INTERNATIONAL
JOURNAL OF COMPARATIVE PSYCHOLOGY

2016, 29
Heather M. Hill
Editor
Peer-reviewed

California Sea Lions (*Zalophus californianus*) Can Follow Human Finger Points and Glances

Thomas Arkwright[1], Raphaelle Malassis[2], Toby Carter[1], and Fabienne Delfour[2, 3]

[1] Anglia Ruskin University, United Kingdom
[2] Paris 13 University, France
[3] Parc Asterix, France

The aim of this study was to determine whether California sea lions (*Zalophus californianus*) are capable of using subtle human gestural cues in a series of object choice tests. Four sea lions, housed at Parc Astérix Dolphinarium (Plailly, France), were tested using three gestural cues: hip-based finger points, chest-based finger points and eye glances (no head movement involved). Above chance performance was found in response to these cues in 4/4, 2/4, and 1/4 sea lions, respectively, suggesting that the sea lions were able to generalize their response from conspicuous pointing gestures to subtle finger pointing, as well as to eye glance cue for one subject. Discrepancies in accuracy rates between the cues confirmed however that conspicuousness of the pointing gesture is determinant for the ability of the sea lions to exploit it efficiently. These findings reinforce the hypothesis that human-socialization of undomesticated species can lead some individuals to develop an affinity for interpreting very subtle human gestural cues.

Humans are able to follow the direction of a pointing finger, head orientated gaze and even an eye-only glance in order to identify an object or location being indicated by a gesture giver. This ability is used in a great number of social interactions to alter the focus of an individual towards a specific object, location or event. Humans have become so proficient at using these gestures in socialisation (Humphrey, 1976) that even those which are only present for extremely short periods of time (such as a split second glance and unconscious cues) can be used as a means of subtle communication between individuals and convey a wealth of information about an individual's emotional state and/or intentions (Frischen, Bayliss, & Tipper, 2007). The range and skill with which humans are able to use gestural cues even at an early age (Brooks & Meltzoff, 2002; Csibra & Volein, 2008; Povinelli, Bierschwale, & Cech, 1999) lead to the discussion of whether non-human animals are also capable of understanding such gestures and applying them in order to locate specific objects, an ability observed in a variety of species including, but not limited to domestic dogs (*Canis familiaris*; Soproni, Miklósi, Topál, & Csányi, 2001; Virányi et al., 2008), grey wolves (*Canis lupus*; Udell, Spencer, Dorey, & Wynne, 2012; Virányi et al., 2008), African elephants (*Loxodonta Africana*; Smet & Byrne, 2013), domestic horses (*Equus caballus*; Proops & McComb, 2010; Proops, Walton, & McComb, 2010), domesticated pigs (*Sus scrofa domestica*; Nawroth, Ebersbach, & Von Borell, 2014), bottlenose dolphins (*Tursiops truncatus*; Xitco, Gory, & Kuczaj, 2001), grey seals (*Halichoerus grypus*; Shapiro, Janik, & Slater, 2003), South African fur Seals (*Arctocephalus pusillus*; Scheumann & Call, 2004), California sea lions (*Zalophus californianus*; Malassis & Delfour, 2015) and all great apes (Call, Hare, & Tomasello, 1998; Itakura & Tanaka, 1998; Tomasello, Call, & Hare, 1998). In comparison with other non-human animals tested, domestic dogs seem especially adept at following human gestural cues to locate objects (Soproni et al., 2001; Virányi et al., 2008).

In addition to this use of pointing some species have also been observed to follow the visual gazes (head and eyes) of both humans and conspecifics to locate an object in both choice experiments and on spontaneous occasions. Species which have demonstrated this gaze tracking ability include domestic dogs and grey wolves (Udell et al., 2012), sooty mangabeys (*Cercocebus atys torquatus*; Tomasello et al., 1998), rhesus macaques (*Macaca mulatta*; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Tomasello et al., 1998), stumptail macaques

Please send correspondence to Thomas Arkwright, Department of Life Sciences, Anglia Ruskin University, Cambridge, United Kingdom. (Email: tom_arkwright1@hotmail.com) https://doi.org/10.46867/ijcp.2016.29.00.02

(*Macaca arctoides*; Tomasello et al., 1998), pigtail macaques (*Macaca nemestrina*; Tomasello et al., 1998), northern bald ibis (*Geronticus eremite*; Loretto, Schloegl, & Bugnyar, 2010), ravens (*Corvus corax*; Bugnyar, Stöwe, & Heinrich, 2004), American crows (*Corvus brachyrhynchos*; Clucas, Marzluff, Mackovjak, & Palmquist, 2013), jackdaws (*Corvus monedula*; Davidson, Clayton, & Thornton, 2015), all four great ape species (Brauer, Call, & Tomasello, 2005), and South African fur seals (Scheumann & Call, 2004). This use of gaze following indicates that some species are able to project another individual's line of sight and then trace that projection to a specific location.

Certain species seem particularly adept at utilising human gestural cues and subtle body orientations to gain potentially important information. In particular, domestic dogs are especially capable at following human gestures (Soproni, Miklósi, Topál, & Csányi, 2002), an ability which could be allocated to the domestication process and their continual close proximity to humans. A recent study showed that dogs follow human gaze into distant space and that their performance could be modulated by training (Wallis et al., 2015). Additionally, human raised Grey wolves have been shown to display a higher level of responsiveness to human gestures than their non-encultured counterparts (Udell et al., 2012; Virányi et al., 2008), indicating that on some level an exposure to humans either from an early age or for an extended period of time allows some species to recognise certain human body movements and orientations and apply that recognition to their advantage (Kaminski, 2009; Proops et al., 2010; Udell, Dorey, & Wynne, 2010).

Studies conducted on human-socialized marine mammals revealed that these animals were also able to follow various pointing gestures in object-choice tasks. Bottlenose dolphins tested on arm points and cross-body points, as well as gazing cue (involving head turn) were successful from the first trials on each of these directional cues (Pack & Herman, 2004). Similar results were obtained in fur seals (Scheumann & Call, 2004). Recently, Malassis and Delfour (2015) also demonstrated in California sea lions (the same individuals which took part in the current study) the ability to exploit human arm pointing and gazes (head turns) to correctly choose a target object at rates exceeding chance.

The aim of this follow-up study was to determine whether California sea lions are capable of using a range of human gestural cues increasing in level of subtlety to locate specific targets in a series of object choice tests. In particular, the sea lions' responses to finger-only points, (hip and chest based), and eye only glances (i.e., without head turn) were assessed.

Method

Subjects

This study was carried out at the Dolphinarium within Parc Astérix theme park, located North of Paris. The subjects were three male and one female California sea lions housed within a dedicated pool area measuring approximately 125 m^2 and with a volume of 313 m^3. The pool area was equipped with both a purpose built beach stretching the length of the enclosure on one side and with a width of 2.5 m, along with indoor housing into which the animals are moved at night or should separation be required for training purposes, for instance. The experiments took place during regular training sessions, which occurred at least twice daily and did not exceed 10 min. On some days, testing sessions were able to be carried out more than twice, although in these instances scheduling precautions were taken to ensure the same animal was not used for all tests, both to ensure minimal impact on the animals' comfort (prolonged exposure to difficult cognitive tasks with variable motivation) and to help keep the daily training routine in place.

The four sea lions were familiar with both shows and training sessions and they knew a wide repertoire of human commands. They were fed with a mixture of herring, capelin and squid during their five daily training sessions. They had to respond to vocal and gestural human commands to be rewarded with a whistle blow and pieces of fish. By the end of a session (including experimental sessions), sea lions received their planned ration, regardless of their performance.

Pretraining

During their daily training sessions, the four sea lions have been trained to respond to several commands which included arm gestures. Two of the commands involved an extended arm pointing toward a general direction: All of the subjects had been trained to return to the water when the trainer extends his/her arm in the direction of the pool, saying "water". The second command was known only by Santo, who had been trained to return a floating toy to the trainer who extended his/her arms in direction of the water and formed a square shape with his two hands. Two other commands, known by the four subjects, involved an extended arm oriented toward the sea lion: with the palm vertical and open, while saying "stay", to make it sit down and wait at a specific place, and with a finger pointed toward the animal, while saying "shy", to make it cover its muzzle with its flipper. These commands were the only ones from their daily training that involved an extended arm and/or finger.

In addition, the four sea lions participated in a previous human pointing gestures experiment including arm pointing, cross-body pointing, elbow pointing, foot pointing and gaze (Malassis & Delfour, 2015). This previous study first assessed sea lions' response to a distal pointing gesture, with a distance of approximately 1 m between the tip of the trainer's finger and the target object. Two subjects, Santo and Smack, responded on the very first trial by moving to the pointed target. They were not rewarded until they touched it with their muzzle, which they both did after a few seconds. After this first trial, they responded to the cues by touching a Frisbee with the muzzle. In contrast, Gonzo and Kaï both attempted to respond to the first distal point by executing previously learned commands (specifically by touching the trainer's pointing hand with their muzzle, or by executing the shy behavior, signaled by the trainers' finger pointed toward the sea lion). Therefore, both were trained with proximal points (30 cm between the tip of the trainers' finger and the target), before to perform the experiment. Two months elapsed between the end of the previous experiment and the beginning of the current experiment.

The individuals that participated in the current experiment were thus not naïve to select, by touching with their muzzle a particular object, indicated by a familiar human body extended gesture. Considering their previous experiences of commands and of target selection according to various pointing gestures, the main aim of this study was to assess California sea lions' abilities to generalize their responses when more subtle trainer's body parts and gestures were used to emit the directional cue.

Desensitization to Experimental Equipment

Prior to testing, each animal was exposed to all equipment which would be used during the experimental period. This was done as part of the daily training regime in order to acclimatize the animals to the new objects. Although the animals had previously been acquainted with the equipment in previous tests on gesture recognition (Malassis & Delfour, 2015), the animals were reacquainted with the objects as it had been two months since the animals had seen or interacted with any of the equipment. Additionally, for a period of approximately two weeks before testing began the experimenter attended routine training sessions, standing in the same spot as in testing and holding the video camera in order to allow the animals to habituate to the presence of an unknown human by their pool and avoid neophobia this might bring about. This was done as while the sea lions are used to being viewed by visitors outside of their enclosure on a daily basis they very rarely encounter new people within the enclosure itself.

General Procedure

The tested animal was not separated from its conspecifics, it was simply led to the part of the enclosure where the experimental setup was located. The remaining three sea lions not being tested during the session underwent regular training sessions, with each animal having its own trainer (i.e., a trainer animal ratio of 1:1). The human that gave the gestural cues in the current experiment was one of the sea lions' customary trainers. Before testing began each animal was paired with a trainer for the duration of the whole experimental period. These pairs were decided based on the relationship between the trainers and animals, specifically, the pairs that work together in regular training. We made sure that all trainers were previously trained to correctly execute each cue and a strong emphasis was put on displaying only gestural and verbal cues defined for each experimental condition throughout each trial to avoid unintentional extra cues.

The sea lions marker, a piece of drainage-linked black rubber matting (60 x 18 x 3 cm) was placed on the floor. The target objects were two green Frisbees (24 cm diameter), placed approximately 1 m from the trainer and 1.8 m diagonally away from the matting on either side (Figure 1). Distance between the trainer and the sea lion was approximately 1.5 m. The layout of the experimental area remained unaltered for the duration of testing, with the distance between trainer and sea lion decreasing to approximately 1 m in Experiment 2 to facilitate an ease in focus for necessary eye contact and glance following. At the beginning of each session (both experiments) all equipment was laid out in the pre-determined fashion (Figure 1) and the sea lion chosen to undergo testing was asked to stand on the marker while the trainer adopted a kneeling position in front of the subject, at which time the experiment began. Correct selection of the target object by the sea lion was rewarded by a piece of fish and social praise. Incorrect choices were not rewarded, the sea lion was instructed to return to the marker and the next trial was immediately performed. If in a trial the sea lion chose one target and then moved to the other, only the sea lion's first response was considered.

In both experiments, sessions were pre-planned using a randomized list of “left/right” choices. The experimenter was the only person knowing the sequence of the commands. Between each trial, the experimenter gave a left/right call. However, the trainers were instructed that if they observed the animal pre-emptively choosing a target before the cue was given they should choose the opposite target, thus encouraging the animal to look at the cue and make a decision based on that, rather than simply guessing before the cue. Additionally, trainers were free to intersperse regular training commands at their discretion, should they note the animal losing concentration or to alleviate any frustration. This was done to prevent any undue stress to the animals participating in the tests. As a result, the number of trials slightly differed across experiments and individuals. The numbers of left and right trials were also sometimes uneven for the same reasons. All sessions and trials were recorded using a handheld video camera for later analysis.

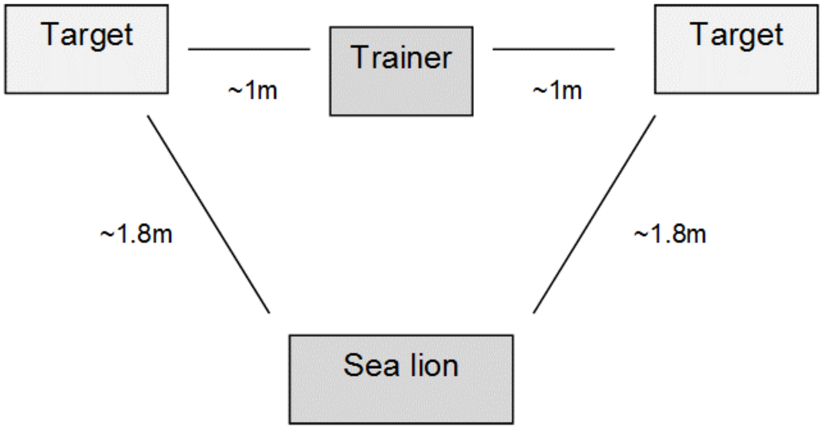

Figure 1. **Overhead view of experimental layout and distances used in Experiment 1.** Distance between the sea lion and each target was decreased to approximately 1.4 m in Experiment 2.

Experiment 1 – Finger Points

The focus of Experiment 1 was the animals responses to hand based gestural cues (finger pointing) directed towards one of two target objects laid out in front of the tested animal (Figure 2). The cue was displayed during 5 s. This experiment combined two differing hand signals:

1. Hip point: While in a kneeling position, the trainers held one flat hand against either hip while extending their index finger in the direction of the target object. It is important to note no crossovers occurred, only the finger on the same side as the chosen target was extended. For this test, a total of 40 trials (20 left sided) were used for three of the sea lions, and 39 trials (19 left) for Gonzo.

2. Chest point: Again in the kneeling position, the trainers held both hands against their hips until a cue was given. Upon receiving the cue the trainer raised one hand to chest height (taking care to avoid any elbow extension which may have led to the animal taking its cue from the “pointing elbow”) and pointed in the direction of the target object on the opposite side (e.g., if the chosen target was on the trainers left, the trainer would use their right hand to produce the gesture). The number of trials performed by each sea lions in this test was as follows: Santo, 42 (22 left sided), Smack: 40 (20 left), Gonzo: 43 (21 left) and Kaï: 39 (20 left).

Throughout this experiment it was important for the trainers to remain as neutral as possible in all gestures but the specified points. As a preventative measure the trainers were asked to focus their gaze (head and eyes) on an imaginary point directly ahead of them while maintaining a consistent forward facing body orientation and no extending limbs.

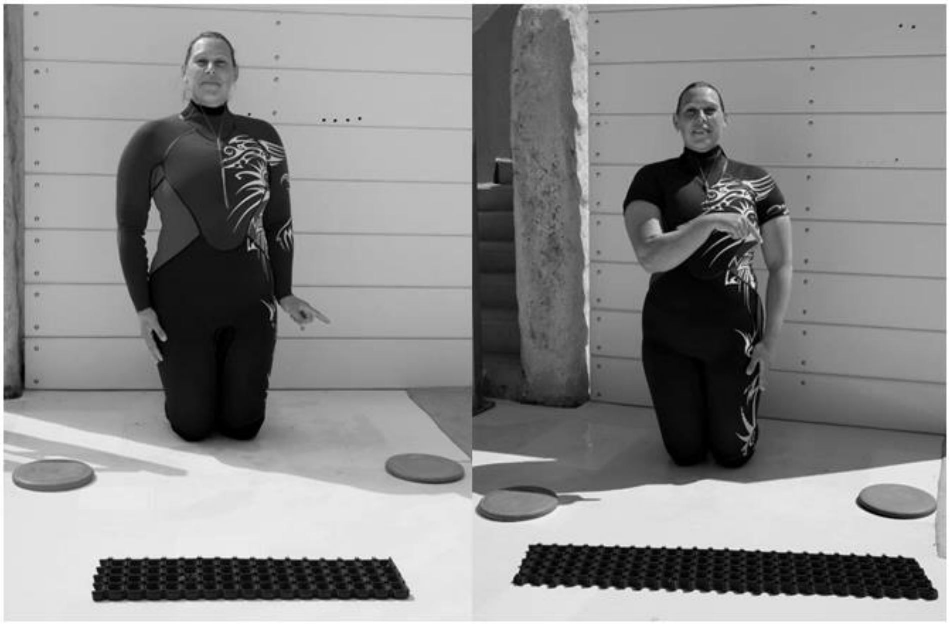

Figure 2. **Trainer performing an example of the hip point cue (left) and chest point cues (right) of Experiment 1.** Note, object spacing in this image is not representative of test conditions.

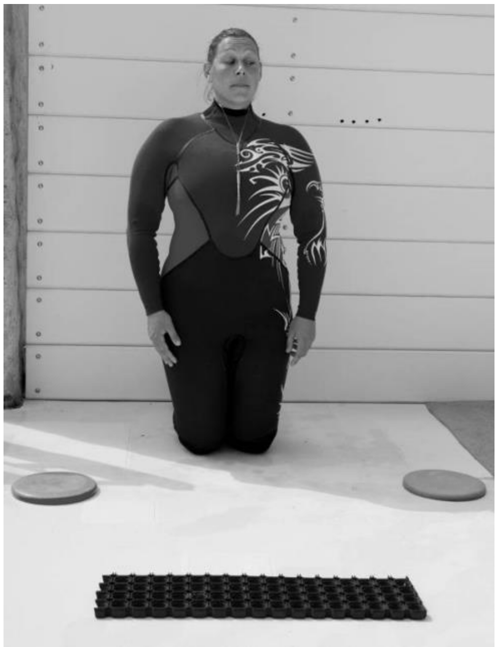

Figure 3. **Trainer performing an example of the eye glance cue of Experiment 2.** Note, object spacing in this image is not representative of test conditions.

Experiment 2 – Eye Glances

The trainer began the session in the kneeling position, with targets 1 m either side. Upon receiving the signal from the experimenter (i.e., left or right callouts) the trainer looked directly at the chosen target for approximately 5 s or until the animal responded, being sure to only use their eyes (i.e., no head turn Figure 3). The number of trials performed by the sea lions was increased for this experiment: Santo, 60 (33 left sided), Smack: 63 (33 left), Gonzo: 97 (48 left) and Kaï: 59 (31 left).

Statistical Analysis

For each experiment and animal, the accuracy of choice response (whether the correct target was chosen upon the test cue being given) was analysed using a binomial test. A chance level of 50% was used, because the sea lions had to choose between two targets. Two-sided permutation tests were used to compare latencies of correct choices between the different cues. Latency was defined as the time period between the trainer presenting the gesture and the sea lion's response of, with the response of the sea lion being defined as the moment the animal participating in the test touched a target with its muzzle. Additionally, the number of correct choices over the ten first trials for each sea lion and cue was reported.

Results

Experiment 1 – Finger points

When presented with hip points, all sea lions individually succeeded following the trainers' cues: Santo was correct on 90% of trials, Smack 95%, Gonzo 89.7%, and Kaï 97.5% (binomial tests, ps ≤ 0.001; Figure 4). Over the 10 first trials, the sea lions were correct on 10, 10, 9, and 9 trials, respectively.

When presented with chest points, only Santo and Kaï displayed correct responses at a frequency significantly different from chance level (Santo: 83.3% correct, $p \leq 0.001$, Kaï: 69.2% correct, $p = 0.012$), whereas contrastingly Smack did not (52.5% correct, $p = 0.437$; Figure 4). Gonzo showed a trend for a greater choice of the correct target (62.8% correct, $p = 0.063$). These results indicate an interindividual variation in the ability to follow the chest point cue contrarily to the hip-based cue. Over the ten first trials, the two successful individuals, Santo and Kaï, responded correctly on 8 and 6 trials, respectively.

Figure 4 shows latencies for each individual and cue (Hip: left; Chest: right). Mean latency of response was higher in the chest compared to the hip condition: 1.6 s (± 0.1 s) and 1.2 s (± 0.2 s), respectively. Permutation tests conducted on the individuals results revealed that Gonzo was faster to respond to the hip compared to the chest cue ($p = 0.006$). Santo and Smack showed a nonsignificant trend in the same direction, ($p = 0 .074$ and $p = 0.100$, respectively). No reliable difference was observed for Kaï ($p = 0.360$).

Both accuracy and latency results indicate that the chest cue was more difficult to use for the sea lions than the hip cue. Two individuals on the four tested showed a successful use of the chest cue, while all of them performed above chance level with the hip cue. Longer latencies also suggest that the sea lions show greater hesitation before to respond to a chest point.

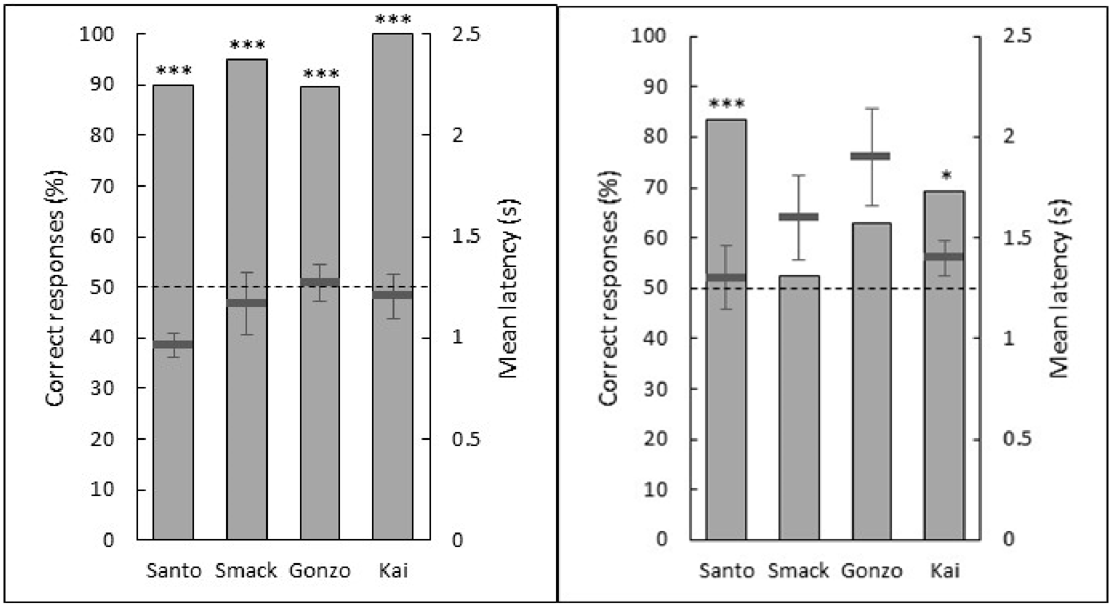

Figure 4. **Results of the hip-based (left) and the chest-based (right) finger points of Experiment 1, for each sea lion.** Bars represent the percentage of correct responses, vertical lines represent mean response latencies, and error bars represent the standard errors. Dotted lines represent chance level (50 %).
*$p \leq 0.05$. ***$p \leq 0.001$.

Experiment 2 – Eye Glances

Trial number differed from the previous experiments and across individuals as a result of the aforementioned concentration and scheduling conflicts: Santo (60), Smack (63), Gonzo (96) and Kaï (59). Additionally, the numbers of left and right trials were also uneven for the same reasons.

One sea lion, Santo, did display correct choices at a frequency significantly greater than expected from chance (68.3% correct, $p = 0.003$) while the others failed (Smack: 57.1% correct, Gonzo: 50.5% correct, Kaï: 55.9% correct, *p*s ≥ 0.157 in all cases; Figure 5). Over the ten first trials, Santo responded correctly on 8 trials.

Mean latency for responses to the eye cue was 1.6 s (± 0.1 s; Figure 5). Permutation tests revealed no difference between chest and eye cues latencies (*p*s ≥ 0.132), but two individuals responded faster to the hip compared to the eye cues (Gonzo: $p = 0.022$; Santo: $p = 0.002$). Smack showed a similar trend ($p = 0.072$). No difference in latencies was observed for Kaï ($p = 0.504$).

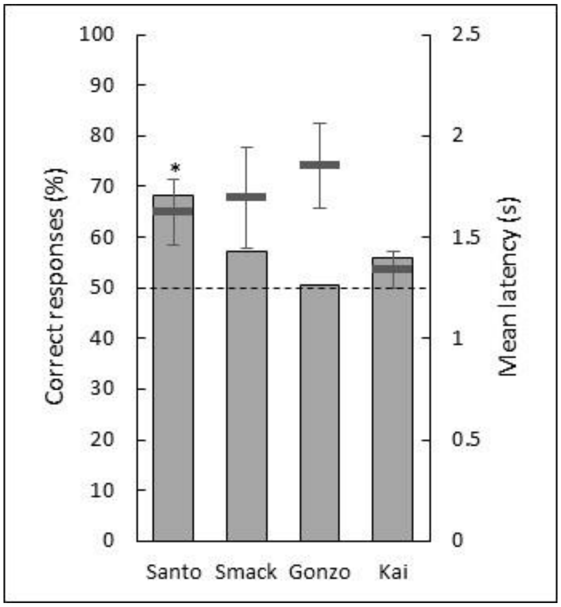

Figure 5. **Results of the eye glance cue of Experiment 2, for each sea lion.** Bars represent the percentage of correct responses, vertical lines represent mean response latencies, and error bars represent the standard errors. Dotted lines represent chance level (50 %).
*$p \leq 0.05$.

Discussion

This study provides some of the first evidence for the use of subtle human gestural cues in California sea lions. The four tested animals successfully used the hip finger point cue to locate and choose the correct target object at a rate exceeding chance. Two sea lions passed the chest point test and one animal was able to repeat this success when presented with the eye glance cue. Data from the 10 first trials analyzed separately suggest that successful exploitation of the cue was present at the onset of the hip-based point experiment for all the sea lions, as well as at the onset of both the chest-based point and the glance experiment for one sea lion, Santo. Taken together, these results indicate that the sea lions were able to quickly generalize from conspicuous pointing gestures presented in a previous study conducted on the same individuals (Malassis & Delfour, 2015), to subtle pointing gestures displayed with an extended fingers. The success of one of the sea lions with the glance cue additionally suggests that sea lions can (1) perceive human eye orientation and (2) exploit it as a directional cue.

However, despite the successful use of each of the tested cues by at least one of the sea lions, performance varied between the cues. For the sea lion(s) that performed above chance level, accuracy was lower in the glance experiment compared to the chest experiment, as well as in the chest experiment compared to the hip experiment. We propose that the differing levels of accuracy demonstrated by the animals towards each cue type is indicative of gesture conspicuousness playing an important role in the sea lions' ability to respond correctly, as it was observed that the more conspicuous the gesture the higher the frequency of correct responses and the shorter the delay between cue presentation and choice. For example, hip points (the most conspicuous gesture) had a higher correct response frequency and shorter response time than either chest points (slightly more subtle than hip points) or eye glances (the least conspicuous gesture tested). It is possible that the inclusion of a protrusion (such as seen in the hip point gesture) may aid animals in their responses to human gestural cues, as the protrusion increases how conspicuous a gesture is by providing a focal point for the animal. This seeming importance of conspicuousness and protrusion has also been observed in previous studies on gestural cue following in other species, with domestic dogs (Lakatos, Soproni, Dóka, & Miklósi, 2009; Soproni et al., 2002), grey wolves (Udell et al., 2012), South African fur seals (Scheumann & Call, 2004) and grey seals (Shapiro et al., 2003), all benefiting from the inclusion of a protruding point, exhibiting an increase in the frequency of correct responses and decreased response latency. In contrast, the chest-based point did not involve a protruding body-part. To our knowledge, two studies before the current one tested finger point following in marine mammals. Scheumann and Call (2004) tested fur seals following a "hand point" similar to the chest-based finger point tested in the current study (i.e., the extended finger did not protrude from the pointer's body torso). They reported failure to follow this hand point in the four tested fur seals. The two tested dolphins succeeded to follow a cross-body point with finger direction as the sole available cue (Pack & Herman, 2004). Previous attempts of testing glance following in both species however led to negative results (Pack & Herman, 2004; Scheumann & Call, 2004). The current study is thus the first that suggests an ability in one individual from a marine mammal species to perceive human glances and to use them as directional cue. One feature of the current study that might explain the success of this subject is the distance and respective position of the trainer and the sea lion. The trainer was 1 m away from the sea lion, on his/her knees. This configuration allowed to execute the chest-based point and the glance cue at the sea lion's eye level. Instead, in the fur seals study as well as in the dolphins experiment, the tested subject was in a pool, and the pointer was sitting or standing on the edge. Possibly, to place the animal and the experimenter at the same level and at very short distance from each other may increase the saliency of these subtle cues. Incidental cueing has been prevented in the current experiment by the instructions and training given to the trainers to avoid performing any gesture other than those defined for each pointing cue. Crucially, they were instructed to look at an imaginary point ahead of them while executing the finger points, to avoid any influence of unintentional eye/head movements. Another way to avoid at least eye movements in this experiment would have been to make the trainers wear tinted sunglasses, or to cover his/her eyes. In addition, the call given by the experimenter to the trainer between each trial to inform him/her about the next target side might have been learned by the sea lions. Current results do not support this last hypothesis: The sea lions performed poorly in the second experiment, compared to the first one. Learning of the auditory signal would predict the opposite. However, we cannot rule out the possibility that the sea lions used these auditory stimuli in addition to the pointing cue.

Although one out of four tested sea lions passed the glance test, the three others were shown to be incapable of using the eye glance cue. Other species have been observed to follow eye glances (both in intra and inter specific situations). It has been theorized that, in its simplest form, the ability to referentially follow the gaze of a conspecific arose as a means of predator avoidance (Gómez, 2005). A more advanced form of gaze following involving projecting another's line of sight around a barrier is thought to exist primarily in species with a complex social structure (Gómez, 2005) such as dogs (Soproni et al., 2002; Virányi et al., 2008), chimpanzees (Melis, Call, & Tomasello, 2006), capuchin monkeys (Mitchell & Anderson, 1997) and more recently California sea lions, with a gaze and arm point cue (Malassis & Delfour, 2015). However, a recent study (Penel & Delfour, 2014) demonstrated limitations in California sea lions' sensitivities to human attentional states. When presented with a human trainer with both clear and tinted sunglasses (so as to hide the eyes) the subjects failed to discriminate between the attentive and inattentive trainers. One possible explanation for this inability could be that eye contact is a non-pertinent gesture and not one used by this species, unlike the great apes, dogs, human-raised wolves and ravens (Brauer et al., 2005; Bugnyar et al., 2004; Udell et al., 2012). Two California sea lions (Santo and Gonzo) were observed to have some difficulty maintaining eye contact throughout glance testing. It is possible that this was due to the animal's difficulty to maintain their concentration and motivation during the tests or eye contact being an agonistic behaviour. It is already known that eye contact is an agonistic behaviour in primates (Coss, Marks, & Ramakrishnan, 2002; Gómez, 1996), domestic dogs (Soproni et al., 2001; Vas, Topál, Gácsi, Miklósi, & Csányi, 2005), harbour seals (*Phoca vitulina*; Sullivan, 1982), and New Zealand fur seals (*Arctocephalus forseri*; Grey, 1992) but no information is available on this being the case in California sea lions. A previous study on this species also suggested that sea lions may possess some form of hierarchal ordering in their social cues, with body orientation being more favorable than head orientation, stating that the sea lions seemingly did not understand the importance of head orientations (Penel & Delfour, 2014). On one occasion in this study it was noted that Kaï (one of the subjects who participated in the current test) chose a trainer whose body pointed towards her, rather than the target trainer with their head orientated towards her. In our case, Santo might have been able to focus on the very subtle glance cue, while the others animals mainly focused their attention to human body parts that are prior in their ordering of possible sources of cues.

Overall, mean response times observed were very low for all cues and all sea lions tested, with slight variations in mean latencies, additionally the results suggest that latency increased with cue difficulty and complexity. This seeming relationship between cue complexity, success rates and response time is a matter observed in previous studies on gesture recognition (Malassis & Delfour, 2015) and sensitivity to human attentional states (Penel & Delfour, 2014). However, the subject Kaï displayed a lower mean latency in the eye glance test than in the chest point test. It is possible that this is the result of Kaï not understanding what was being asked her and so rather than taking the time to make an informed decision she instead 'guessed' which target she should choose, resulting in a lower mean latency, a very similar observation to what was seen in the study conducted by Penel and Delfour (2014). Santo displayed a similar latency pattern to Gonzo and Smack, but displayed a greater increase in latency between the chest and eye tests than was observed in the other participant animals. This increase in latency is particularly interesting as Santo was the only animal to pass this test.

It has been demonstrated that domestic dogs in particular are especially adept at following human points (both whole limb extensions and finger points; Soproni et al., 2002). This ability to use human gestures so efficiently could be regarded as being the result of the domestication process, as generations of selective breeding for human companions would likely result in such sensitivity. That being said, previous studies looking at grey wolves showed that hand reared individuals (Virányi et al., 2008) or those exposed to humans on a regular basis (Udell et al., 2012) display a high level of responsiveness to human gestural cues, lending support to the theory that exposure to humans for prolonged periods of time and human socializing sensitise animals to human gestures and cues (Kaminski, 2009; Proops et al., 2010; Udell et al., 2010). The tested sea lions which, while not domesticated, not only spend a great deal of time around humans, but are also trained to follow specific 'commands' and gestures as part of their daily lives. This result suggests that our subjects are sensitive to human gestures, and are capable of spontaneously following new gestures as a result of their daily contact based exposure to humans.

References

Brauer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze into distant space and around barriers. *Journal of Comparative Psychology*, *117*, 145—154.

Brooks, R., & Meltzoff, A. (2002). The importance of eyes: How infants interpret adult looking behaviour. *Developmental Psychology*, *38*, 958—966.

Bugnyar, T., Stöwe, M., & Heinrich, B. (2004). Ravens (*Corvus corax*) follow gaze direction of humans around corners. *Proceedings of the Royal Society of Biological Sciences*, *271*, 1331—1336.

Call, J., Hare, B., & Tomasello, M. (1998). Chimpanzee gaze following in an object choice task. *Animal Cognition*, *1*, 89—99.

Clucas, B., Marzluff, J. M., Mackovjak, D., & Palmquist, I. (2013). Do American crows pay attention to human gaze and facial expressions?. *Ethology*, *119*, 296—302.

Coss, R. G., Marks, S., & Ramakrishnan, U. (2002). Early environment shapes the development of gaze aversion by wild bonnet macaques (*Macaca radiata*). *Primates*, *43*, 217—222.

Csibra, G., & Volein, A. (2008). Infants can infer the presence of hidden objects from referential gaze information. *British Journal of Developmental Psychology*, *26*, 1—11.

Davidson, G. L., Clayton, N. S., & Thornton, A. (2015). Wild jackdaws, *Corvus monedula*, recognize individual humans and may respond to gaze direction with defensive behaviour. *Animal Behaviour*, *108*, 17—24.

Emery, N. J., Lorincz. E. N., Perrett. D. I., Oram., M. W., & Baker, C. I. (1997). Gaze following and joint attention in Rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, *111*, 286—293.

Frischen, A., Bayliss, A., & Tipper, S. (2007). Gaze cueing of attention. *Psychology Bulletin*, *113*, 694—724.

Gómez, J. C. (1996). Ostensive behaviour in great apes: The role of eye contact. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 131—151). Cambridge, United Kingdom: Cambridge University Press.

Gómez, J. C. (2005). Species comparative studies and cognitive development. *Trends in Cognitive Sciences*, *9*, 118—125.

Grey, P. (1992). Agonistic behaviour in female New Zealand fur seals *Arctocephalus forseri*, *Ethology*, *92*, 70—80.

Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303—317). Cambridge, United Kingdom: Cambridge University Press.

Itakura, S., & Tanaka, M. (1998). Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orang-utan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology*, *112*, 119—126.

Kaminski, J. (2009). Dogs (*Canis familiaris*) are adapted to receive human communication. In A. Berthoz & Y. Christen (Eds.), *Neurobiology of "Umwelt"* (pp.103—107). Berlin, Germany: Springer Berlin Heidelberg.

Lakatos, G., Soproni, K., Dóka, A., & Miklósi, A. (2009). A comparative approach to dogs' (*Canis familiaris*) and human infants' comprehension of various forms of pointing gestures. *Animal Cognition*, *12,* 621—31.

Loretto, M., Schloegl, C., & Bugnyar, Y. (2010). Northern bald Ibises follow others' gaze into distant space but not behind barriers. *Biology Letters*, *6*, 14—17.

Malassis, R., & Delfour, F. (2015). Sea lions' (*Zalophus californianus*) use of human pointing gestures as referential cues. *Learning & Behavior*, *43*, 101—112.

Melis, A. P., Call, J., & Tomasello, M. (2006). Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology*, *120*, 154—162.

Mitchell, R. W., & Anderson, J. R. (1997). Pointing, withholding information, and deception in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *111*, 351–361.

Nawroth, C., Ebersbach, M., & Von Borell, E. (2014). Juvenile domestic pigs (*Sus scrofa domestica*) use human-given cues in an object choice task. *Animal Cognition*, *17*, 1—13.

Pack, A., & Herman, L. M. (2004). Bottlenosed dolphins (*Tursiops truncatus*) comprehend the referent of both static and dynamic human gazing and pointing in an object-choice task. *Journal of Comparative Psychology*, *118*, 160–171.

Penel, M., & Delfour, F. (2014). Are California sea lions (*Zalophus californianus*) sensitive to the attentional state of their caretakers?. *Animal Behaviour and Cognition*, *1*, 434—445.

Povinelli, D. J., Bierschwale, D. T., & Cech. C. G. (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, *17*, 37–60.

Proops, L., & McComb, K. (2010). Attributing attention: The use of human-given cues by domestic horses (*Equus caballus*). *Animal Cognition*, *13*, 197—205.

Proops, L., Walton, M., & McComb, K. (2010). The use of human-given cues by domestic horses (*Equus caballus*) during an object choice task. *Animal Behaviour*, 79, 1205—1209.

Scheumann, M., & Call, J. (2004). The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). *Animal Cognition*, *7,* 224—230.

Shapiro, A., Janik, V., & Slater, P. J. B. (2003). A gray seal's (*Halichoerus grypus*) responses to experimenter-given pointing and directional cues. *Journal of Comparative Psychology*, *117*, 355—362.

Smet, A. F., & Byrne, R. W. (2013). African elephants can use human pointing cues to find hidden food. *Current Biology*, *23*, 2033—2037.

Soproni, K., Miklósi, Á., Topál, J., & Csányi, V. (2001). Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *Journal of Comparative Psychology*, *115*, 122—126.

Soproni, K., Miklósi, Á., Topál, J., & Csányi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, *116*, 27—34.

Sullivan, R. (1982). Agonistic behaviour and dominance relationships in the harbour seal *phocea vitulina*. *Journal of Mammalogy*, *63*, 554—569.

Tomasello, M., Call., J, & Hare., B. (1998). Five primate species follow the gaze of conspecifics. *Animal Behaviour*, *55*, 1063—1069.

Udell, M. A., Dorey, N. R., & Wynne, C. D. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, *85*, 327—345.

Udell, M. A. R., Spencer, J. M., Dorey, N. R., & Wynne, C. D. L. (2012). Human-socialized Wolves follow diverse human gestures… and they may not be alone. *International Journal of Comparative Psychology*, *25*, 97—117.

Vas, J., Topál, J., Gácsi, M., Miklósi, A., & Csányi, V. (2005). A friend or an enemy? Dogs’ reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Applied Animal Behaviour Science*, *94*, 99—115.

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., & Miklósi, A. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, *11*, 373—387.

Wallis, L. J., Range, F., Müller, C. A., Serisier, S., Huber, L., & Virányi, Z. (2015). Training for eye contact modulates gaze following in dogs. *Animal Behaviour*, *106*, 27—35.

Xitco, M. J., Gory, J. D., & Kuczaj, S. A. II. (2001). Spontaneous pointing by bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*, *4*, 115–123.

Submitted: *January 28th, 2015*

Resubmitted: *July 7th, 2016*

Accepted: *October 4th, 2016*