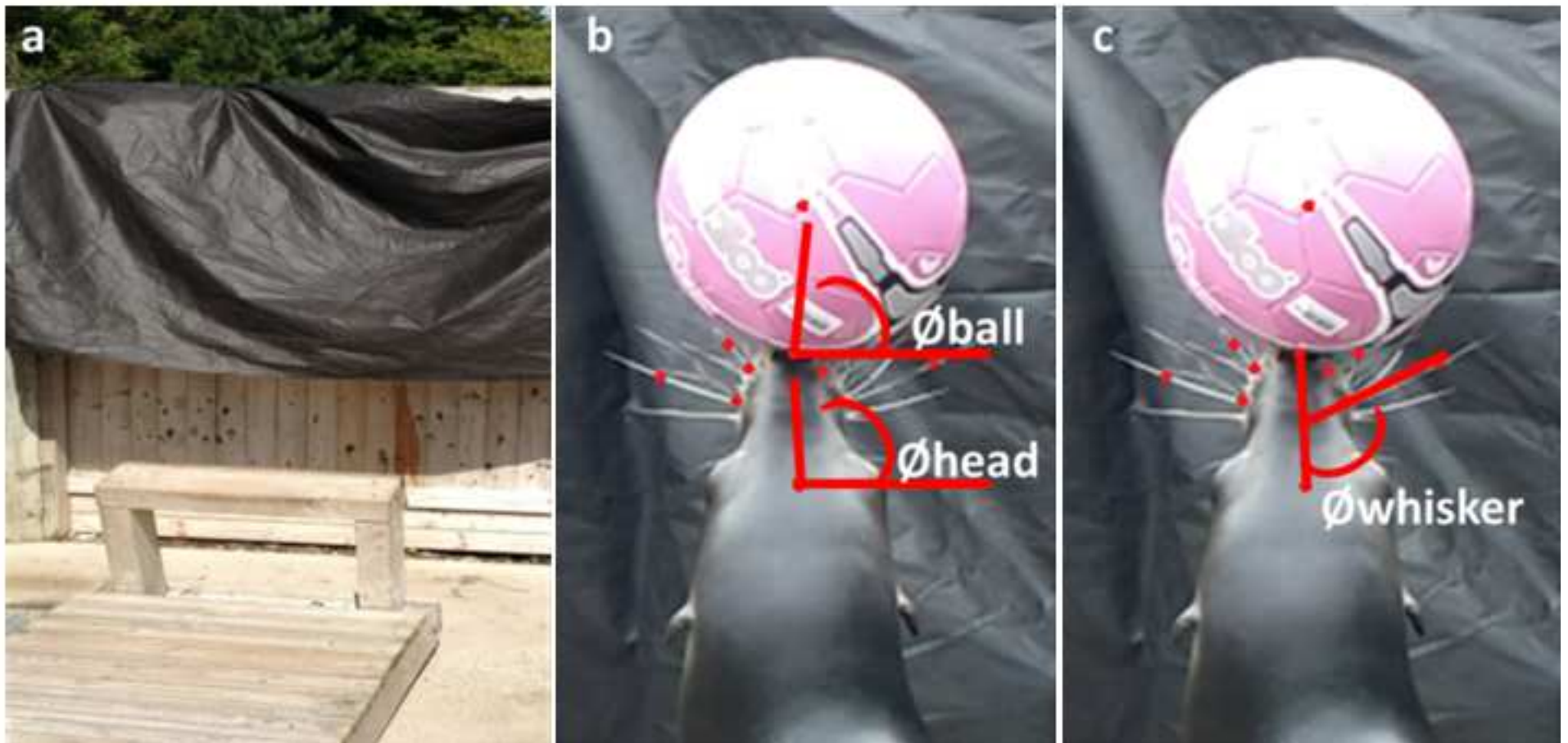


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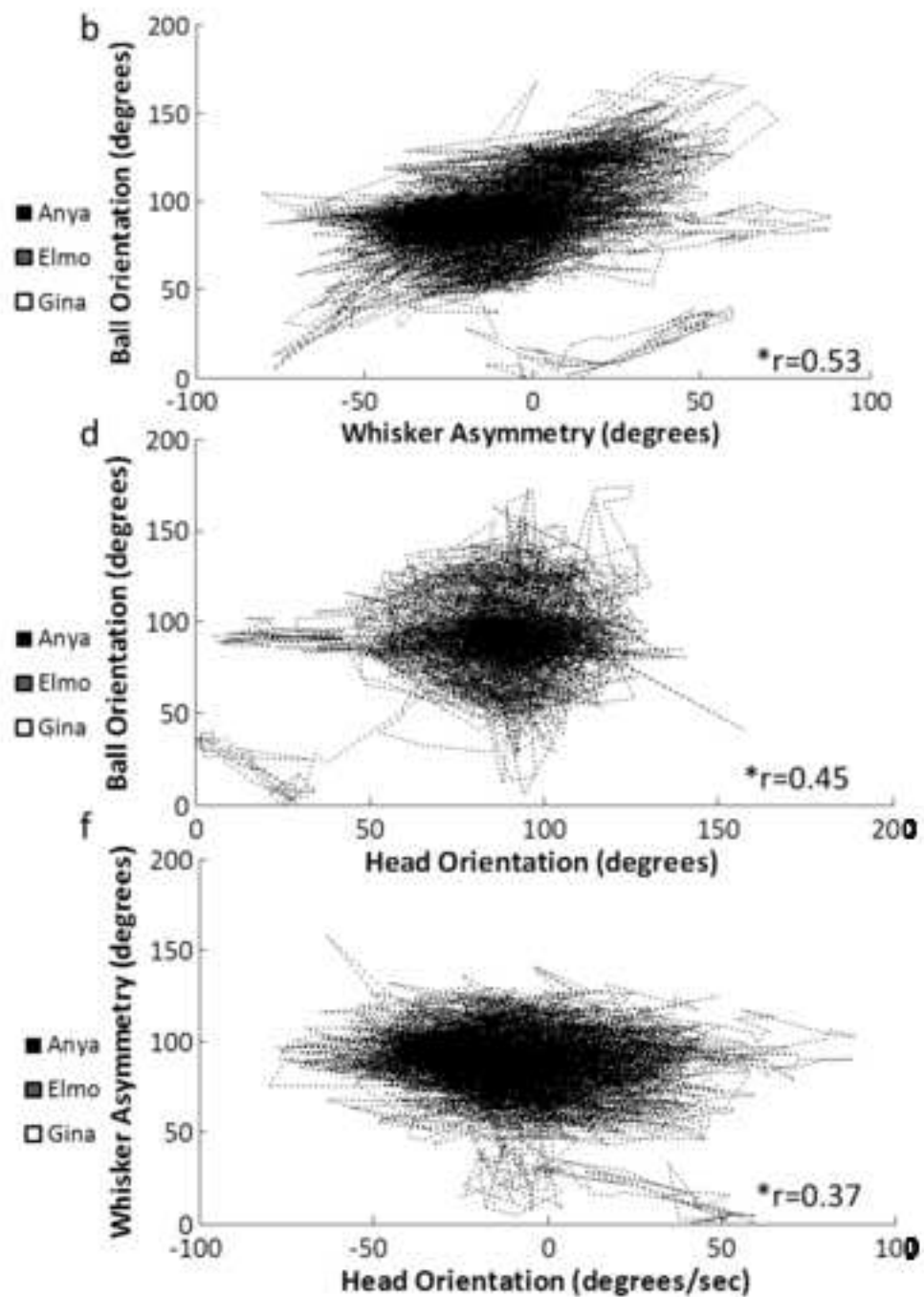
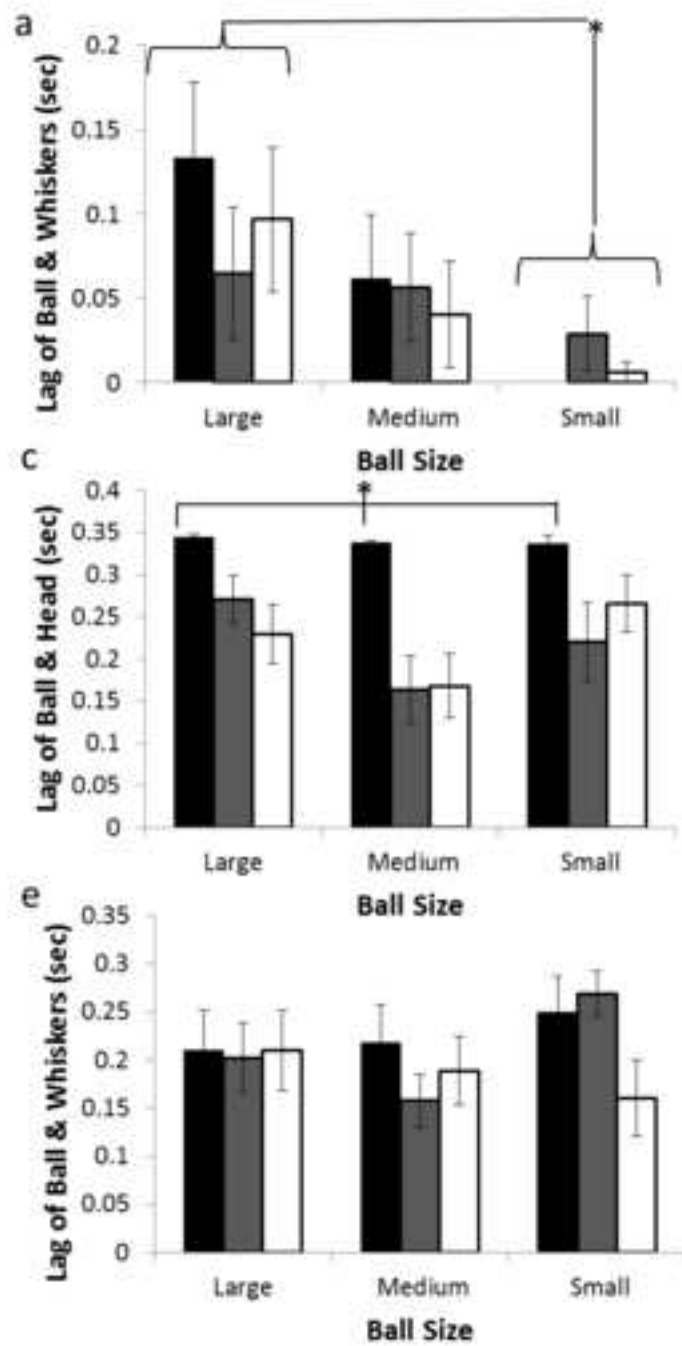




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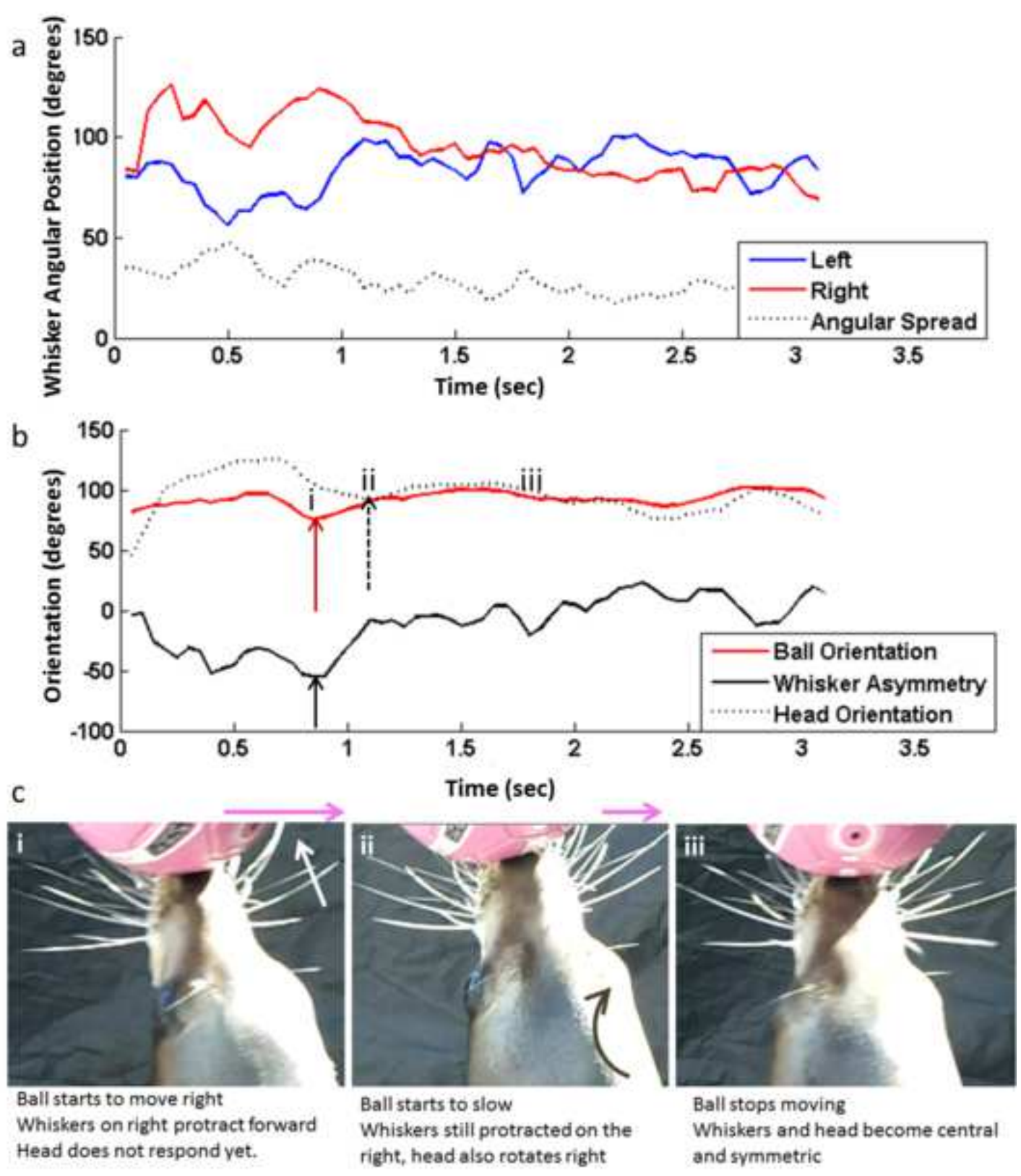


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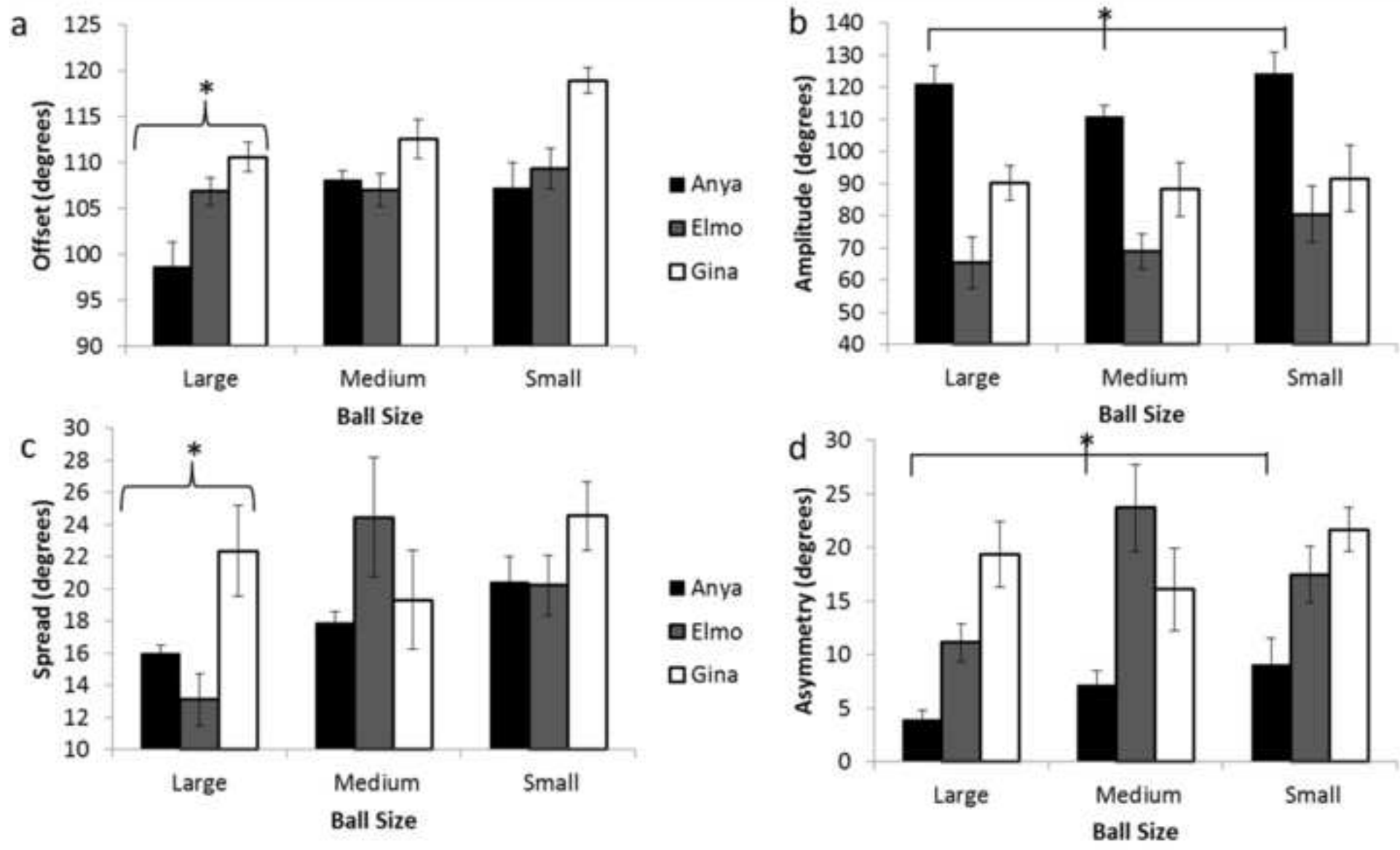


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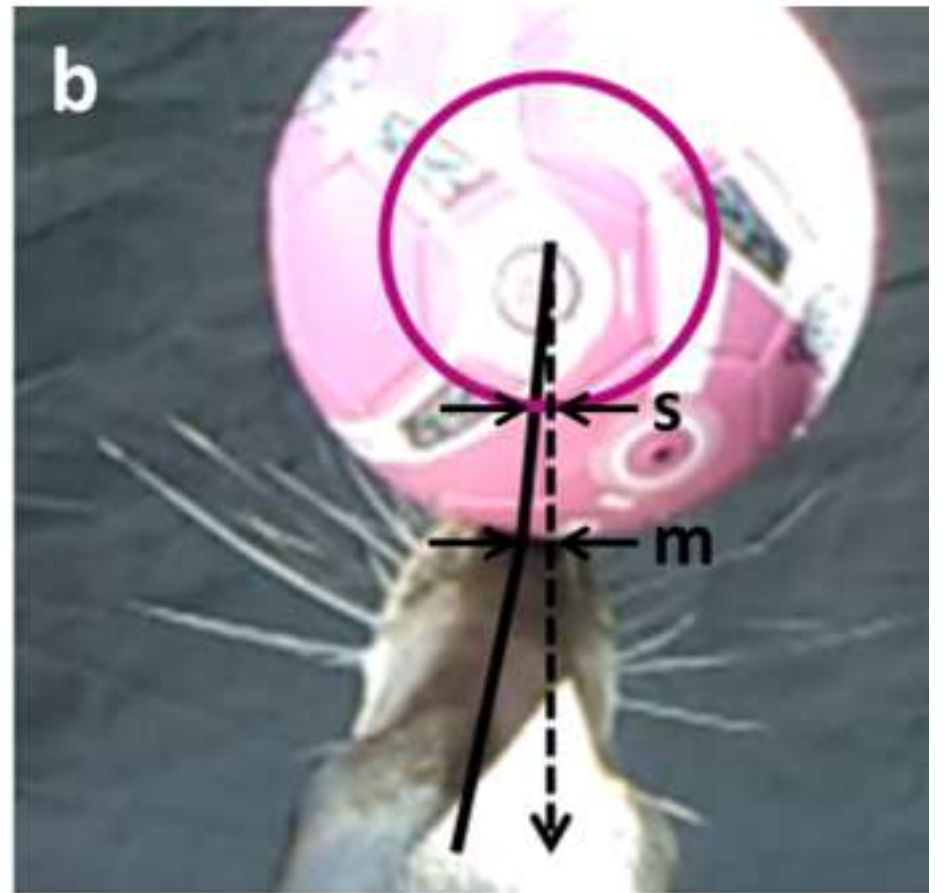
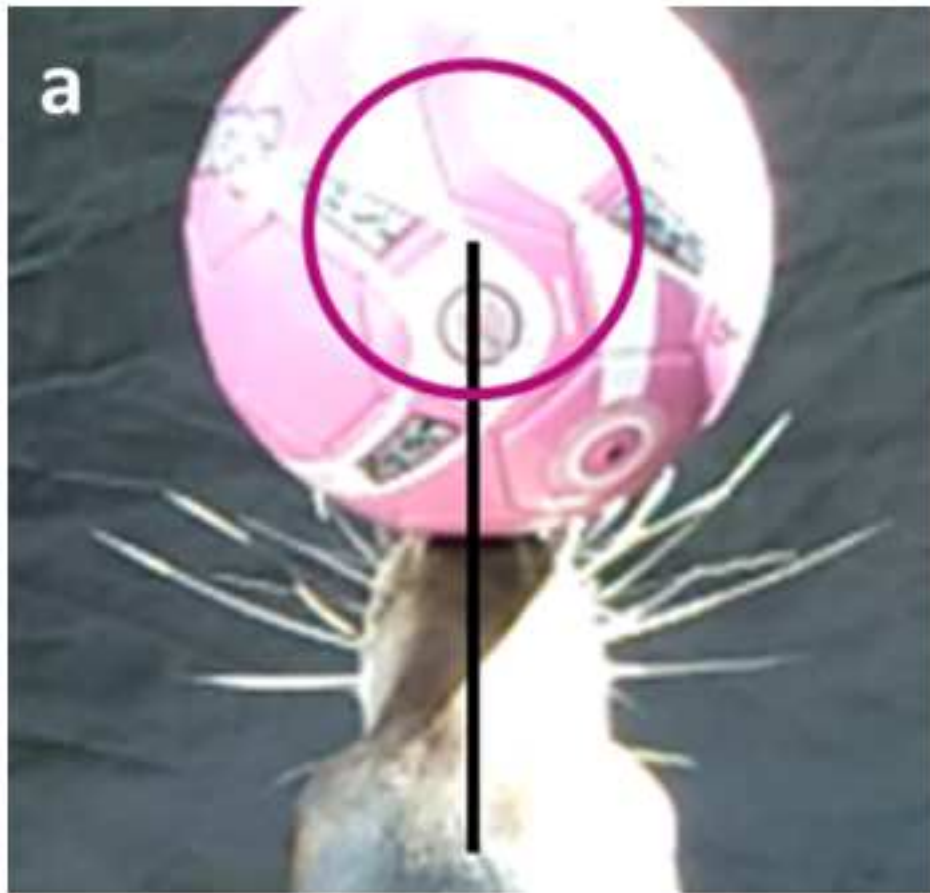


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Supplementary Movie 1

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