How harbour seals *(Phoca vitulina)* encode goals relative to landmarks

Eric Maaß & Frederike D. Hanke*

University of Rostock, Institute for Biosciences, Neuroethology, Albert-Einstein-Str. 3, 18059 Rostock, Germany

*Author of correspondence

Phone +49 381 666 97 19 14

Fax +49 381 666 97 19 35

frederike.hanke@uni-rostock.de

ORCID orcid.org/0000_0002_1737_3861

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Summary Statement

When encoding goals in respect to landmarks, harbour seals choose the strategy depending on context but predominantly use a directional vector strategy.

Abstract

Visual landmarks are defined as object with prominent shape or size that distinguish themselves from the background. With the help of landmarks, animals can orient themselves in their natural environment. Yet, the way in which landmarks are perceived and encoded has previously only been described in insects, fish, birds, reptilians and terrestrial mammals. The present study aimed to provide insight into how a marine mammal, the harbour seal, is encoding goals relative to landmarks. In our expansion test, three harbour seals were trained to find a goal inside an array of landmarks. After diagonal, horizontal or vertical expansion of the landmark array, the search behaviour displayed by the animals was documented and analyzed regarding the underlying encoding strategy. The harbour seals mainly encoded directional vector information from landmarks and did neither search arbitrarily around a landmark nor used a rule-based approach. Depending on the number of landmarks available within the array, the search behaviour of some harbor seals changed, indicating flexibility in landmark-based search. Our results present first insight in how a semi-aquatic predator could encode landmark information when swimming along the coastline in search for a goal-location.

Introduction

In all moving organisms, the need to remember the locations of foraging sites, sleeping grounds, nests and even items not immediately visible in the environment is vital. Under many circumstances, organisms are guided to goal-locations by landmarks. Landmarks are defined as objects with specific characteristics such as a prominent shape or size with which it clearly contrasts from the background (Yesiltepe, Conroy Dalton et al. 2021). The use of visual landmarks for goal localization has been documented in multiple species including bees (Cartwright and Collett 1983), birds (see for example Cheng 1989, Cheng and Sherry 1992, Spetch 1995), fish (Burt and Macias Garcia 2003), dogs (Fiset 2007), rodents (see for example Cook and Tauro 1999), turtles (Lopez, Gómez et al. 2001) and several non-human primates (see for example MacDonald, Spetch et al. 2004, Marsh, Spetch et al. 2011). In contrast, the role of landmarks and landmark orientation has not been experimentally studied in marine mammals yet although the behaviour of wild animals has already been assumed to be based on landmarks. Matsumura et al. (2011) speculated that wild elephant seals close to the coast were guided by landmarks in the final phase of migrating back to their natal beach. Grey seals crossing the channel switched their navigational strategy when they were reaching familiar areas close to the coast in which local cues such as landmarks might have guided their journeys (Chevaillier, Karpytchev et al. 2014).

In this study, we aimed at describing whether and how the position of a goal is memorized in respect to landmarks by a marine mammal, the harbour seal. Harbour seals that commute between the coast and the open ocean appear to be very suitable subjects for assessing the role of landmarks, as previous studies revealed an extraordinary ability to return to previous haul-out places along the coast after foraging in deeper waters (Brown and Mate 1983, Stewart 1984, Suryan and Harvey 1998, Steingass, Horning et al. 2019, Vance, Hooker et al. 2021). While in the open ocean, landmarks may not be continuously available, the coastline offers many landmarks, such as rock formations, sandbanks, or anthropogenic structures, to be used for orientation or specifically for homing.

We used a classic experimental approach to study the use of landmarks and the underlying strategies in harbour seals, the expansion test. This experimental paradigm was previously established including numerous animals (Wehner and Räber 1979; Cartwright and Collett 1983, Spetch, Cheng et al. 1996, Spetch, Cheng et al. 1997, MacDonald, Spetch et al. 2004, Potì, Bartolommei et al. 2005, Potì, Kanngiesser et al. 2010, Marsh, Spetch et al. 2011). First, the subject is trained to locate a hidden item or goal within an array of landmarks. Afterwards, the array is then expanded, meaning that the distances between the landmarks are modified, but the geometrical relationship may remain constant in some but may change in other expansion schemes. The peak search areas of the animals are subsequently analysed to unravel the underlying strategy (Marsh, Spetch et al. 2011).

There are at least three different strategies describing how a landmark is used for orientation and navigation (Marsh, Spetch et al. 2011). Landmarks can serve as beacons (Fig. 1); thus, the organisms search for a goal near an individual landmark in an undirected way. This beacon-strategy was described for rats (Cook and Tauro 1999), turtles (Lopez, Gómez et al. 2001), monkeys (Potì, Bartolommei et al. 2005) and human children (MacDonald, Spetch et al. 2004).

Another group of animals seems to encode distance and direction between a goal and one or multiple landmarks (Fig. 1). This second strategy has been called directional vector-strategy, and it is defined as averaging of familiar directional vectors between a goal and a landmark (Cheng 1989, Cheng et al. 2006). It can be differentiated from the undirected search of a beacon-strategy in that the animals search in relation to a single landmark, but they combine multiple landmarks or the entire landmark array to determine the direction and length of the vector (Marsh, Spetch et al. 2011). This type of landmark use was documented in gerbils (Collett, Cartwright et al. 1986), pigeons (Spetch, Cheng et al. 1996, Spetch, Cheng et al. 1997) and primates (Potì, Bartolommei et al. 2005, Potì, Kanngiesser et al. 2010).

Those organisms that apply a third strategy, the rule-based-strategy, operate with the configuration of an entire array of landmarks and encode the position of the goal in relation to all available landmarks (Fig. 1). So far, only adult humans were documented to use this strategy ad hoc (MacDonald, Spetch et al. 2004). Studies on landmark use in bees indicated that the responses of bees also followed a rule-based approach. However, their search behaviour might also be explained by comparing a 2D-snapshot of the landmarks with images stored in memory (Cartwright and Collett 1983). Interestingly, some birds and primates, among others, seem to be able to learn this strategy when trained in paradigms that forced the animals to rely on the configuration of the array (Jones, Antoniadis et al. 2002, Potì, Kanngiesser et al. 2010).

In our study, we designed an expansion experiment to unravel the strategy of landmark use by harbour seals by first using an array of four landmarks (experiment 1). Subsequently, in experiment 2, we reduced the number of landmarks within the array to two landmarks and ultimately to a single landmark to determine, whether the seals' strategy would change with less goal-defining information available.

Material & Methods

Experimental Animal

The experiment was conducted with three adult male harbor seals (*Phoca vitulina*) named "Nick" (21 years old; length: 173 cm; mean weight: 121 kg), "Filou" (14 years old; length: 165 cm; mean weight: 109 kg), and "Moe" (14 years old; length: 151 cm; mean weight 91 kg) at the Marine Science Center of the University of Rostock, Germany. All seals had previously participated in numerous, but different scientific experiments (see for example Kowalewsky, Dambach et al. 2006, Schulte-Pelkum et al. 2007, Byl, Miersch et al. 2016, Niesterok, Krüger et al. 2017, Krüger, Hanke et al. 2018, Maaß and Hanke 2021). They were housed with nine other harbor seals, two California sea lions *(Zalophus californianus*), and a South African fur seal *(Arctocephalus pusillus pusillus)* in a seawater enclosure. The seals were mainly fed freshly thawed cut herring *(Clupea harengus)* and sprats *(Sprattus sprattus)*. During the experiment and the general training, the animals received 1-5 kg of fish a day depending on season and motivation, meaning eagerness to participate during training and during experiments. We performed experiments three to four days a week. The experiment took place in an enclosure (7 m x 12 m) separated from the main enclosure.

The experiments carried out in this study were in accordance with the European Communities Council Directive of September 22nd, 2010, (2010/63/EU) and the German Animal Welfare Act of 2006. The individuals used in the study were not subject to pain, suffering or injury therefore no approval or notification was required.

Experimental Setup

The experimental setup consisted of a ring-station (Fig. 2 A) that served as the starting point for the animal in each trial. This station was opposed to a 2 m x 2 m integral foam wall (Fig. 2 A, 3) with integrated LED lights, which served to present the stimuli. The wall was fully submerged with the upper rim 20 cm below the water surface. In total, 121 LED lamps (Luckylight, Shenzhen, China Ø 10 mm; 8000 mcd, cold-white, radiation angle 20 deg) were inserted in the wall in 11 rows and 11 columns (Fig. 2, 3). The LEDs were 15 cm apart from each other; the outermost LEDs were 25 cm apart from the aluminium frame surrounding the wall. Every LED was connected to a control panel (Fig. 2 C) installed at a distance of 5 m to the wall. The control panel served as a miniature version of the LED-wall equipped with 22 light-switches, which allowed controlling the LEDs from afar. Two cameras (Eyoyo 1000 TVL Waterproof Camera; Eyoyo Shenzhen, Guangdong, China) on aluminium mountings were placed to the left (2 m afar) and right (3 m afar) of the LED wall and served to observe the animals' performances on two LCD monitors during the experiment. A third camera (GoPro Hero 7 Black Edition; GoPro San Mateo, CA, USA) on the right aluminium mounting recorded the experiment for later analysis. During the experimental sessions, the experimenter hid behind an opaque visual cover to avoid secondary cueing. The influence of secondary cues from the experimenter was additionally prohibited as the seal swam away from the experimenter when indicating its response at the LED wall.

General Experimental Procedure

After entering the enclosure, the animal was asked to swim to and rest in its ring station. At the same time, the experimenter hid behind the opaque visual cover next to the control panel. After the experimenter had switched on the specific landmark array of the respective trial, the seal was indicated to leave its station by a short whistle and had to approach the wall to indicate its response by touching the position where it assumed the goal was with its snout (Fig. 2 C). After every correct response, the animal received up to three (pieces of) fish from the experimenter. An incorrect response was answered by the German word for no "nein", and no reward was given. After the feedback, the animal had to swim back to its station for a new trial to begin. The duration of the inter-trial interval was approximately 60 - 90 s.

Experiment 1

Stimulus

The stimulus presented was an LED-array consisting of four lit LEDs (Fig. 1, 2, 3). The task for the animal was to find the goal in the middle of the array. For each trial, the LED-array configuration was varied in its absolute position on the LED wall following a pre-set schedule. A total of 81 target locations could be chosen for each trial. In order to systematically vary the position of the LED array, we divided the wall into four quadrants and an overlapping area (Fig. 3). During a session, the LED array was placed four (during testing) or six (in training) times in each quadrant and the overlapping area resulting in a session of 20 or 30 trials respectively.

Pretraining

Pretraining started with the animal swimming from its ring-station towards the panel touching a target held at the goal-location by an assistant from above the array. Over the course of pretraining, the response target was successively reduced in size. During these familiarization trials, a correct answer was defined as the animal swimming to the target ball and touching it with its snout for three seconds. After successfully completing ten correct trials per target in succession, trials without assistant and target ball were interspersed. The number of interspersed trials varied between 5 and 25 trials, depending on the animals' performance and motivation, meaning if the seal continued to respond even without assistant and was eager to participate in the training, more trials without assistance were conducted in comparison to sessions in which the animal was responding more hesitantly without guidance and was generally cooperating less well.

Training phase

In the training phase, the LED array was presented, and the animal was required to touch the goal-location with its snout. An incorrect answer was defined as the animals touching elsewhere on the LED wall. Training was continued until the animal reached a learning criterion of 80 % correct choices in two consecutive sessions.

Testing phase

During the testing phase, test trials were interspersed into the session. In test trials, the landmark array was expanded either diagonally, horizontally, or vertically. Diagonal expansion resulted in the LEDs of the array to be 90 cm apart from each other, instead of being 30 cm apart as during baseline trials (Fig. 3 B). During horizontal expansion, the two landmarks on the right and left kept their position relative to each other; however, these two pairs were moved 90 cm apart horizontally (Fig. 3 C). In a vertical expansion, the two upper and the two lower LEDs kept their position, but those two pairs were moved 90 cm apart vertically (Fig. 3 D).

During the testing phase, the sessions consisted of 19 baseline trials and one test trial. The test trial consisted of one of the expansions and was interspersed at random, however, it was never included as first and last trial of the 20-trials session. Baseline trials were ended by feedback from the experimenter, either reinforcement or a verbal no. No feedback was given in the test trials. We performed 10 test trials for each expansion, resulting in 30 test sessions overall. We kept the number of expansion trials per session small, as we were interested in the spontaneous instead of a learned reaction of the seals to the expansion.

Experiment 2A

Stimulus

In this experiment, two landmarks were lit in every trial (Fig. 3 E). The landmarks were aligned in the horizontal dimension of the search space. The goal was located between the landmarks but at a perpendicular distance away from and below the line connecting the two landmarks.

Training and testing phase

The training phase was conducted as described for experiment 1. In the testing phase, test trials were interspersed in which the two-landmark array was expanded in the left-right dimension of the search space, meaning the distance between the landmarks was increased. After expansion, the two landmarks were 90 cm apart from each other, instead of 30 cm as during training (Fig. 3 E). In each testing session, the LED array was placed in each quadrant four times and five times in the overlapping area, resulting in 19 baseline trials and one additional test trial. The position of the LED array in the test trial was chosen at random, but over the course of the sessions, the position occurred equally often in the quadrants and the overlapping area, which resulted in six test trials per area. Again, no feedback or reward was given for the seals' answers in test trials. Altogether 30 sessions were run resulting in 30 responses to the expanded array per animal.

Experiment 2B

After completing the testing phase of experiment 2A, we conducted a brief follow-up test. In these sessions, test trials with a single landmark were interspersed into the baseline trials with a two-landmark array to determine how the seals would respond to a further reduction of the number of landmarks. We conducted two sessions with 25 baseline trials and 5 test trials.

Data Analysis

We performed all statistical tests with an alpha level of 0.05 in Microsoft Excel (Version: Office 2019; Redmond, Washington, USA) and IBM SPSS (v.26; International Business Machines Corporation Armonk, New York, USA). During analysis, we focussed on the first choices the animals made when performing the control and test trials in all phases of the experiment; it needs to be noted, that the seals hardly, meaning only two to six times in each experiment, gave second responses. In order to unravel the underlying strategy of landmark perception, we performed an analysis similar to Marsh, Spetch et al. (2011). According to their analysis, the three landmark-based strategies predict specific hypothetical goal-locations, with corresponding peak search areas. Since Marsh and colleagues could not differentiate between the beacon-strategy and the vector-strategy due to an overlap of the hypothetical goal-locations, we redefined the goal-locations to clearly separate the goal-locations for the beacon- and the vector-strategy (Fig. 1). We then determined the frequency of searches that fell into each of the hypothetical goal-locations and performed binomial tests to determine whether the answers of the animal that were directed towards each area differed from what would be expected by chance. Similar to Marsh, Spetch et al. (2011), we compared the frequency of searches per area with the expected frequency of searches in the areas according to the number of possible goal-locations (see Fig. 1) in the area (1 goal-location for the rule-based-strategy = 1 % chance, 8 or 4 goal-locations for the vector-strategy = 10 % or 5 % chance and 28 or 14 goal-locations for the landmark strategy = 34 % or 17 % chance in experiment 1 or experiment 2). Our analysis assumes that a random or indirect search would target any LED in the area of the respective strategy.

Results

Experiment 1

The seals needed 746 trials in 37 sessions (Nick), 995 trials in 34 Sessions (Filou), and 1,725 trials in 59 sessions (Moe) to meet the learning criterion in the training phase. In the testing phase, the seals chose the goal-location of the landmark array with 87.7 % (Nick), 91.9 % (Moe), and 97.6 % (Filou) of the choices in the baseline trials. During the expansion trials, the seals directed all their searches to locations inside the landmark boundary area (Fig. 1). Inside the landmark boundary area, irrespective of the type of expansion, all three seals prioritised their searches in the regions predicted by the vector-strategy more than expected by chance (binomial test: $p < 0.05$; Fig 3, Tab. 1). No animal directed its search according to a rule-based-strategy, which, in our configuration, would have resulted in choosing the centre of the expanded array. While focussing their searches in the surrounding of landmarks, Moe and Filou mostly responded to an LED that adopted the same angle and distance to a landmark as the goal during the baseline trials and the trials in the training sessions (Fig. 4). However, the seals favoured LEDs at the training angle and distance to different landmarks. Filou preferred the LED defined by the training vector from the top-right landmark, whereas Moe also preferred to answer at the position defined by the training vector but with respect to the top-left landmark. Both animals thus responded as in the training phase and with the same distance to the landmarks but orientated to different landmarks. Nick, on the other hand, favoured two different positions, one defined by the training vector, and one defined by a length of 15 cm with an angle of 45° counter-clockwise from the training vector.

The animals' responses were predominantly related to the two uppermost landmarks. Filou and Nick selected a location in the upper half of the wall in all of their searches. With 85 % of its responses to the upper half of the wall, even Moe mainly directed its search to the upper two locations and only went to locations in the lower half of the configuration wall three times; then the seal gave responses with respect to the lower landmarks consistent with its responses to the upper landmarks.

Experiment 2

All animals needed only two training sessions including 60 trials to complete the learning criterion for experiment 2. In the testing phase, 92.3 % (Nick), 96.3 % (Moe), and 99.1 % (Filou) of the baseline trials were directed to the goal-location of the unexpanded landmark array. In the testing phase of experiment 2A, the seals directed all their searches inside the landmark boundary area of the expanded array (Fig. 1; binomial test: $p < 0.05$). Taking a closer look at the responses within the landmark boundary area, all seals prioritised their searches in the regions predicted by the vector- and the beacon-strategy more than expected by chance (Fig. 5, Tab. 1; $p < 0.05$). No search was ever in line with rule-based searching, thus to the middle of the array or in triangular form.

In this experiment, Filou again preferably chose to respond at a single vector from a landmark (Fig. 5 A), thus searching for the goal at the same vector as in the baseline/training condition, but he did not discriminate between the left and right landmark; instead, he always searched at the same vector irrespective in relation to which landmark. On the contrary, Moe's searches were directed to locations defined by three different vectors: the training vector, a vector 45° counter-clockwise to the training vector with a length of 21 cm and a vector 45° clockwise to the training vector with a length of 15 cm with almost the same frequency (Fig. 5 A). Nick again, as in experiment 1, favoured the training vector and the vector 45° clockwise to the training vector with a length of 15 cm.

In experiment 2B, all seals maintained a high performance as 95.5 % of the baseline trials were in the correct location of the unexpanded landmark array for Moe and Nick. Filou did not make any mistakes at all in the baseline trials. In the control trials, Filou responded at a location defined by the training vector relative to the landmark in 90 % of the trials (Fig. 5 B). In contrast, Moe's and Nick's responses were distributed over locations defined by the training vector and by a vector directly underneath the landmark. Both animals responded with the training vector in 50 % of the trials (Fig. 5 B).

Discussion

In this study, it was determined how harbour seals encode positional information in respect to landmarks. The seals learnt the experimental paradigm within 746 – 1,725 trials. For comparison, orang-utans needed several thousand trials to acquire the basic task in a comparable study (Marsh, Spetch et al. 2011). The relatively fast acquisition process in harbour seals supports findings from previous studies that had revealed excellent access to as well as high performance in visuo-spatial tasks (Renouf and Gaborko 1989, Mauck and Dehnhardt 2007).

In the testing phase of the first experiment, in which the four-landmark array was expanded, the seals mostly showed responses to locations in the dimension parallel to the shift and no shift in searching in the perpendicular dimension. The search behaviour of the seals was consistent with a directional vector-strategy as previously described for e.g. non-human primates and gerbils, among others (Collett, Cartwright et al. 1986, MacDonald, Spetch et al.

2004, Potì, Bartolommei et al. 2005, Potì, Kanngiesser et al. 2010). The seals mostly kept the same distance and angle towards a landmark that they had experienced during training; they chose the goal in line with the training vector. Filou mainly applied one vector, the appropriate vector to locate the goal with respect to the top-right landmark, irrespective to which landmark, which was most apparent in experiment 2B. Moe even chose three different training vectors depending on the specific landmark he was targeting. Moreover, all seals responded inside the landmark array. Overall these observations stress the high directionality of their response behaviour; their responses were clearly more directed than predicted by the alternative strategy, the beacon-strategy.

The ability to memorize and apply a vector would allow seals to relocate a specific goal with respect to (a) landmark(s) precisely. The application of a directional vector-strategy would furthermore enable seals to use landmarks for piloting. When encountering (a) landmark(s), seals would be required to determine the correct, previously memorized/learnt vector, including directional as well as distance information, with respect to the landmark(s), leading the seals to the next station on its journey and/or finally towards its end-goal. This piloting-strategy would benefit from the previously reported abilities of seals to estimate distances (Maaß and Hanke 2021) and to keep a straight path (Vance, Hooker et al. 2021). Our results thus allow the formulation of new hypotheses on landmark orientation or orientation/navigation in general to be tested in the future in an attempt to explain the well-documented navigational abilities of seals that are commuting between the open ocean and the coast.

The response behaviour in the baseline trials of experiment 1 shows that the animals must have identified individual as well as groups of landmarks inside the array; the correct identification of the middle of the array requires the determination of upper versus lower landmarks and left versus right landmarks. For this identification process, the seals could have used cues, such as the setup's position in the water column, the relative position of the seal to the setup during stationing/approaching, their own position in the water column. These cues were available in our experiment. However, it needs to be stressed that, in our experiment, the bespoken cues did not interfere with the experimental paradigm, as only the landmarks defined the goal precisely, thus the seals were forced to use the LED landmark array to solve the task.

In the test trials, the seals were mainly answering in the upper half of the panel. The focus of the seals to the upper landmarks might result from the asymmetry of the seals' visual field in the vertical meridian (Hanke et al. 2006). Due to their dorsal eye position, harbour seals have a large dorsal, but only a small ventral visual field (see Supplementary Figure 1). Thus, when approaching the panel, the two upper landmarks remained within in the visual field longer than the two lower landmarks. Thus they localized the goal with respect to the upper two landmarks that defined the goal most precisely. When transiting to experiment 2A, the seals' responses clearly indicate that the top two landmarks provide enough orientation cues to be used for goal localization.

The analysis of the results obtained in the two-landmark array experiment revealed that the response behaviour was in line with the directional vector- and the beacon-strategy but did not correspond with a rule-based approach. The number of responses in line with a beacon-strategy increased in experiment 2 in comparison to experiment 1; seal Nick even predominantly answered in line with a beacon-strategy. Thus, with reduced landmark information, it seemed more difficult for the seals to obtain/memorize the angular information of goal versus landmark. In conclusion, the amount of information available in the environment determines the strategy chosen by the seals and the accuracy of the search behaviour. Flexibility in landmark-based search is vital, allowing the seals to optimize their search in respect to the information available.

From experiment 1 to experiment 2, the seals slightly or clearly shifted their search strategy. Differential use of search strategies in different experimental conditions was already documented for e.g. human children and capuchin monkeys (MacDonald, Spetch et al. 2004, Potì, Bartolommei et al. 2005). Whereas the human children seem to choose a strategy depending on their age (towards using a rule-based-strategy when adult), the capuchin monkeys switched their strategy according to the complexity of the task. In contrast to our seals, the primates used a beacon-strategy when confronted with a four-landmark-configuration but shifted to a directional vector-strategy when confronted with a two-landmark-configuration. This discrepancy needs to be worked on in future experiments.

In all our experiments, the harbour seals did not implement a rule-based approach in the sense of "find-the-middle" or "complete the triangular form" to find the goal in the landmark array, which would have resulted in a higher frequency of searches in the respective positions of the expanded array. Adult humans responded according to a rule-based-strategy during expansion by answering directly in the middle of the array or by maintaining a triangular shape in tests with two landmarks, which they also expressed verbally when asked about the strategy they had followed during testing (Spetch, Cheng et al. 1996, Spetch, Cheng et al. 1997, MacDonald, Spetch et al. 2004). Even though the seals did not spontaneously use a rule-based approach in the current study, seals might be capable of using such an approach when forced to rely on a rule with a different experimental paradigm, in line with previous studies including birds and primates (Spetch, Cheng et al. 1997, Potì, Bartolommei et al. 2005). When these organisms were asked to respond to the middle of two landmarks that varied in inter-landmark distance they adopted a rule-based-strategy (Kamil and Jones 1997, Jones, Antoniadis et al. 2002, Spetch, Rust et al. 2003, Potì, Kanngiesser et al. 2010). A comparable experiment conducted with harbour seals could reveal whether seals also switch to a rule-based-strategy depending on context/task. This context-dependent shift of strategies seems possible, as it would be in line with experimental evidence just mentioned and as the seals showed a change of their response behaviour with the modifications of the landmark array from experiment 1 to experiment 2.

In conclusion, we could show that harbour seals can learn to locate a goal with the help of landmarks and that they preferably choose the vector(s), including direction and distance information, relative to (a) landmark(s) memorized during training. However, the encoding of goals with respect to landmarks is adjusted with respect to the specific environment as indicated by the context-dependent shifts in search strategy, a flexibility that seems to be adaptive in a complex environment.

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Journal of Experimental Biology • Accepted manuscript

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Figures and Table

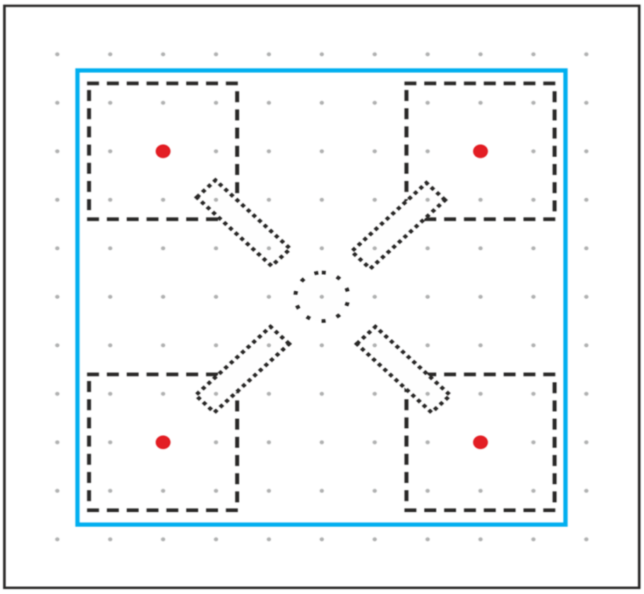

Figure 1 Search areas predicted by a beacon-strategy (*squared dashed lines*), a rule-based strategy (*dotted circle*) and a directional vector-strategy (*dotted rectangle*) in an expansion test. Red dots represent the landmarks within a four-landmark array, and the blue line indicates the landmark boundary area (modified after Marsh, Spetch et al. 2011, Potì et al. 2010)

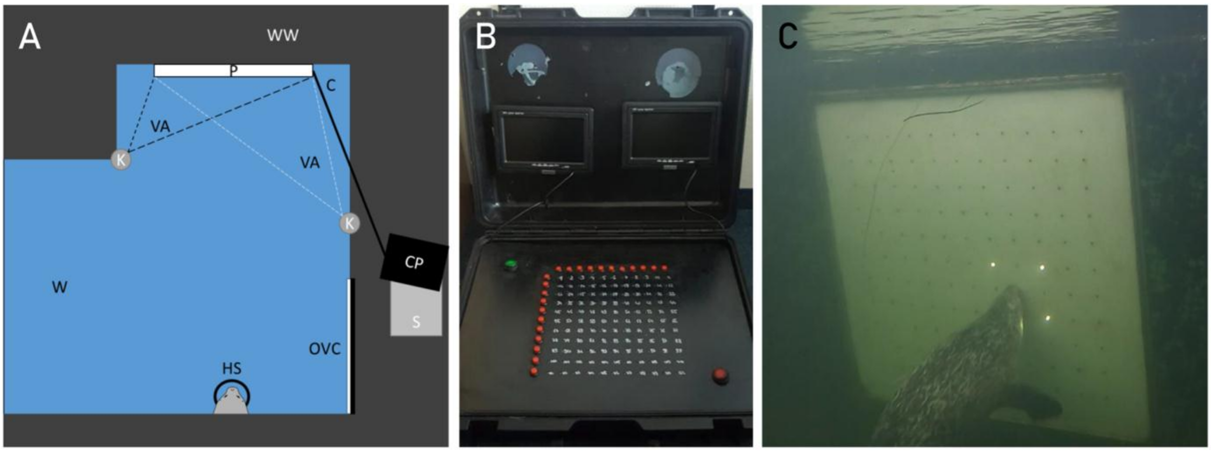

Figure 2 Experimental setup. A schematic top view of the experimental basin, in which the experiment took place, with the walkway (WW) and the water area (W). The experimenter sat on the walkway (position S) behind an opaque visual cover (OVC) to avoid secondary cueing and set the landmark array with the help of the control panel (CP) connected to the submerged LED panel (P) with a cable (C). At the beginning of a trial, the seal was stationing in a hoop station (HS). Upon signal, it was swimming towards the submerged LED panel (P) indicating with its snout where it assumed the goal. The LED panel was within the viewing angle (VA) of three cameras mounted on two mountings (K; two cameras on the right-hand side) which allowed to oversee the response behaviour of the seal at the panel as well as to control stimulus presentation. B Control panel with which the specific LED landmark array could be set on the submerged LED panel from a distance. C Submerged LED-panel in a training situation with the seal Nick giving a response at the goal-location.

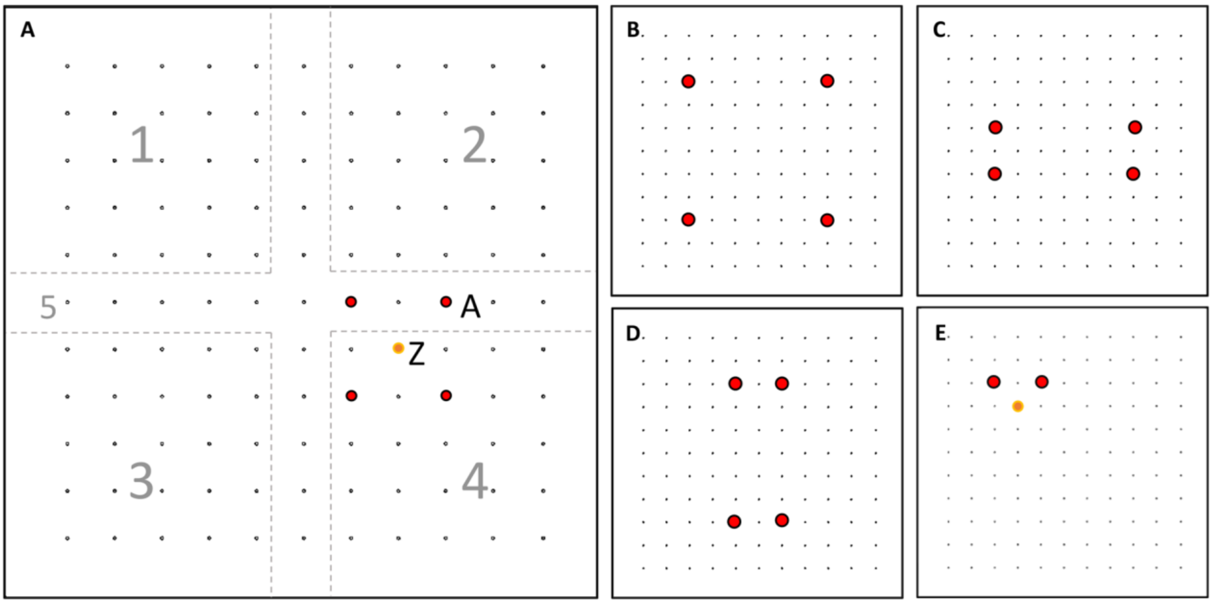

Figure 3 Landmark array on the LED panel during baseline and test trials in experiment 1 and 2. To a plastic foam wall, 121 LED-lights were attached. In every trial of experiment 1, four LEDs (red dots) were lit and served as landmark array (A). The task of the animal was to touch an unlit LED, the goal (Z; for representation, this unlit LED is here marked by a yellow dot; however, during the experiment, Z remained unmarked) in the middle of the landmark array. The position of the array was shifted to all quadrants (1-4) and the overlap area (5); see text for details. (B), (C) and (D) show the different types of expansion the seals experienced during the test trials of experiment 1: (B) diagonal expansion, (C) horizontal expansion and (D) vertical expansion. (E) Landmark array of experiment 2 as presented during baseline trials. The array consisted of 2 lit LEDs. The goal the animals needed to respond to is marked with a yellow dot; however, during the experiment the goal remained unmarked.

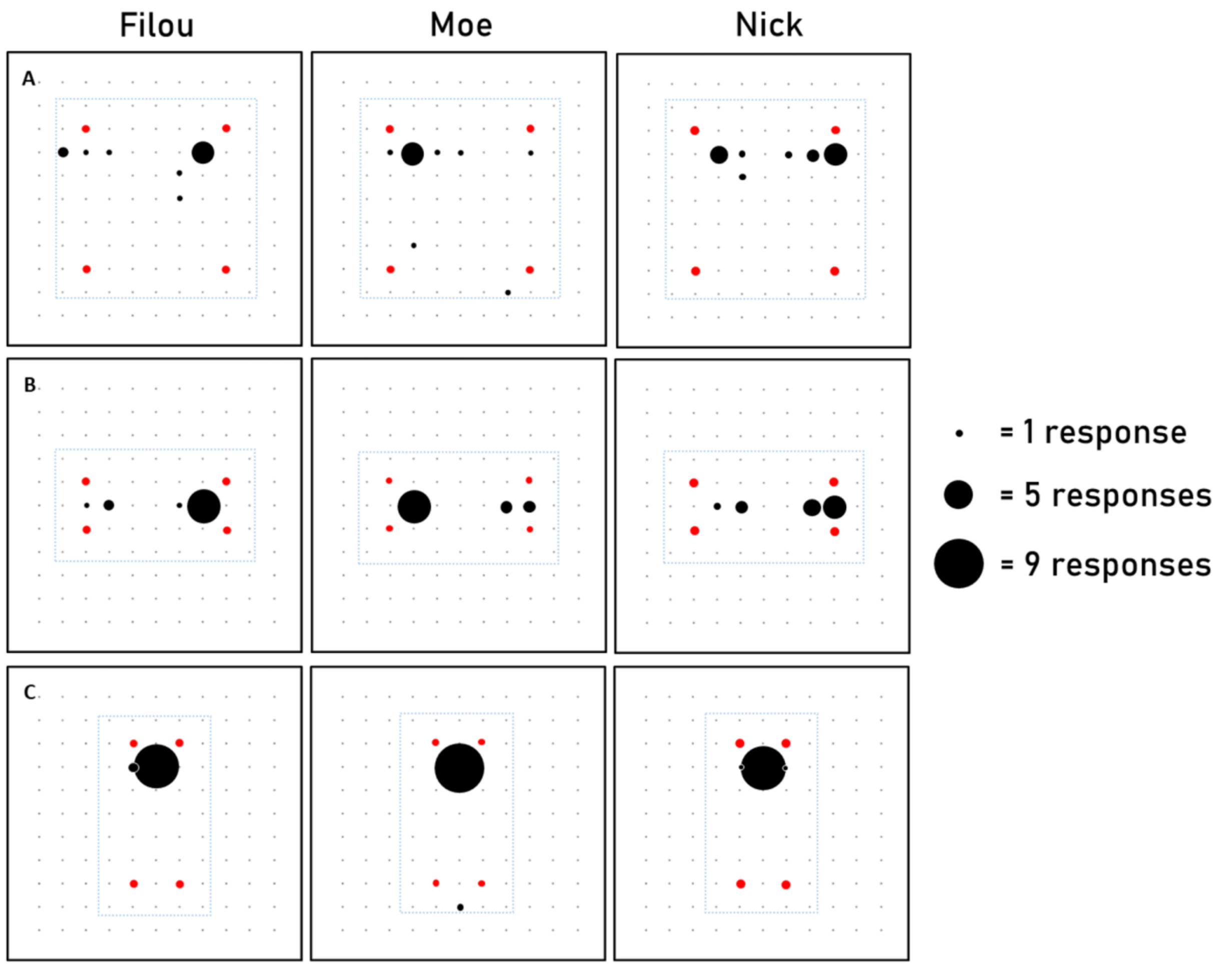

Figure 4 Response behaviour of seal Filou (left), seal Moe (center) and seal Nick (right) in respect to the (A) diagonal expansion, (B) horizontal expansion, and (C) vertical expansion of the four-landmark array (experiment 1). Black circles represent the responses of the seals with the number of responses per position coded by the size of the circles: the largest circle represents the highest number of responses at a position, as indicated on the right side of the figure. Conventions as in Fig. 1 and 3, array is again always shown in the middle of the LED-wall although its position was varied across the LED-wall over trials.

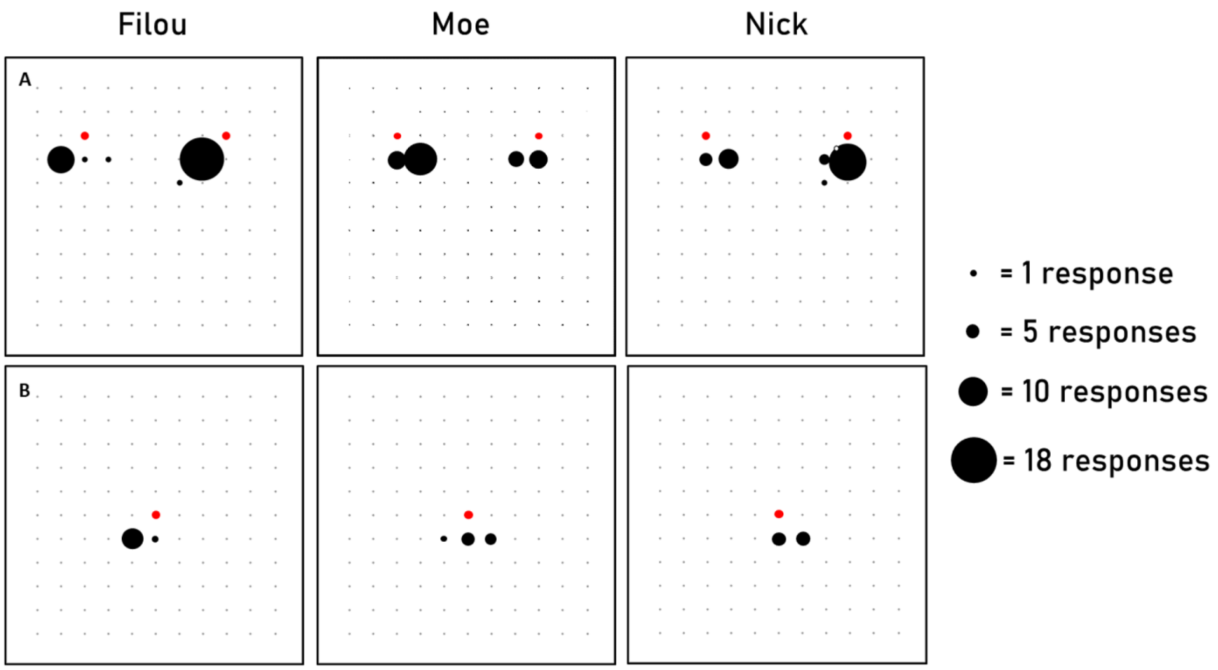

Figure 5 Response behaviour of seal Filou (left), seal Moe (center) and seal Nick (right) in (A) the expansion trials of experiment 2A and (B) experiment 2B. Results are visualized as in Fig. 4 and the conventions of all other figures. Please note, that in experiment 2A, each seal performed 30 test trials and one test trial was interspersed in a session of 20 trials, while in experiment 2B each seal performed five test trials in each of the two sessions of 30 trials.

Table 1 Number of searches in the expansion test trials of experiment 1 and 2 in the hypothetical goal-locations predicted by the three different strategies (beacon, vector, rule-based strategy) for the three different types of expansion (diagonal, horizontal, vertical expansion). Numbers written in italics indicate percentages higher than expected by chance (α-level 0.05). Note that the chance level was different for each of the landmark strategies in the two experiments (see Data Analysis).

Experiment	Subject	Expansion	Hypothetical Goal-Locations			
			Beacon	Vector	Rule-Based	Other[1]
Exp. 1	Filou	Diagonal	3	*6*	0	1
		Horizontal	2	*8*	0	0
		Vertical	3	*6*	0	1
		Overall	8	20	0	2
	Moe	Diagonal	2	*5*	0	3
		Horizontal	1	*9*	0	0
		Vertical	2	*8*	0	0
		Overall	5	22	0	3
	Nick	Diagonal	3	*5*	0	2
		Horizontal	2	*8*	0	0
		Vertical	6	*4*	0	0
		Overall	11	17	0	2
Exp. 2	Filou	Horizontal	*12*	*18*	0	0
	Moe	Horizontal	*12*	*18*	0	0
	Nick	Horizontal	*19*	*10*	0	1

[1] 'Other' defines any position chosen by the seals not in line with the goal-locations predicted by the beacon-, vector-, or rule-based-strategy.

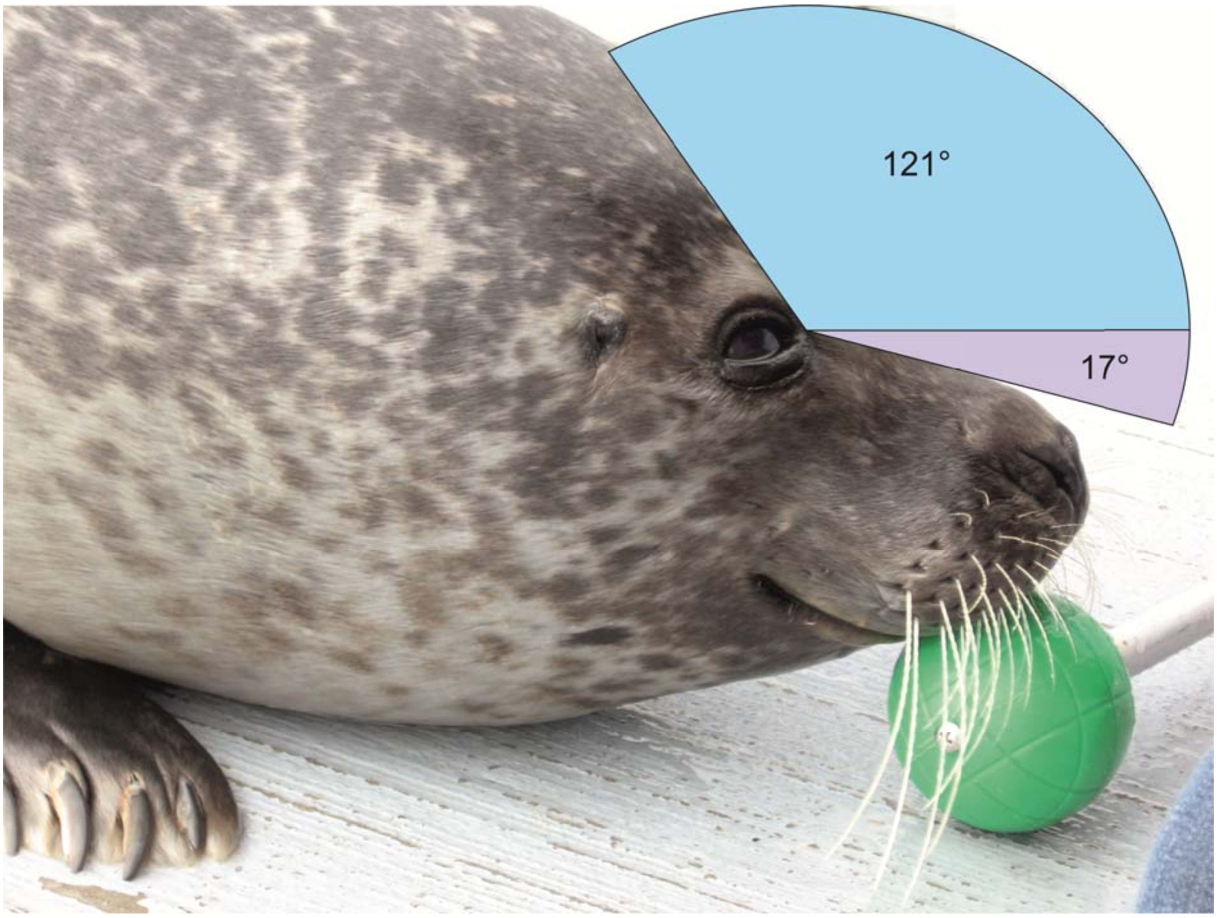

Fig. S1. Dynamic visual field of a harbor seal. Ha bor seals have a large dorsal but only small ventral dynamic visual field. When eye movements are prohibited, the dorsal visual field is still extending over 69 deg. The ventral visual field is reduced to 12 deg without eye movements (data taken from Hanke et al. 2006)