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RESEARCH ARTICLE

A harbour seal (*Phoca vitulina*) can learn geometrical relationships between landmarks

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ABSTRACT

Marine mammals travel the world's oceans. Some species regularly return to specific places to breathe, haul-out or breed. However, the mechanisms they use to return are unknown. Theoretically, landmarks could mediate the localisation of these places. Occasionally, it might be beneficial or even required to localise places using geometrical information provided by landmarks such as to apply a 'middle rule'. Here, we trained a harbour seal to find its goal in the middle of numerous vertically and horizontally orientated two-landmark arrays. During testing, the seal was confronted with unfamiliar two-landmark arrays. After having successfully learnt to respond to the midpoint of multiple two-landmark arrays, the seal directly and consistently followed a 'middle rule' during testing. It chose the midpoint of the two-landmark arrays with high precision. Harbour seals with the ability to localise goals based on geometrical information would be able to home in on places even from unknown positions relative to goal-defining features. Altogether, the results obtained with our harbour seal individual in the present and a previous study, examining the basis of landmark orientation, provide evidence that this seal can use landmark information very flexibly. Depending on context, this flexibility is adaptive to an environment in which the information content can vary over time.

KEY WORDS: Spatial strategies, Navigation, Rule-based searching, Cognitive map, Pinnipeds

INTRODUCTION

Many animals are guided to, for example, their nests or burrows by landmarks (Healy, 1998). Generally, a landmark is defined as an object or stimulus that is contrasting from the background or is prominent in it and that is used for navigation and orientation (Lynch, 1960). Landmarks might also guide marine mammals when revisiting certain feeding areas, breeding grounds or, in amphibiously living species, haul-out places (Liebsch, 2006). In the first approach to marine mammal landmark orientation (Maaß and Hanke, 2022), we tested how harbour seals encode goals in respect to landmarks in a transformational approach – the expansion test. In an expansion test, the subjects are first trained to find a goal inside or in relation to a landmark array (e.g. Cheng and Spetch, 1998). After accurately locating the goal, the array was expanded, meaning the distances and/or the geometrical relationship between the landmarks were altered. The subsequent analysis then focused

on the subject's search behaviour and how it was altered by the experimental manipulations. When exposing harbour seals to an expanded four-landmark array, the seals indicated the position of the goal at the specific angle and distance of goal to landmark as experienced during training, they applied a directional vector strategy for goal localisation (see Fig. S1 for the visualization of the different goal localisation strategies). In the second part of the experiment with a two-landmark array, the search behaviour of one of the three seals additionally suggested the use of landmarks as beacons, which resulted in an undirected search in the vicinity of a landmark. However, the seals never searched configurationally, which would have resulted in a search behaviour in line with an underlying rule such as 'the goal is in the middle of the landmarks', or 'the goal completes a triangle'.

The findings obtained in harbour seals are consistent with the search behaviour of various organisms tested in expansion tests (Collett et al., 1986; Spetch et al., 1996; Spetch et al., 1997; Potì et al., 2005; Kelly et al., 2008; Potì et al., 2010). Here, mostly the directional vector and beacon strategy were spontaneously chosen when animals were tested in single goal–landmark relationships as experienced by our harbour seals. Only humans spontaneously, meaning without prior training, and consistently adopted a configurational or rule-based approach (Spetch et al., 1996; Spetch et al., 1997; MacDonald et al., 2004). However, this midpoint encoding only emerged later during child development, and the researchers hypothesized that the advent of adopting a middle-rule correlates with the knowledge of the corresponding spatial wording (Simms and Gentner, 2019). Yet even though humans use this type of landmark encoding after reaching a certain age ad hoc, individuals of some animal species have demonstrated the use of relational information in experiments conducted with multiple goal–landmark relationships (Kamil and Jones, 1997; Kamil and Jones, 2000; Jones et al., 2002; Spetch et al., 2003; Potì et al., 2005; Sturz and Katz, 2009). Thus, it appears that the encoding of landmarks is context dependent.

Context-dependent search behaviour, or more generally the flexibility to apply all three possible goal localisation strategies, would be highly advantageous for harbour seals or for marine mammals in general. A directional vector and a beacon strategy allow localising a goal with respect to familiar landmarks that can be individually identified, for example, on the basis of feature information. However, if these features cannot be resolved from a distance or are not stable over time, rule-based searching would be more effective for goal localisation. The ability to use relational information from familiar landmarks would enable a harbour seal to localise a goal even from places it has never been before. More generally, behavioural flexibility is essential for species living in complex environments, such as marine mammals, which might require the organisms to adapt quickly to changing conditions or simply to different circumstances (Robinson, 1985; Kamil and Mauldin, 1988; Jones, 2006; Nowak and Lee, 2013). To investigate

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the degree of flexibility underlying goal localisation based on landmarks, we assessed whether a harbour seal would start to show rule-based searching with multiple goal–landmark relationships that triggered the use of relational goal searching in other species.

MATERIALS AND METHODS
Experimental animal
The experiment was conducted with one adult male harbour seal (*Phoca vitulina* Linnaeus 1758) named 'Moe' (14 years old) at the Marine Science Center of the University of Rostock, Germany. The seal had already participated in the previous experiment on landmark encoding (Maaß and Hanke, 2022). The setup of the previous experiment was also used in the present study, thus the seal was already familiar with the setup. The seal was housed with 11 other harbour seals, two sub-adult California sea lions (*Zalophus californianus*) and an adult South African fur seal (*Arctocephalus pusillus*) in a seawater enclosure. The seal was 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, with experiments running 3 to 4 days a week.

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

Experimental setup
The experiment took place in a small enclosure of the large facility. Here, a 2×2 m integral foam panel (Fig. 1) was fully submerged with the upper frame 20 cm below the water surface. A total of 121 LED lights (Luckylight, Shenzhen, China, Ø 10 mm; 8000 mcd, cold white, radiation angle 20 deg), arranged in 11 columns and rows, were embedded in the panel. The LEDs were 15 cm apart from each other; the outermost LEDs were 25 cm apart from the aluminium frame surrounding the wall. Each LED was connected to a control panel installed at a distance of 5 m to the wall. In order to control the LEDs from afar, the control panel served as a miniature version of the LED panel equipped with 22 light switches. Three cameras (two Eyoyo 1000 TVL Waterproof Camera, Eyoyo Shenzhen, Guangdong, China, and one GoPro Hero 7 Black Edition, GoPro San Mateo, CA, USA) on aluminium mountings were used to observe and document the animal's behaviour. To prevent secondary cueing, the experimenter hid behind an opaque visual cover.

Stimuli
The stimuli presented were LED landmark arrays consisting of two lit LEDs (Fig. 1). For each trial, the LED array configuration was varied in its absolute position on the LED wall following a pre-set schedule. In order to systematically and evenly vary the position of the LED array over the entire LED wall, we divided the wall into four quadrants and an overlapping area (Fig. 1A). During a session, the LED array was placed four (during testing) or up to six times (in training) in each quadrant and the overlapping area, resulting in a session of 20 to 32 trials.

During training, four different landmark configurations were shown to the seal either separately (stages 1–4) or several combined in one session (stages 5–7), thereby increasing the complexity of the task continuously as preparation for the testing phase with sessions that ultimately included a multitude of LED landmark arrays (see
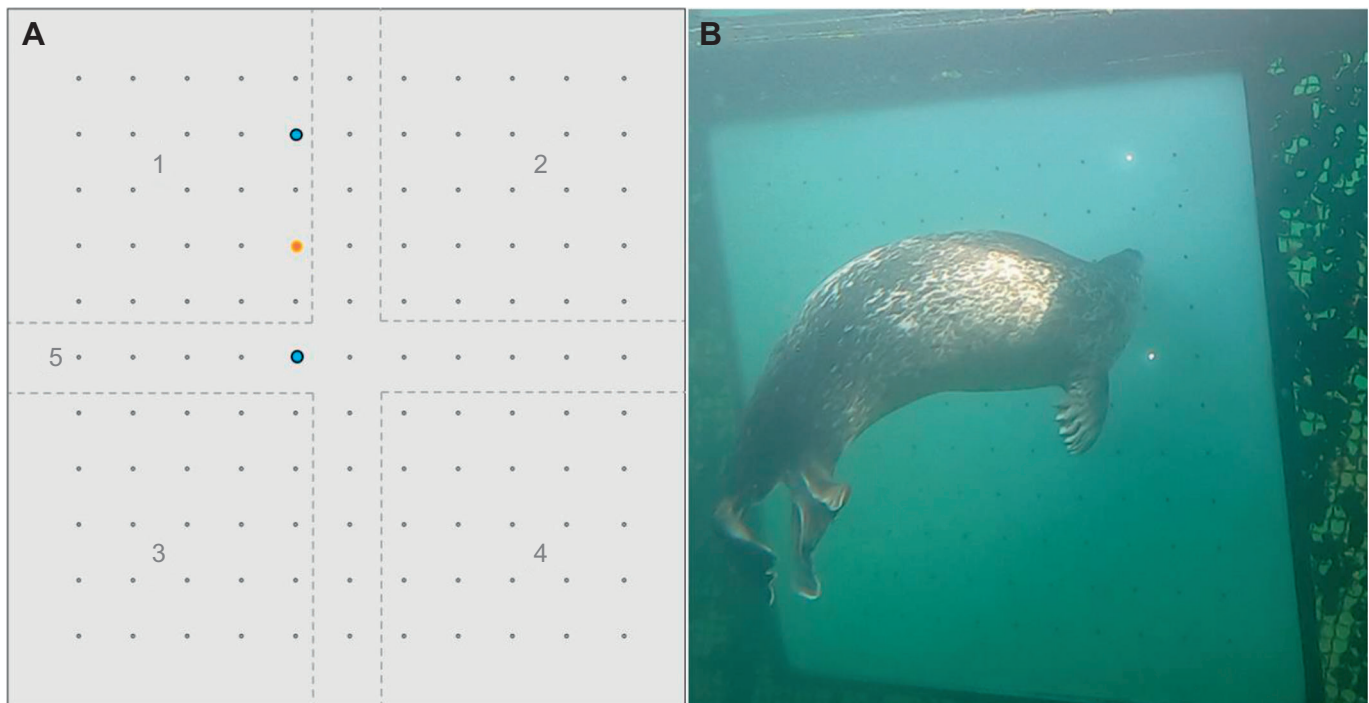

Fig. 1. Experimental setup from the seal's point of view and *in situ* as well as the seal's response behaviour when making a correct response to the middle of the two-LED landmark array. (A) On a plastic foam wall, we fixed 121 LED lights. In every trial, two LEDs (blue dots) were lit and served as the two-LED landmark array. The distance between the landmarks was altered in the different stages of training and during testing. The task of the animal was to touch an unlit LED, the goal, in the middle of the two landmarks (for representation, this unlit LED is here marked by a yellow dot; however, during the experiment, it remained unmarked). The position of the array was shifted to all quadrants (1–4) and the overlap area (5); see Materials and Methods for details. (B) A typical response behaviour of the seal when presented with the 3LEDv configuration of the experiment in the training phase.

below). The suite of landmark configurations for the different stages (Table 1) was chosen to make the seal familiar with LED landmark arrays with various inter-landmark distances as well as two orientations of the LED landmark array. Altogether, we used all horizontal and vertical two-LED landmark array configurations that were possible to present on our 11×11 LED panel with some variation in absolute position on the board (Fig. 1).

First, two LEDs, serving as landmarks, were shown that were spaced 60 cm apart and aligned vertically (Fig. 1; 3LEDv, stage 1). Second, we presented two landmarks 90 cm apart from each other, also aligned vertically (5LEDv, stage 2). Third, the configuration of stage 1 but with the LEDs aligned horizontally (3LEDh, stage 3) was shown to the seal. Fourth, we presented the landmarks with a distance of 120 cm from each other (7LEDh, stage 4) and with horizontal orientation. After stage 4, a session was composed of 3LEDh and 7LEDh in stage 5, of 3LEDh, 7LEDh and 3LEDv in stage 6, and of all four two-LED landmark arrays used in stages 1–4 combined in one session in stage 7.

In the test trials, a two-LED landmark array with the LEDs aligned either horizontally or vertically and 30 cm (1LEDv and 1LEDh) or 150 cm (9LEDv and 9LEDh) apart from each other was shown to the seal. The inclusion of new inter-landmark distances in the test trials smaller and bigger than the distances used in the training phase as well as in the baseline trials served to evaluate whether the seal's search behaviour fulfilled the requirements of 'geometric rule'-learning in accordance with Kamil and Jones (2000). We also introduced two variants of the familiar two-LED landmark arrays 5LEDv and 7LEDh by rotating the arrays by 90 deg, thus 5LEDh and 7LEDv, to increase the number of test trials. Testing resumed until each test stimulus was presented eight or nine times.

Experimental procedure

At the beginning of the trial, the animal was resting in a ring station opposite the LED panel. After the experimenter had switched on the specific two-LED landmark array of the respective trial, the seal was indicated to leave its station by a short whistle and approached the wall. At the wall (Fig. 1), the seal had to put its snout at the position, where it assumed the goal. The seal was required to touch the goal location in the middle of the LEDs with its snout. An incorrect answer was defined as the seal stationing elsewhere on the LED wall. After every correct response, the animal received a food reward. An incorrect response was followed 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 the next trial to start.

When presented with one (stages 1-4), two (stage 5) or three (stage 6) two-LED landmark arrays, a session consisted of 20–30 trials, whereas with four two-LED landmark arrays (stage 7), the number of trials was increased to 32 trials, allowing the presentation of arrays in the different areas of the panel with equal percentage as done in the previous stages. Every stage of training was concluded when the animal reached the learning criterion set to a performance of ≥80% correct responses to be reached in two consecutive sessions.

In the subsequent testing phase, a session was composed of 20 baseline and two test trials. The test trials were randomly integrated into the sessions, but never as first or last trial. In the baseline trials, the trials followed the schedule as for phase 7 of training and thus consisted of all four two-LED landmark arrays that had been used during training again presented in pseudorandomised order and equally distributed among the quadrants and the overlapping area.

Table 1. Overview of all stages of training and testing

Phase	Stage	Landmark array configuration	Inter-landmark distance (cm)	Orientation	Performance in first trial	Trials to LC in stages 1–7	Times tested in testing phase
Training	1	3LEDv	60	Vertical	IC	337	
	2	5LEDv	90	Vertical	IC	340	
	3	3LEDh	60	Horizontal	IC	372	
	4	7LEDh	120	Horizontal	IC	467	
	5	3LEDh	60	Horizontal	C	130	
		7LEDh	120	Horizontal	–		
	6	3LEDh	60	Horizontal	–	232	
		7LEDh	120	Horizontal	–		
		3LEDv	60	Vertical	C		
	7	3LEDh	60	Horizontal	–	84	
		7LEDh	120	Horizontal	–		
		3LEDv	60	Vertical	–		
		5LEDv	90	Vertical	IC		
Testing	Baseline trials	3LEDh	60	Horizontal	–		130
		7LEDh	120	Horizontal	–		130
		3LEDv	60	Vertical	–		130
		5LEDv	90	Vertical	–		130
	Test trials	1LEDh	30	Horizontal	C		8
		1LEDv	30	Vertical	C		8
		5LEDh	90	Horizontal	C		9
		7LEDv	120	Vertical	C		8
		9LEDh	150	Horizontal	C		8
		9LEDv	150	Vertical	C		9

Displayed are the specific configurations shown to the seal including the orientation of the two-LED landmark array (either vertical or horizontal) and the distance between the two LEDs of the two-LED landmark arrays (in cm) as well as the performance of the seal in the very first trial of presentation of the LED landmark array configuration or in the first trial after reintroduction (see 3LEDv in training stage 6, and 5LEDv in training stage 7; C, correct meaning response at midpoint; IC, incorrect meaning response not at midpoint; –, the configuration had already been tested in the directly proceeding training stage), the trials the animal needed to reach the learning criterion (LC) in the training phase and the number of trials in which each configuration was tested during the testing phase.

Data analysis

We analysed the performance of the seal during the training and testing phase (Table 1). During all trials, we noted whether the seal was giving a response at the midpoint (C; 'correct') or not (IC; 'incorrect'). Throughout the test trials, the position, meaning the LED on the panel the seal was stationing at when giving its response, was documented. If the seal was deviating from the middle of the landmark array, we described the deviations as the number of LEDs from the midpoint (1) in the linear direction, the error in distance along the line connecting the two LEDs of the landmark array, and (2) in the orthogonal direction, when the seal's responses occurred on the line(s) above or below (horizontal configurations) or on the line(s) to the left or right (vertical configurations) of the midpoint of the landmark array. These errors could be negative (e.g. when answering to the left of the midpoint regarding the linear error and below the midpoint regarding the orthogonal error for horizontal configurations), as well as positive (e.g. when answering to the right of the midpoint regarding the linear error and above the midpoint regarding the orthogonal error for horizontal configurations).

The seal's performance in the testing phase was statistically analysed to test whether the seal's performance in the first test trials with all fully or partially novel configurations taken together deviated significantly from chance performance (binomial test). For this first-trial analysis, we defined a lower and upper chance level (see also Spetch et al., 1996). The lower chance level was 1 in 121 or 0.83% as the seal could have answered at any of the 121 LEDs of the LED panel. As the upper chance level, we used the error rate of the seal during the last training phase (the seal made 18 errors within 84 trials corresponding to 21.43%). A performance significantly different from chance level in all six first trials of the testing phase together was considered evidence for the seal responding in line with a middle rule.

We assessed whether the performance in all 50 test trials and the 520 baseline trials was similar or significantly different to the seal's performance in stage 7 of the training phase (χ^2 tests). Analysis of the baseline trials was done to evaluate the motivation of the animal to cooperate during the testing phase. A comparably high motivation of the seal in the testing phase versus stage 7 needed to be documented as a prerequisite for analysing the test trials.

Additionally, we analysed whether the seal's performance differed significantly between test conditions [binomial generalised linear model (GLM)]. For this statistical calculation, the seal's performance in the 50 test trials was coded in binary form as either correct (C) or incorrect (IC). We ran an analysis using the following fixed factors: orientation (horizontal versus vertical landmark array configuration), inter-landmark distance (four-level factor: 1LED, 5LEDs, 7LEDs or 9LEDs), degree of novelty of LED landmark array configuration (fully versus partially novel LED landmark array configuration) and the two-way interaction between inter-landmark distance and orientation (see Table S2 for model comparison).

Finally, we analysed whether the absolute size of the error (Kamil and Jones, 2000) differed significantly by the type of error (linear or orthogonal), inter-landmark distance and orientation using a repeated-measures ANOVA (GLM). For all analyses, we used JASP (JASP Team 2020, Version 0.14.1, University of Amsterdam, Amsterdam, The Netherlands).

RESULTS

During training, the seal learnt to respond to the middle of four two-LED landmark arrays in 84–467 trials, with only 84 trials to criterion in the last stage of training (Table 1, Fig. 2). However, throughout the training phase, the seal did not direct its response to the midpoint of the two-LED landmark array in the first trials after the introduction of new two-LED landmark array configurations in
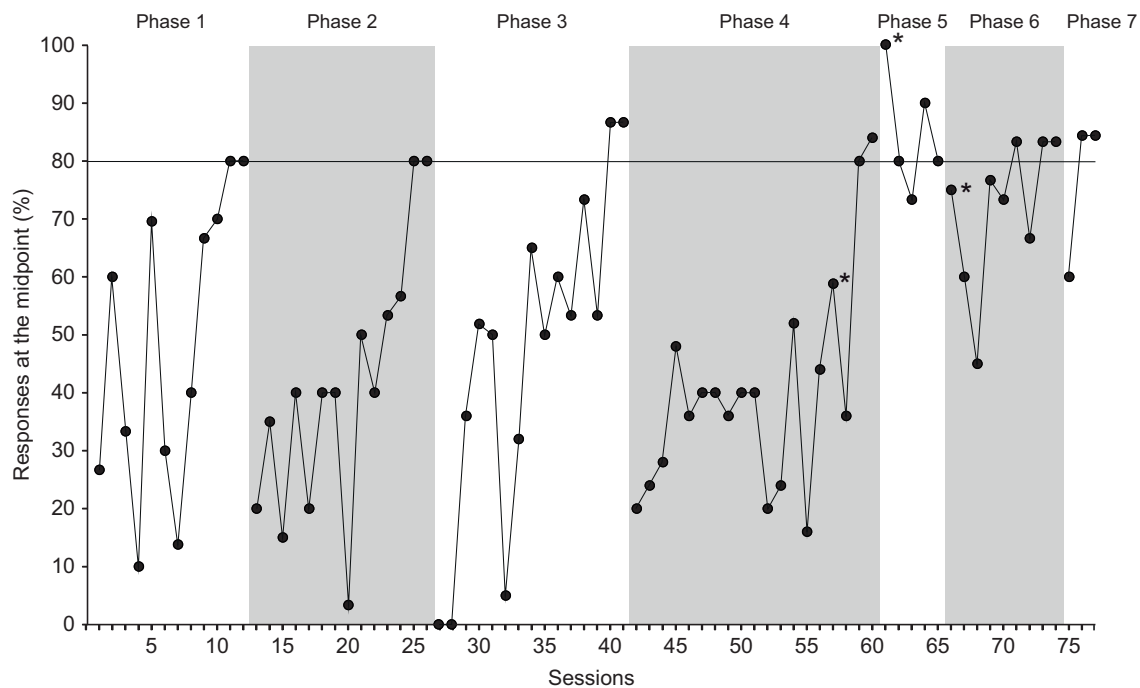

Fig. 2. Learning curve of the training phase of the experiment. Percentages of responses at the midpoint for each session during training phases 1–7. Each session was composed of 20–30 trials. The black horizontal line indicates the learning criterion that the animal had to reach, which was defined as a performance of ≥80% correct response at the midpoint in two consecutive sessions. In sessions 57, 61 and 66 (*), the sessions were terminated before the seal performed at least 20 trials owing to poor motivation of the animal (session 57) or weather conditions and turbidity hindering a normal experimental procedure (sessions 61 and 66).

stages 1 to 4. Thus, the animal did not show a positive transfer between consecutive new configurations. Even upon reintroduction of configurations in stages 5–7 (Table 1), the first trial of the seal was only directed at the midpoint for two of the three configurations.

In the testing phase, Moe chose the midpoint between the two landmarks in all first trials of presentation of the six two-LED landmark array configurations (Table 1, Table S1). The first trial analysis revealed that the seals' performance of 100% correct in all six first trials of the testing phase was significantly better than chance level (binomial test: $P<0.001$; for chance level 0.83% and 21.43%, $N=6$). Having a look at the seal's performance in the entire testing phase, the animal responded at the midpoint between the two landmarks in 76% of all test trials (12 ICs, 38 Cs; Table S1). This was similar to its performance in stage 7 of the training phase ($\chi^2=0.12$, $P=0.73$). In 24% of the test trials, the seal made errors that were all distributed in close proximity (–1 to +2 LEDs) to the midpoint (Fig. 3; Table S1, Fig. S2). The seal made small linear or orthogonal errors in 14% and 10% of the test trials, respectively, but it never deviated from the midpoint linearly and orthogonally in one trial. Accordingly, the seal's search behaviour was consistent with a relational 'middle' strategy or rule-based searching. During the testing phase, the seal kept performing the baseline trials with high accuracy by answering at the midpoint in 89% of all baseline trials in the testing phase, and was performing significantly better than in stage 7 of the training phase ($\chi^2=7.29$, $P=0.007$), indicating that the seal showed a high degree of cooperation.

Detailed analysis of the test trials revealed that, in the testing phase, the performance of the seal was not related to any feature of the LED landmark array configuration (binomial GLM, $\chi^2_{45}=4.759$, $P>0.05$, McFadden $R^2=0.09$; Table S2, Fig. S2). In detail: the seal's performance was not significantly different when comparing its performance across inter-landmark distances ($z=-1.13$, $P=0.26$, 75% for 1LED and 7LEDs, 89% for 5LEDs, 71% for 9LEDs) or across orientations ($z=-1.23$, $P=0.22$, 80% for horizontal and 73% for vertical LED landmark arrays). In addition, the interaction between orientation and inter-landmark distance was not significant ($z=1.78$, $P=0.07$). The performance was not significantly different regarding the LED landmark array configuration with different degree of novelty ($z=-0.79$, $P=0.43$, 73% for fully novel and 82% for partially novel LED landmark array configurations). In this context, it needs to be noted that, with stage 6, the seal rotated its body axis by 90 deg when approaching vertical configurations.

Notably, for the absolute size of the error, we found that there was a statistically significant interaction between type of error and inter-landmark distance (interaction effect: $F_{1,47}=9.27$, $P<0.01$, $\eta^2=0.08$; e.g. in the 9LED configuration the animal made larger linear than orthogonal errors, whereas the reverse was true for the 1LED configuration. There was no interaction between type of error and orientation ($F_{1,47}=2.04$, $P=0.16$, $\eta^2=0.02$). None of the main effects of the GLM was significant (Table S3).

DISCUSSION

In the present experiment, the seal directly, i.e. in the first trials, responded at the midpoint between two landmarks during the testing phase. It showed midpoint-responding when confronted with two-LED landmark arrays with unfamiliar inter-landmark distances in two orientations (fully novel configurations), and even with inter-landmark distances outside the range presented in the training phase. The seal also instantly showed responses to the midpoint in test trials that included LED landmark arrays with inter-landmark distances known from training, that were, however, presented with changed orientation (partially novel configurations). Taking all test trials together, the seal kept responding at the midpoint of all LED landmark arrays with a high performance, irrespective of whether experiencing fully or partially novel LED landmark arrays. The seal's behaviour was thus in line with a relational middle rule or rule-based searching (Kamil and Jones, 2000).

The seal's responses at the midpoint supporting the application of a middle rule generally required two processes to have taken place: the animal needed to determine (1) the line connecting the two landmarks, a directional problem, and then (2) the midpoint between the landmarks on that line, a distance problem (Kamil and Jones, 1997). In accordance, the seal might have also applied both processes when confronted with the 1LED landmark array configurations in the testing phase. However, its behaviour as response to the 1LED landmark array configurations could also be explained on the basis of the first process only, as after determining the line between the landmarks, the seal had only one LED between the landmarks left to answer to; indeed, the seal did not make linear errors when presented with this configuration (Fig. 4). We consider it most likely that the seal used a middle-rule throughout the testing phase owing to its overall high accuracy of responding to the midpoint, even when it was confronted with configurations that required it to be more decisive than the 1LED configuration. In a future experiment, the seal's performance could be further
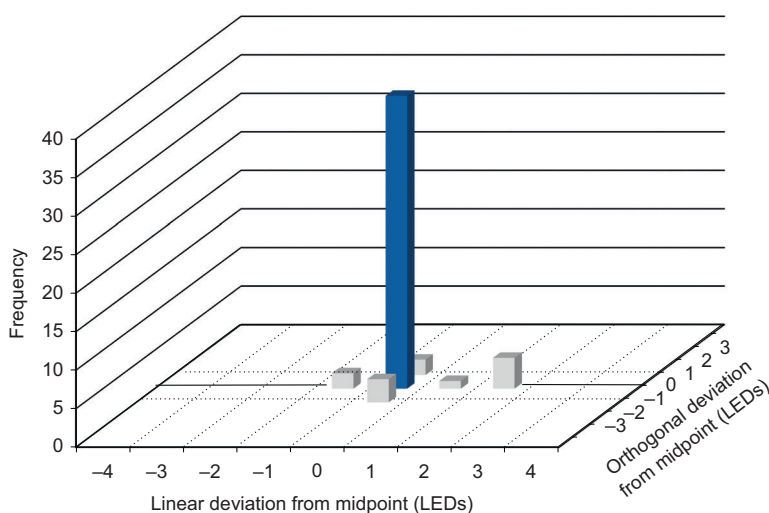

Fig. 3. The seal's search behaviour summarised for all test trials ($N=50$) over all two-LED landmark array configurations. The absolute frequency of responses at a specific position relative to the midpoint (at the origin of the coordinate system). To depict the error in deviation from the midpoint for all configurations in one graph irrespective of absolute orientation on the panel, the absolute orientation of the landmark array, either vertical or horizontal, was neglected, and errors for both landmark array orientation were plotted as if the landmark array had always been horizontal. The line on which the landmarks of the two-LED landmark array were positioned is indicated by the black line. For a more detailed depiction, see Fig. S3.
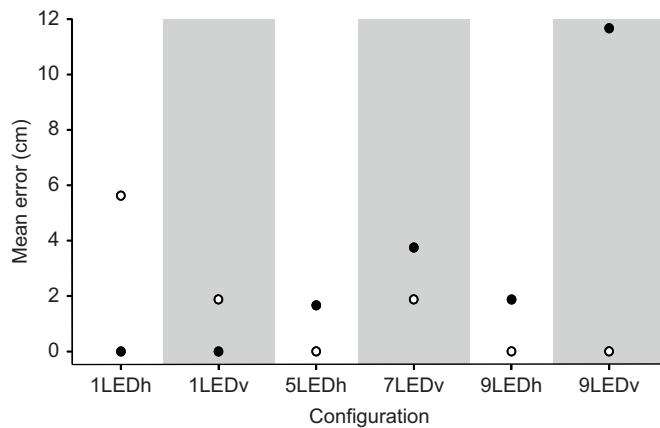
Fig. 4. Mean linear (filled circles) and orthogonal error (open circles) for each configuration presented in the testing phase (note that the distance between two LEDs on the LED panel was 15 cm). The errors occurring as a response to vertical configurations are highlighted with a grey background. Each data point represents the average error of eight or nine presentations (see Materials and Methods for details).

characterised with an experimental setup allowing a continuum of responses between the landmarks, which would make a determination of the precision of responding at the midpoint and of distance judgment even with short distances between landmarks possible.

In general, the seal's directional judgments were very accurate. When analysing the errors made by the seal in the testing phase, it made more linear than orthogonal errors the longer the inter-landmark distance, whereas the reverse was true for shorter inter-landmark distances. This overall finding hints at distance and direction being judged independently as it was also assumed for Clark's nutcrackers (Kamil and Jones, 1997; Kamil and Jones, 2000). The 'largest' directional problem that the seal needed to solve was to assess the orientation, vertical versus horizontal, of the landmark array. It solved this directional problem with ease and even without any significant difference in performance regarding configurations with horizontal or vertical orientation. Most likely the comparable performance resulted from or was at least supported by the body rotations the seal showed when confronted with vertical configurations from training stage 6 onwards. By these body rotations, the seal transformed a vertical into a horizontal configuration, which it might have figured out by chance, or by mentally rotating the configurations, an aspect that was investigated in a California sea lion (Mauck and Dehnhardt, 1997; Stich et al., 2003). The seal might have shown this rotatory behaviour owing to specific characteristics of the eye. On the harbour seal's retina, a horizontal visual streak with an increased ganglion cell density can be found in addition to an area centralis (Hanke et al., 2009). The visual streak provides the seal with a horizontal axis of high resolution, and it was previously speculated that it might be used to sample events taking place at the sea floor or at the water surface, which are strong horizontal reference planes in the habitat of seals, with high accuracy. The body rotations shown by our experimental animal in our study might have served to align the eye's axis of best resolution, the horizontal, with the two-LED landmark array. Thus, the seal might have optimised visual resolution by using the degrees of freedom of body rotations available to it underwater. As seals regularly change their body orientation underwater, they might perceive objects from different perspectives, which could ultimately lead to a different organization of visual perception, as already

proposed by Schusterman and Thomas (1966), and consequently in solutions of directional problems different from terrestrial animals.

The seal's rotatory behaviour could also hint at the mechanism underlying its responses at the midpoint of the LED landmark array. To assess the midpoint, the seal might have balanced the input from the two landmarks to both eyes, which would have ultimately led it to the midpoint. In order to use the equal forces to both eyes for the vertical LED landmark array, rotating the body is a prerequisite. The mechanism of midpoint-responding needs to be addressed in future experiments.

Although the seal answered in line with a relational middle-rule in the testing phase, it did not directly swim to the midpoint between the landmarks in the first trial of a new landmark configuration in the training phase. Thus, it seemed that the seal had to learn to respond to the midpoint for every new landmark configuration in the training phase, even though the animal showed that it was capable of finding the midpoint in the first trials of re-introduced configurations in stages 5 and 6. Possibly the seal discovered the underlying principle 'respond to the middle' during stage 7 in which four configurations were presented and in which the seal reached the learning criterion within only 84 trials. It then continued to apply the middle rule to every configuration in the testing phase. Thus, only after training with several configurations, albeit only four configurations, including multiple goal–landmark distances, the seal used configurational information for goal localisation, which would make its behaviour in these tasks comparable to that of Clark's nutcrackers (Kamil and Jones, 2000). The transition from stimulus-specific responses shown during early training to finally responding in line with an underlying principle, such as 'respond at the midpoint' or 'same versus different', has been shown in previous cognitive experiments with harbour seals (e.g. Mauck and Dehnhardt, 2005; Scholtyssek et al., 2013). However, acquisition of midpoint-responding for the first configurations was much faster in our study than in the previous seal cognitive experiments, most likely as the seal had already gained some experience with the setup and LED landmark arrays in our previous study (Maaß and Hanke, 2022), and in other species trained in comparable tasks (Marsh et al., 2011).

Taking the results of the previous expansion test (Maaß and Hanke, 2022) and the current experiment into account, the findings obtained in three harbour seal individuals might indicate that seals can apply all three strategies for goal localisation depending on context. This putative flexibility seems adaptive for seals, and also for other species that revealed a shift between strategies depending on experimental paradigm (for Clark's nutcrackers, see Kamil and Jones, 1997 and Kelly et al., 2008; for pigeons, see Spetch et al., 1997, 2003; and for primates, see Potì et al., 2005, 2010), as it would allow them to choose appropriate/adequate solutions quickly and dynamically. Generally, it needs to be stressed that cognitive/behavioural flexibility allows adaptations in real-time, which is an important aspect to consider even in the face of climate change or when assessing the impact of anthropogenic interventions in the ocean, the habitat of marine mammals. Behavioural flexibility has previously been addressed in harbour seals in reversal learning experiments (Erdsack et al., 2022; Niesterok et al., 2022). Although they successfully reversed a spatial task, only one out of four seals solved a serial visual reversal learning experiment. The flexibility with which seals generally respond to spatial information as well as their generally good access to visuo-spatial information (Renouf and Gaborko, 1989; Mauck and Dehnhardt, 2007; Maaß and Hanke, 2021) seems highly adaptive in a species navigating the open ocean and being a central place forager.

With our two studies on goal localisation (Maaß and Hanke, 2022; present study) with respect to small and artificial landmarks presented on a board with restricted size, we gained first insight into how seals, the experimental animal of the present study and two additional seal individuals in the previous study, use goal-defining features for goal localisation. Future experiments could document the goal localisation behaviour of harbour seals in respect to naturally occurring and larger landmarks in a large-scale orientation task. These experiments would be the basis for understanding landmark orientation/navigation in wild pinnipeds, which has previously been speculated about in studies that analysed the movements of wild seals, grey seals and Weddell seals in their habitat (Matsumura et al., 2011; Chevaillier et al., 2014; Fuiman et al., 2020). Although, to our knowledge, landmark orientation/navigation has not been mentioned regarding wild harbour seals, it seems very likely that harbour seals, often staying close to the shore, use landmarks for many reasons, such as the localisation of haul-out places. A configurational use of landmarks, if also shown in future experiments as just described, might be particularly useful when distant landmarks are the only goal-defining elements, available as has already been suggested for nutcrackers (Kamil and Jones, 2000). It might even allow the animals to find their goal from novel positions, also called non-route-based familiar landmark navigation by Bingman (1998), which would also need to be shown in a future experiment. This type of landmark navigation would be in line with spatial information being represented in the form of a cognitive map (Tolman, 1948; O'Keefe and Nadel, 1978; Gallistel, 1990; Gallistel and Cramer, 1996), an aspect that has previously only recently been implied in a marine mammal (Beltran et al., 2022).

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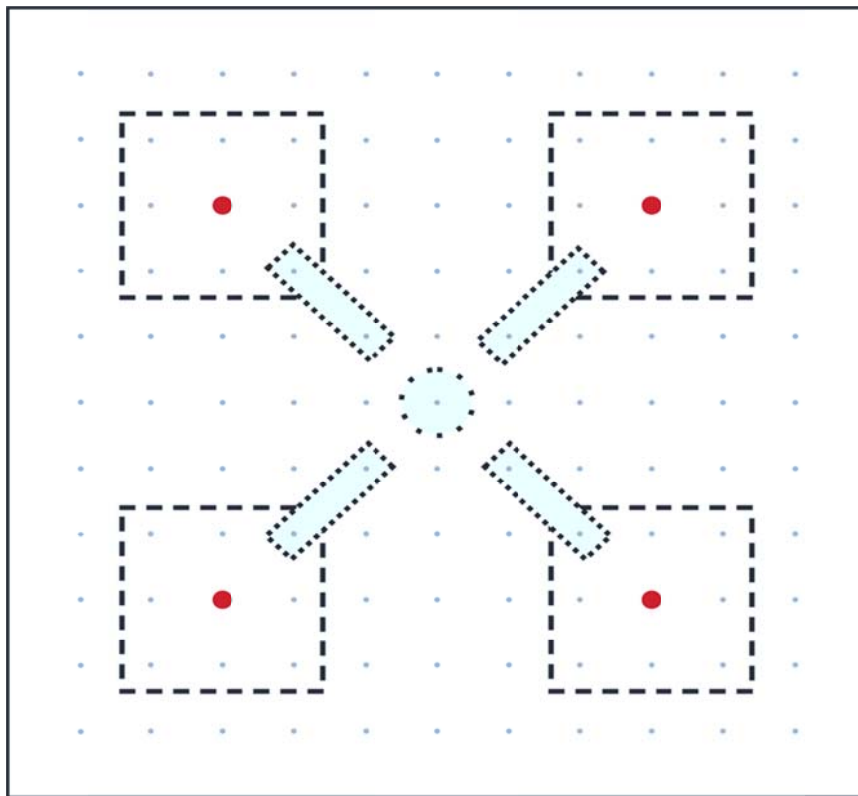
Fig.S1. Predicted search areas after expanding a landmark array consisting of four landmarks (red dots). The search areas in line with a beacon strategy (squared dashed line), a rule-based strategy (dotted circle) and a directional vector strategy (dotted rectangles) are shown (modified after Marsh et al., 2011; Potì et al., 2010).
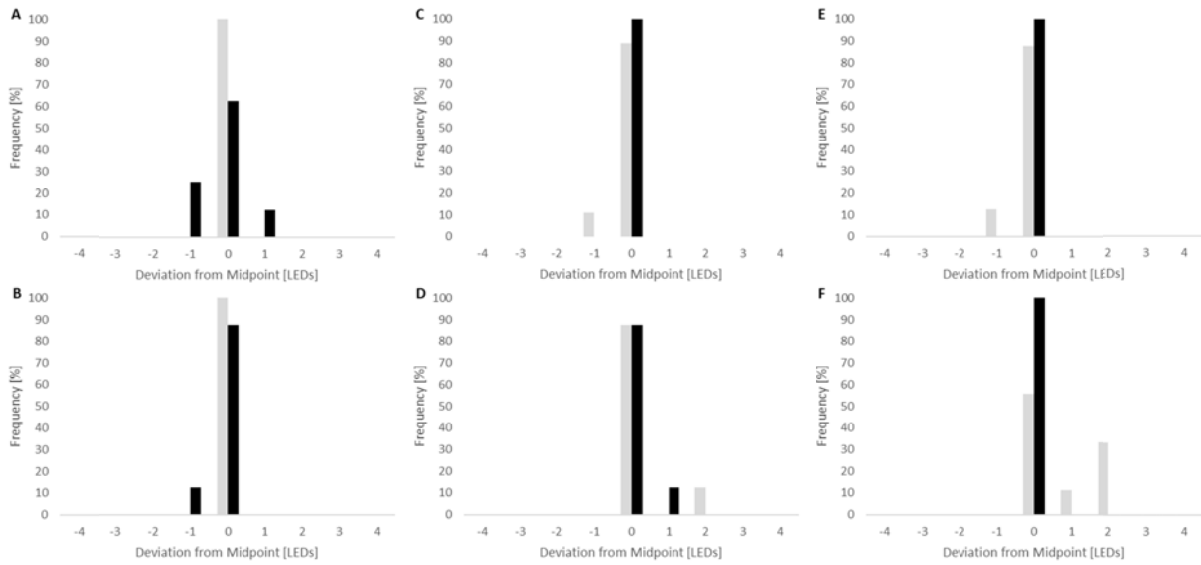
Fig. S2. Search behaviour of the seal during the test trials of the experiment for each configuration separately. A shows the 1LEDh configurati n (N = 8), B the 1LEDv configuration (N = 8), C the 5LEDh configuration (N = 9), D the 7LEDv configuration (N = 8), E the 9LEDh configuration (N =8) and F the 9LEDv configuration (N = 9). Depicted is the frequency [%] with which the seal hose the specific point along the linear (light grey bars) and the orthogonal (black bars) axis of the landmark configuration.

Table S1. Overview of the seal's search behaviour in the testing phase of the experiment during each test-trial (N=8-9). The responses of the seal are indicated as linear (L) and/or orthogonal (O) deviations from the midpoint in number of LEDs away from the midpoint. A response at the midpoint is indicated with 0. Deviations in linear direction (L) were defined as deviations occurring along the line connecting the two LEDs of the array, negative numbers show deviations to the left of the midpoint and positive numbers to the right of the midpoint in the horizontal configuration whereas for vertical configurations negative numbers are a deviation below the midpoint and positive numbers a deviation above the midpoint. Conversely, deviations in orthogonal direction (O) are defined as the seal's response occurring on the LED line(s) above (positive) or below (negative) the midpoint of the array in horizontal configurations and to the left (negative) and right (positive) in vertical configurations (see Method section).

Testtrial #	1 LEDh		1 LEDv		5 LEDh		7 LEDv		9 LEDh		9 LEDv	
	L	O	L	O	L	O	L	O	L	O	L	O
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	0	0	0	0	0	0	0	0	0
3	0	0	0	-1	0	0	0	1	1	0	1	0
4	0	-1	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0
6	0	-1	0	0	0	0	0	0	0	0	2	0
7	0	0	0	0	-1	0	0	0	0	0	2	0
8	0	0	0	0	0	0	2	0	0	0	2	0
9					0	0					0	0

Table S2. Overview of the results of the binomial general linear model. We calculated the effect of different fixed factors on the performance of the seal. The performance in every test trial was categorised as correct ("C", 1) or incorrect ("IC", 0). Fixed factors were the orientation (horizontal versus vertical), the inter-landmark distance (1LED, 3LEDs, 5LEDs, or 9LEDs), the degree of novelty of the LED landmark configuration (fully versus partially novel), and the two-way interaction between orientation and inter-landmark distance. Logistic regression for errors with orientation, inter-landmark distance and degree of novelty as fixed factors and the two-way interaction between inter-landmark distance and orientation

Model Summary - errors

Model	Deviance	AIC	BIC	df	X^2	p	McFadden R^2	Nagelkerke R^2	Tjur R^2	Cox & Snell R^2
H_0	55.1080	57.1080	59.0200	49						
H_1	50.3492	60.3492	69.9093	45	4.7588	0.3130	0.0864	0.1359	0.0965	0.0908

Coefficients

	Estimate	Standard Error	z	Wald Test Wald Statistic	df	p	95% Confidence interval Lower bound	Upper bound
(Intercept)	-0.3686	0.8253	-0.4466	0.1994	1	0.6552	-1.9860	1.2489
Inter-landmark distance	-0.1860	0.1640	-1.1343	1.2866	1	0.2567	-0.5074	0.1354
Orientation (vertical vs horizontal)	-1.7480	1.4167	-1.2339	1.5225	1	0.2172	-4.5247	1.0286
Degree of Novelty (partial vs fully)	-0.6092	0.7732	-0.7880	0.6209	1	0.4307	-2.1247	0.9062
Inter-landmark distance * Orientation	0.4025	0.2255	1.7847	3.1852	1	0.0743	-0.0395	0.8445

Note. errors level '1' coded as class 1.

The above model is not statistically significantly better than a model without the two-way interaction, $\chi^2(1,45) = 3.653$, p = .056, a model having only inter-landmark distance as fixed factor, $\chi^2(1,45) = 4.656$, $p = 0.199$; having only orientation as fixed factor, $\chi^2(1,45) = 4.319$, $p = 0.23$; having only the factor degree of novelty as fixed factor, $\chi^2(1,45) = 4.168$, $p = 0.244$; having inter-landmark distance and degree of novelty as fixed factors, $\chi^2(1,45) = 4.011$, $p = 0.135$; having orientation and inter-landmark distance as fixed factors, $\chi^2(1,45) = 4.26$, $p = 0.119$; or having orientation and degree of novelty as fixed factors, $\chi^2(1,45) = 3.764$, $p = 0.152$.

Table S3. Overview of the results for the GLM (repeated measurement ANOVA) with abs olute s iz e of the error as outcome and types of errors (linear or orthogonal), inter-landmark distance and orientation as fixed factors. Note that hypothetically the seal could make both types of errors in a single trial (but he did not).

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2
error type (linear or orthogonal)	0.6988	1	0.6988	3.5747	0.0648	0.0325
error type ✳Orientation	0.3996	1	0.3996	2.0440	0.1594	0.0186
error type ✳ Inter-landmark distance	1.8119	1	1.8119	9.2685	0.0038	0.0844
Residuals	9.1881	47	0.1955			

Note. Type III Sum of Squares

Between Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2
orientation	0.2997	1	0.2997	1.5792	0.2151	0.0140
magnitude	0.1601	1	0.1601	0.8438	0.3630	0.0075
Residuals	8.9199	47	0.1898			

Note. Type III Sum of Squares