Spatial Orientation in Harbour Seals

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Eric Maaß, geb. am 09.08.1990 in Berlin-Lichtenberg

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Gutachterin: Prof. Dr. Frederike Diana Hanke, Universität Rostock, Institut für Neuroethologie

Gutachterin: Prof. Dr. Kristy Biolsi, St. Francis College, Department of Psychology

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Für Jürgen und Helga

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Summary

Harbour seals, as semi-aquatic predators, commute regularly between haul-out places and feeding grounds. How the animals orientate themselves and navigate towards their goal has so far only been examined in an indirect way. Hereby, either tags were used to analyse the seals' trajectories or specific sensory systems were analysed regarding the question of whether they could contribute towards orientation and navigation. Thus, direct investigation into the orientation and navigation mechanisms of harbour seals has been missing until now. In the present thesis, I examine the basis of two mechanisms that seals could use to navigate and orientate themselves in their natural habitat. First, close to the shore, the seal could eventually rely on landmarks to indicate the position of its haul-out place. An expansion test was conducted to investigate how landmark information could be encoded by the seal and revealed that the seals spontaneously use vector information and, in a second experiment, could be trained to localise the goal based on relational information. These two studies thus unravelled the strategies of landmark use by seals and demonstrated a high degree of flexibility and adaptability in their natural habitat, in which conditions are expected to change continuously. Second, path integration – integrating distance and directional information into a homing vector – would be a promising navigational mechanism for a seal. In order to integrate paths, the seals have to be able to estimate distances. The seal's general ability to estimate and reproduce distances was examined in this thesis in distance reproduction tasks. I found that the seals could be very precise in estimating distances, especially when repeatedly swimming a specific distance, but even when blindfolded. A seal could benefit from distance estimation as part of path integration or on its own, such as when travelling to a specific place on a straight path.

The present thesis thus demonstrates the first evidence of direct experimental approaches towards two different mechanisms of orientation and navigation in harbour seals. Though viewed separately in this thesis, both mechanisms could also contribute to and complement each other, which would be an excellent point for further investigation.

Zusammenfassung

Seehunde, als semi-aquatische Raubtiere, schwimmen regelmäßig zwischen ihren Liegeplätzen und ihren Nahrungsgründen hin und zurück. Wie sie sich dabei orientieren/navigieren wurde bisher jedoch nur auf indirektem Wege untersucht. Einzelne Tiere wurden entweder mit Sendern versehen oder Sinnessysteme wurden auf ihre Eignung für Orientierung und Navigation untersucht. Ein direkter Ansatz zur Untersuchung fehlte demnach bis jetzt. In der hier vorliegenden Dissertation präsentiere ich nun die Grundlagen von zwei verschiedenen Mechanismen, mit denen sich Seehunden in ihrem natürlichen Lebensraum zurechtfinden könnten. Zuerst könnten die Tiere z.B. in Küstennähe Landmarken nutzen, welche zu ihren Liegeplätzen weisen. Ein Expansionstest wurde deshalb durchgeführt, um zu erörtern wie Seehunde Landmarkeninformationen verarbeiten und konnte zeigen, dass Seehunde spontan Vektorinformationen nutzen und wie ein zweites Experiment ergab, auch trainiert werden können, das Ziel basierend auf relationalen Informationen zu finden. Beide Studien konnten somit die Strategien der Landmarkennutzung aufzeigen, welche hochgradig flexibel und damit angepasst an ihr sich ständig im Wandel befindliches natürliches Habitat zu sein scheinen. Zweitens könnte Wegintegration, also die Integration von Wegstrecken und Richtungsinformationen in einem heimwärts-gerichteten Vektor ein vielversprechender Navigationsmechanismus für Robben sein. Um Wegintegration zu betreiben, muss das Tier in der Lage sein, Distanzen abzuschätzen, eine Fähigkeit, die auch in dieser Dissertation mit Hilfe einer Reproduktionsaufgabe untersucht wurde. Ich konnte zeigen, dass Seehunde hierbei sehr präzise sein können, gerade wenn sie eine Distanz wiederholt abschwimmen, sowie auch unter visueller Maskierung. Eine Robbe könnte demnach von der Nutzung der Distanzabschätzung profitieren, ob im Zusammenhang mit Wegintegration, oder allein, wenn sie einen geraden Weg eingeschlagen hat.

Die vorliegende Dissertation konnte also zum ersten Mal in direkten experimentellen Ansätzen zwei verschiedene Mechanismen der Orientierung und Navigation bei Seehunden untersuchen. Auch wenn, beide Mechanismen hierbei separat betrachtet werden, könnten Sie auch zusammenspielen und sich gegenseitig ergänzen, was eine exzellente Grundlage für weitere Untersuchungen bildet.

1. General Introduction

1.1. There and Back Again: Harbour Seal Behaviour in its Natural Environment

Harbour seals (*Phoca vitulina*) are semi-aquatic mammals. They inhabit bays, estuaries, intertidal areas and rivers all the way to the continental slope in the northern hemisphere (Webber et al. 2015). The animals can often be found hauling out on rocks or sandy beaches. However, for a considerable amount of time, harbour seals leave their haul-out places mostly to go foraging. From tagging studies, the paths taken by the seals have been well-described. The trajectories of seals illustrate that the animals cover dozens of kilometres on their journey (Bjørge et al. 1995, Tougaard et al. 2008, Cunningham et al. 2009, Peterson et al. 2012, Vance et al. 2021). During these trips, seals either follow the coastline or swim towards the open ocean, where some of them even stay for days (Vance et al. 2021). Interestingly, some animals visit specific foraging places repeatedly (Iorio-Merlo et al. 2022). After foraging, the seals return to specific haul-out places (Vance et al. 2021). Revisiting certain areas of interest, often over kilometres, such as haul-out places and foraging grounds, demonstrates that the seals are well orientated in their habitat (Vance et al. 2021). However, the mechanisms of orientation and navigation behind these movements are mostly unknown or subject to speculation.

1.2. Speculations about Mechanisms of Orientation and Navigation in Harbour Seals

Many researchers have already speculated about the mechanisms of orientation and navigation underlying the movements of harbour seals. These speculations arose from laboratory experiments focussing on sensory perception. Information from the senses is most likely required if (1) the seal wants to determine its own position in relation to a reference (orientation, see Schone 2014) or if (2) the seal wants to chart a course from its current position towards a remote goal (navigation, see Schone 2014). The following paragraphs will give an overview of what is known about the sensory systems and mechanisms involved in navigation and orientation, for which well-controlled laboratory experiments and also studies in the wild have been performed.

Mauck et al. speculated about harbour seals using astronavigation (Mauck et al. 2005, Mauck et al. 2008). In their first study, Mauck et al. (2005) examined how bright a star has to be in order to be perceivable by a harbour seal. The seal tested was able to perceive stars down to a stellar magnitude of 4.4 on a scale ranging from 1 (bright) to 6 (faint). Thus, the seal could use numerous stars, including the signs of the zodiac, for astronavigation. In a subsequent study, Mauck et al. (2008) additionally demonstrated that seals can identify and swim towards a lodestar within a full projection of the night sky. Thus, harbour seals possess the prerequisites for astronavigation, which awaits confirmation in a future experiment.

Harbour seals could also use their high sensitivity to dimethyl sulphide (DMS) as an odorant cue to guide them to areas of high marine productivity (Kowalewsky et al. 2006). In these high-productivity areas, abiotic factors, such as solar radiation or the availability of nutrients, support the growth of marine phytoplankton. When this phytoplankton is grazed by zooplankton, DMS is released into the atmosphere (Savoca and Nevitt 2014). These high-productivity areas could be interesting for seals, as the zooplankton ultimately attracts organisms, which the seals prey upon. The use of high-productivity areas by seals was indicated when a population of harbour seals changed their foraging behaviour (dive duration and dive length) with the occurrence of upwelling events bringing prey species closer into reach of the seals (Blanchet et al. 2015). Studies including baleen whales (Bouchard et al. 2019) and sea birds (Nevitt and Haberman 2003, Wright et al. 2011) illustrated that whales, for example, were generally attracted and stayed longer in areas with chemical cues present (here krill extract), and that they modified their acoustic behaviour when DMS was present (Bouchard et al. 2019). Leach's storm petrels (*Oceanodroma leucorhoa*) approached DMS-exposed areas nearly twice as often as areas in which control solutions were put out (Nevitt and Haberman 2003). Similar aspects, such as harbour seals being directly attracted by DMS or following DMS gradients, still need to be experimentally demonstrated.

Similarly, speculation also arose about salinity gradients and their use for orientation and navigation (Sticken and Dehnhardt 2000). The laboratory experiment by Sticken and Dehnhardt (2000) showed that harbour seals can detect small differences in salinity, which would enable them to compare salinities on their routes. This way, the animals could, for example, be guided into estuaries by following a gradient of decreasing salinity, making a gustatory cue valuable in the navigation and orientation context.

Other sensory systems that could enable harbour seals to orientate or navigate in their environment, are their hydrodynamic and acoustic senses. The hydrodynamic sense of seals, mediated by their elaborate vibrissal system (Dehnhardt et al. 2014), could help in the determination or modification of their movement direction by using temporally or permanently stable currents. One example could involve sensing the systematic change of direction of water flow with the tides, which could provide essential hydrodynamic information for orientation (Hanke and Dehnhardt 2018). The harbour seal's well-developed auditory system (Hanke and Reichmuth 2022) might allow seals to perceive soundscapes underwater for orientation, as has been suggested in the context of whale orientation by Norris (1967).

Seal orientation/navigation on the basis of the Earth's magnetic field or polarized light from the sun or the moon has also been hypothesized (Renouf 1989, Hanke et al. 2013). Yet, so far, only two studies have examined harbour seal magnetoreception (Renouf, 1989; Hanke et al., unpublished data) and one polarization vision (Hanke et al. 2013). However, none of these studies provided evidence for either cue being perceivable by harbour seals. Thus, it is uncertain whether harbour seals can perceive magnetic cues or polarized light and whether these play a role in the context of orientation and navigation.

In general, there are two mechanisms that have been repeatedly raised with respect to marine mammal navigation and orientation. These could be based on a multitude of different sensory inputs that have not yet been investigated in harbour seals: *landmark orientation* and *path integration*. The idea of landmark orientation was raised when performing experiments with ice-living seals (Fuiman et al. 2020) and when observing wild elephant seals (Matsumura et al. 2011). The latter study suggested that those seals might orientate themselves with the help of visual landmarks when at the surface and might keep their initial course even after submerging in a spiralling manner. For harbour seals, who also frequent coastlines where landmarks are available for orientation, no evidence is available with respect to landmark orientation and no study has so far been undertaken to examine landmark orientation.

In the absence of landmarks, an alternative navigational mechanism is path integration (for a review see e.g. Etienne and Jeffery 2004). The data obtained by Fuiman and colleagues (2020) demonstrated that ice-living Weddell seals (*Leptonychotes weddellii*) might use path integration in order to find their way back to their breathing holes. The study suggests that the seals integrate distance and direction information in order to obtain a homing vector, which would lead them straight back to their origin – their breathing hole. While path integration allows homing after tortuous outbound paths, seals could also keep track of the distance travelled to a specific area on a straight path and reverse the path during homing. This easiest form of path integration is called *path return*. Experiments directly showing the abilities of seals to perform path integration, or its prerequisites, are missing so far.

This thesis addresses basic questions with respect to both mechanisms – landmark orientation as well as path integration. In detail, the studies demonstrate how a marine mammal (1) localises a goal with the help of landmarks (see 1.3 and the following sections) and (2) estimates distances, which, as just outlined, is a crucial component for path integration and beyond (see Chapter 1.4 and the following sections).

The following sections will give a deeper insight into the mechanisms of landmark orientation and path integration and the corresponding experiments in this thesis.

1.3. Landmark Orientation/Navigation

Landmarks are objects that can be distinguished from a distance – by a seal or any other animal – or are prominent in their shapes and can thus be used as guides towards a specific location or more generally help an animal to orientate itself (Yesiltepe et al. 2021). Visual landmarks, for instance, can be natural structures such as seamounts and the coastline itself or anthropogenic objects such as lighthouses or offshore windfarms. Harbour seals have been shown to generally use anthropogenic structures such as pipelines as linear landscape features on their routes (Russell et al. 2014). For some populations of humpback whales (*Megaptera novaeangliae*), the use of the coastline as a landmark has been postulated while the animals were swimming, for example, from Antarctica to Australia (Bingman and Cheng 2005, Rozhok 2008). The cracking of ice around a breathing hole might also serve as an acoustic landmark to be used for the localisation of and homing in on a breathing hole (Wartzok et al. 1992). Besides visual and acoustic landmarks, speculation has also arisen about the existence and use of magnetic landmarks, such as local small-scale changes in the Earth's magnetic field (Walker et al. 1992). These so-called magnetic anomalies occur when hard substrates contain magnetic materials, such as iron. The presence or absence of these formations might increase or decrease the magnetic field near the hard substrate (Klinowska 1985). Animals might then use anomalies for navigation. Researchers have speculated about cetacean navigation being based on the Earth's magnetic field in general and anomalies in particular, as temporal local variation in the strength of the Earth's magnetic field has been linked to stranding events (Klinowska 1985, Kirschvink et al. 1986). Thus, as landmarks can come in a multitude of forms and might be available close to shore but also in the open ocean, landmark orientation and navigation in marine mammals seems likely and thus a promising area of research.

Landmarks in the environment can contribute to different mechanisms of either navigation or orientation (Yoder et al. 2011). A single visual landmark could, for example, serve as an orientation point for the seal in order to determine its own position in relation to the landmark. If the landmark provides further information in the form of features or is associated with further instructions on how to reach the seal's desired destination, the seal could also use it for navigation and thus for the computation/execution of a planned trajectory (Yoder et al. 2011). Co-occurring additional landmarks could also be used in determining the distance between objects or between oneself and other objects in the form of *piloting*. Piloting describes the process of determining the location between some visual items (e.g., landmarks) and oneself during navigation. The navigator's position is determined with the help of the vectors relative to the landmarks (Zhang and Mou 2017). With multiple landmarks en route, the seals could compart their pathway in smaller segments from landmark to landmark, like humans would with the help of specific sights in a new city to find their way back to the hotel room (also called *route following*).

Additionally, landmarks not only function as objects serving orientation and navigation at a distance. Harbour seals could also use them for goal localisation. If a landmark is closely associated with a goal, it could very well provide information on where the goal can be found with respect to the landmark, which is the topic of the next chapter.

1.3.1. Goal Localisation

There are three main strategies that various organisms have been shown to apply when localising goals with respect to landmarks. The encoding of landmarks is therefore not uniform across species (Marsh et al. 2011); different species use different ways of landmark encoding or even apply multiple strategies (Kamil and Jones 2000, MacDonald et al. 2004, Potì et al. 2010). First, when encountering a visual landmark, the animal perceives the landmark as a beacon, a conspicuous object associated with the goal. Using the landmark as a beacon leads the animal omnidirectionally searching for the goal in the vicinity of the landmark. This *beacon strategy* has been found, for example, in rats, turtles, monkeys and human children (Cook and Tauro 1999, Lopez et al. 2001, MacDonald et al. 2004, Potì et al. 2005).

When applying the *directional vector strategy*, the goal is not encoded in relation to a single landmark, but instead information from multiple landmarks is obtained in the form of a vector, thus including distance and direction information that clearly guides the animal to the goal (Marsh et al. 2011). This type of landmark use has been found in gerbils (Collett et al. 1986), pigeons (Spetch et al. 1996, Spetch et al. 1997), and primates (Potì et al. 2005, Potì et al. 2010).

Lastly, a goal can be localised applying a *rule-based* strategy. Using this approach, an animal can operate with the configuration of an entire array of landmarks and encode the position of the goal in relation to all available landmarks. The goal, for example, could be surrounded by three landmarks that form a triangle. Encoding the goal with the help of a rule-based approach, it doesn't matter how the landmarks are aligned or from which position the animals approach the array, as the goal is always in the middle of the landmark array, and thus a "rule" underlines this search strategy. Until now, the spontaneous application of a rule-based strategy has only been demonstrated by human subjects after reaching a certain age (MacDonald et al. 2004). However, a few species, such as birds and monkeys, have demonstrated that they could learn to adopt a rule-based approach with experience when locating a goal inside a landmark array (Kamil and Jones 1997, 2000, Jones et al. 2002, Spetch et al. 2003, Potì et al. 2005, Sturz and Katz 2009).

Some of the aforementioned species have been described as using different strategies depending on context (Kamil and Jones 2000, Potì et al. 2005, Sturz and Katz 2009, Potì et al. 2010). This flexible use of goal localisation strategies with respect to landmarks might be adaptive, as it allows animals to choose the most reliable strategy under specific circumstances.

The experimental approach to analysing which strategy an organism spontaneously uses after training is the so-called *transformational approach*. Using this approach, the spatial arrangement of goal-defining landmarks relative to one another and/or to the goal is altered during the course of the experiment. In displacement experiments, landmarks that have defined the goal over time are displaced to a different location. This type of experiment was first performed on digger wasps (Tinbergen 1972) and illustrated that the wasps memorized the entrance of their nest with the help of landmarks, in this case pine cones. The wasps failed to locate the correct nest entrance upon displacement of the landmarks and instead searched for their nest entrance at a location relative to the landmarks as during training conditions. Apart from insects, the landmark-displacement technique has over the course of centuries been used to show that many species use landmarks for goal localisation including rodents (Collett et al. 1986), birds (Spetch et al. 1992), cephalopods (Mather 1991), fish (Reese 1989, de Perera Burt and Macias Garcia 2003) and reptiles (Lopez et al. 2001).

Subsequently, numerous studies have tested how various species encode goals with respect to landmarks by altering the distance between landmarks in an entire landmark array systematically. This alteration results in an expansion or contraction of landmark arrays while keeping the relational properties of single landmarks to each other constant. Accordingly, these experiments have been labelled *expansion tests* (Spetch et al. 1992, Spetch et al. 1996, Spetch et al. 1997). Usually, the animal is first trained to find a goal among an array of prominent landmarks. The position of the array may be translocated across the experimental setup to avoid the animal using the goal's absolute position. However, the landmark array's geometric properties remain constant until the animal learns the task. In subsequent test trials, the landmark array is expanded or contracted. The search and response behaviour during the test trials with the expanded or contracted landmark array can then provide information on the encoding of goals with respect to landmarks and which of the previously mentioned search strategies was predominantly chosen or chosen under specific circumstances (see Marsh et al. 2011).

In order to investigate whether and how harbour seals encode goals with respect to landmarks, two experiments, outlined in the following chapters, were conducted as part of this dissertation project, both adopting the transformational approach.

1.3.2. Experiment 1: Landmark Encoding in Harbour Seals

The first experiment (Maaß, E., & Hanke, F. D. (2022): *How harbour seals (Phoca vitulina) encode goals relative to landmarks*. Journal of Experimental Biology, 225(5): jeb243870) was designed in order to unravel which strategy of goal localisation with respect to an entire landmark array harbour seals would spontaneously choose. Up until this point, no experiment had been performed regarding landmark use in marine mammals, even though, as mentioned before (see Chapter 1.3), marine mammals could benefit from using external landmark information when orientating and navigating themselves in their habitat.

The experiment was performed using an expansion test as an experimental paradigm. Three seals were trained to find a hidden goal within an array of landmarks. In the experiment, LED lights served as landmarks, and the goal was always in the middle of the landmark array. After the seals had learnt the basic task of indicating the position of the goal in the middle of a four-landmark array, the landmark array was expanded in test trials, and the seals' search behaviour was documented. The seals' search behaviour in the test was consistent with the directional-vector strategy, also found in birds, gerbils and primates (Collett et al. 1986, MacDonald et al. 2004, Potì et al. 2005, Kelly et al. 2008, Potì et al. 2010). In a subsequent experiment, I reduced the number of landmarks in order to evaluate whether the landmark encoding strategy would change with the number of landmarks present. When presented with an array with only two landmarks, and with the goal of forming a triangle with respect to the landmarks, some seals additionally opted for the use of the landmarks as beacons, thus choosing to search for the goal in the direct vicinity of the landmarks, similar to rats, turtles, monkeys and human children (Cook and Tauro 1999, Lopez et al. 2001, MacDonald et al. 2004, Potì et al. 2010). The results obtained in this study illustrate how harbour seals spontaneously use landmarks to locate a goal: preferably, seals use vectors consisting of directional and distance information with respect to the landmarks. Yet, they also demonstrate a context-dependent switch in search strategy when the amount of landmark information is reduced. The context-dependent switch between strategies might be adaptive in the seals' complex environment, as it allows the seal to localise the goal when landmarks of different quantities and qualities (landmarks serving as beacons or providing directional information) are available. The results obtained in this experiment are the first on goal localisation with the help of landmarks in harbour seals. They provide the basis for further investigations on the abilities of harbour seals to use landmarks for goal localisation as well as generally for navigation and orientation (see Chapter 1.2).

1.3.3. Experiment 2: Moe in the Middle: Can a Harbour Seal Learn Geometrical Relations?

The first study on the localisation of goals with respect to landmarks in harbour seals revealed that seals spontaneously adopt two of the three strategies that were demonstrated in previous studies on goal localisation, including other organisms (see Chapter 1.3.2). Seals, however, had never showed search behaviour consistent with a rule-based approach. As mentioned before (see Chapter 1.3.1), other species demonstrated that they could learn to search using a rule or geometric relations when the experimental design was adjusted (Kamil and Jones 1997, Jones et al. 2002, Spetch et al. 2003, Potì et al. 2010). A follow-up study (Maaß, E., Miersch, L., Pfuhl, G., & Hanke, F. D. (2022). *A harbour seal (Phoca vitulina) can learn geometrical relations between landmarks.* Journal of Experimental Biology, 225(24), jeb244544) was thus designed to address the question of whether seals could learn to use relational information, when confronted with a similar experimental design that sparked the use of relational information in other species (Kamil and Jones 1997, Jones et al. 2002, Spetch et al. 2003, Potì et al. 2010). I was interested to see whether a comparable experimental approach would enable a harbour seal to use the landmark's relationships for goal localisation.

In this experiment, the same experimental setup was used as in the preceding experiment (see Chapter 1.3.1). In contrast to the first experiment, the goal in this experiment formed a line with the landmarks, and the seal had to locate the goal at the midpoint of the line connecting the two landmarks of various landmark arrays, which differed in interlandmark-distance and orientation. In one session, up to four different landmark arrays were presented to the seal. After the seal showed high precision in finding the midpoint, it was presented with unfamiliar landmark configurations of two orientations with unknown inter-landmark distances. The seal chose the midpoint in the first trial of the presentation of all new landmark configurations. It thus reacted according to the rule-based approach when encoding goals relative to landmarks. This finding demonstrates that with extensive training and the presentation of numerous landmark arrays varying in inter-landmark distances and orientation the use of a rule-based approach can be triggered in seals. As seals seem to be able to use relational information, they could be able to find goal locations regardless of their own position towards the landmarks. In particular, rule-based goal localisation would be beneficial when distant landmarks are the only goal-defining features (Kamil and Jones 2000) and when these are approached from entirely new positions in line with non-route-based familiar landmark navigation (Bingman 1998). Altogether, these studies demonstrate that harbour seals are very flexible with respect to information provided by landmarks. Future research could assess the role of landmarks, for example, in the context of a putative map of the environment (see Chapter 1.5).

1.4. Path Integration

Path integration is the ability to integrate directions steered and distances travelled during an outbound trip into a homing vector that enables the animal to find the way back to its origin or to any point along its outbound path (Mittelstaedt and Mittelstaedt 1982, Bigel and Ellard 2000, Etienne and Jeffery 2004).

In general, path integration can be based on external (*allothetic* path integration) or internal (*idiothetic* path integration) information. External information used for path integration can be derived from vision (Etienne and Jeffery, 2004), magnetoreception (Kimchi et al. 2004), or audition (Müller and Schnitzler 2000, Yovel and Ulanvosky 2017). Internal information refers, for instance, to information obtained from the vestibular system or proprioception (Mittelstaedt and Glasauer 1991). The fact that path integration can rely on a multitude of information makes path integration a promising navigational mechanism to look at in marine mammals. It would allow seals to home under conditions in which external information is available and reliable, but also in their seemingly low-structured environment, using, for example, information from self-motion to integrate a homing vector.

Until now, a multitude of taxa (insects, birds, mammals, fish, and reptiles) have been tested for their ability to perform path integration, ranging from insects to humans (Mittelstaedt and Mittelstaedt 1980, Müller and Wehner 1988, Moller and Görner 1994, Benhamou 1997, Seguinot et al. 1998, Durier and Rivault 1999, Collett and Collett 2000, Layne 2003, Etienne and Jeffery 2004, Kautzky and Thurley 2016). Detailed knowledge about path integration and the underlying mechanisms was most prominently obtained in desert ants (Müller and Wehner 1988, Wittlinger et al. 2006, Ronacher 2020, Wehner 2020).

In marine mammals, path integration was first suggested for Weddell seals by Fuiman et al. (2020). The approach in that study assumed that the seal's inbound path back to the breathing hole would be straighter than its outbound path, as the computation of a homing vector allows the seals to home in on the breathing hole on the shortest path. The analysis of the Weddell seal's movement was in line with this prediction from path integration. However, the study could not exclude alternative mechanisms of homing, and a direct investigation of path integration is missing for any marine mammal so far.

One reason for this lack of experimental studies has certainly been the difficulty of examining path integration in wild animals. When looking at the track of a tagged seal, it has to be noted that the movements of the animal might be guided into a general direction but can be very long, or tortuous and ambiguous (see Chapter 1.5). During these trips, the seal might well switch among different orientation mechanisms, thus not all movements can be attributed to path integration. In its simplest form, a harbour seal could use path integration to swim straight to, for example, a familiar foraging ground (Iorio-Merlo et al. 2022) and home in on a haul-out place subsequently by turning 180 degrees and travelling the distance swum on the outbound path back. This form of path integration is called *path return*. It would require the seal to keep and reverse its course and to reproduce a previously swum distance. Thus, the third study included in this thesis focuses on the question of whether a harbour seal can estimate and reproduce distances (see Chapter 1.4.1). As distance estimation is an integral part and a prerequisite for path integration, estimating distances could not only contribute to path integration (gathering information about distance and direction), but it could also help the seals efficiently commute in their natural environment.

1.4.1. Distance Estimation

The ability to estimate distances has been tested mostly on human subjects (Klatzky et al. 1990). In such studies, humans have proven that they can estimate distances to a previously viewed target location or the length of a path they have previously been led on. The researchers documented a high accuracy of reproduction with an error of 20–35% of the path length or slightly better (Klatzky et al. 1990, Bigel and Ellard 2000). Interestingly, the absolute error increased the longer the distance travelled (Lappe et al. 2007, Lappe et al. 2011, Lakshminarasimhan et al. 2018, Stangl et al. 2020). This increase in error when travelling larger distances might be explained by the organism accumulating more and more data about the path or route the longer it travels. The error either accumulates due to noise stemming from the velocity input of the integration (Stangl et al. 2020), a bias in the estimation of self-motion speed (Lakshminarasimhan et al. 2018), or a leak occurs (Lappe et al. 2007, Lappe et al. 2011), depending on the model used for the calculation. Regardless of why larger distances were underestimated, it results in the animal stopping too early, which could be adaptive. It was speculated that a positional error could lead the animal into a familiar area in the vicinity of the goal (Etienne and Jeffery 2004). In the vicinity of the goal, other mechanisms of orientation, such as the previously mentioned landmarks, could then help to pinpoint the goal (see Chapter 1.3).

Researchers have discerned possible mechanisms on which distance estimation could be based: (1) timing (Kautzky and Thurley 2016); (2) double integration of linear acceleration (Israël and Berthoz 1989, Israël et al. 1993); (3) optic flow (Sun et al. 2004, Lappe et al. 2007); (4) energy consumption (Kooyman et al. 1973, Castellini et al. 1992, Ponganis et al. 1993, Sparling and Fedak 2004); (5) monitoring the output of a central pattern generator (Marder and Bucher 2001, Wehner 2020); or (6) proprioceptive cues measuring locomotor activity (Etienne and Jeffery 2004, Freas and Cheng 2022).

If distance estimation abilities were shown in harbour seals, distance estimation could potentially be based on these cues, too. Recent work on the timing abilities of seals has shown that harbour seals have a well-developed sense of time (Heinrich et al. 2016, Heinrich et al. 2020, Heinrich et al. 2022). This ability could be used to measure distance when swimming velocity is continuously taken into consideration. The harbour seal's ability to perceive optic flow (Gläser et al. 2014) could also allow the determination of distance travelled. Hereby, the idea that swimming past particles in the water column generates optic flow fields to be analysed in numerous behavioural contexts is appealing, as previously particles were considered to only be detrimental to vision. Seals could also measure their energy consumption while travelling. One way to measure the energy consumed would be to determine the metabolic rate (Kooyman et al. 1973, Castellini et al. 1992, Ponganis et al. 1993, Sparling and Fedak 2004). In the species tested, the metabolic rate decreased more slowly with slower swimming speeds and extended dive durations. Since it is speculated that the seals keep track of their metabolic rates in order to determine when to breathe, the depletion of the metabolic rate could be used for distance estimation as well, as longer distances covered by the seal would result in low oxygen stores (Castellini et al. 1992). Pinnipeds could also keep track of distances travelled by using information from locomotion such as the number of strokes, which can be considered an oscillator (Cheng 2022, Freas and Cheng 2022). If this were the mechanism, the more oscillating movements performed, the larger the distance covered would be. To conclude, a multitude of mechanisms may allow seals to estimate distances.

Distance estimation itself (not its underlying mechanisms) has been investigated using various experimental paradigms. Some experiments required the subjects to actively walk up to a goal (see Corlett et al., 1985; Elliot, 1986; Loomis et al. 1993; or Bigel and Ellard, 2000). Other experiments included passive locomotion in reality or virtual reality (Israel et al. 1993, Georges-François et al. 1995, Israël et al. 1997, Lappe et al. 2011, Keil et al. 2021). Here, the subjects were, for example, passively transported on a sledge (Israël et al. 1997) or sat in front of a computer and used a joystick to move inside a virtual reality environment (Keil et al. 2021). The task the subjects had to fulfil during the experiments, irrespective of whether they were actively or passively moving, was mostly a production task, requiring the subjects to, for example, walk a specific distance, or a reproduction task, requiring the subjects to reproduce a previously experienced distance (Loomis et al. 1993). In visual distance estimation experiments, the subjects were usually presented with an object at a specific distance (Bigel and Ellard 2000). Subsequently, the goal vanished, and the subjects had to move themselves actively or passively to where they anticipated the goal to be.

In numerous further experiments, the information the subjects could use during the task varied. For instance, blindfolding the subjects inhibited the use of visual information, such as landmarks or optic flow (Frenz et al. 2003, Frenz and Lappe 2005), while asking the participant to repeatedly say a specific word inhibited step-counting. Even the role of neurological structures, such as the labyrinth in distance estimation has been tested (Glasauer et al. 1994). Thus, using a production or reproduction approach allows an analysis of the general ability of distance estimation and enables the researchers to examine the effect of different conditions on performance.

I conducted an experiment in which a seal had to estimate and finally reproduce a distance to address the seal's distance estimation abilities with respect to numerous specific research questions.

1.4.2. Experiment 3: Are we there yet? Distance Estimation in a Harbour Seal

In this experiment (Maaß, E., and Hanke, F. D. (2021), "*Distance Estimation in Reproduction Tasks in a Harbour Seal (Phoca vitulina)*," Water 13.7: 938), I examined whether harbour seals can generally estimate and reproduce distances. With a well-functioning distance estimation ability, seals could prevent errors in orientation and conserve energy over the course of their journeys.

I asked the seal to perform a distance reproduction task along a belt system that floated atop the water surface. The belt served as a measuring tape. Two target balls were attached to the belt and mounted at predetermined, but changing locations and were separated by the distance, which had to be reproduced by the experimental subject. In a single trial, the animal started from a hoop station and swam towards the first target, indicating the start of the standard distance interval. After touching the first target, the seal swam towards the second target ball, indicating the end of the standard distance interval and the beginning of the reproduction interval. After touching the second ball, the seal then had to reproduce the standard distance by swimming further along the belt. Ultimately, the seal stopped, where it assumed it had reproduced the previously covered distance. An observer evaluated the distance swum by the seal and communicated this distance swum to the experimenter, allowing for differential reinforcement depending on the precision of reproduction. In contrast to the experiments mentioned in Chapter 1.4.1, I did not allow the seal to swim back to the origin of the path. Instead, I let the animal swim further. This procedure prevented the use of secondary cues from the starting point, which might have allowed solving the task. I also varied the distances to be estimated as well as the starting position of the reproduction alongside the belt to avoid the use of secondary external cues from the facility for solving the task. During training, the seal achieved a precision with an (absolute) error of 12 to 31% when reproducing distances from 1 m to 11 m. This precision is comparable to the precision of humans in similar tasks (Ellard et al. 1984, Bigel and Ellard 2000). In a concluding control session with interspersed unknown distances, the absolute error of distance reproduction was 39%, yet smaller for distances over 10 m. Interestingly, the seals demonstrated a specific motion pattern for specific distances that were to be estimated, thus nurturing speculations about motoric cues as mechanisms for distance estimation (see Chapter 1.4.1).

In a subsequent test, the maximum precision the seal could reach after repeatedly swimming and estimating single distances was determined. In the wild, seals often frequent specific haul-out places and specific foraging grounds (Vance et al. 2021, Iorio-Merlo et al. 2022). Repeatedly swimming a distance could positively influence the ability to estimate distances, meaning accuracy could be higher, which was assessed in this part of the experiment. Using the staircase method, the tolerance range within which the seal had to reproduce the distance to obtain a reward was decreased, whenever the seal could reproduce the distance well inside the previous tolerance range. The seal here demonstrated a minimal absolute error of 6.4% after extensive training. This result implies that with experience of a path and the distance covered en route, a harbour seal is highly accurate in distance estimation.

In the last part of the experiment, I evaluated the influence of the visual system on the seals' precision during distance estimation. Therefore, in this final part of the experiment, trials were interspersed with the animal being blindfolded with a stocking mask. Thus, the animal could not rely on visual cues for distance estimation. The results showed that trials in which the seals swam without visual input were performed with similar precision as trials with visual input. This finding suggests that the presence of visual information might be helpful for distance estimation, but in the absence of visual cues, the seal is still able to estimate distances. Seals can thus use distance estimation even under environmental conditions that inhibit the use of visual information, such as at depth or at night. This study revealed the general distance estimation and reproduction abilities of harbour seals. These abilities are informative in the context of path integration, or generally, for navigating towards a goal.

1.5. In the Distance…

The experiments in this dissertation project demonstrated the fundamental abilities of harbour seals that might play a role in the context of navigation and orientation. For both abilities – goal localisation with the help of landmarks as well as distance estimation – the present thesis can serve as a cornerstone for further research in the field of orientation and navigation.

In the context of path integration, it would be interesting to investigate how directional information is processed by the seal and which type of input is needed to determine and keep a direction in addition to keeping track of distances covered. Keeping a course is an interesting question in marine mammals per se, as marine mammals have been shown to keep courses over long distances (Horton et al. 2011, Chevaillier et al. 2014). Analysing veering, even, for example, in the absence of visual cues, might thus reveal astonishing precision in marine mammals. In humans, it has been shown that without visual input, the straightness of the pathways decreased with distance and ultimately led humans to walk in loops (Souman et al. 2009). One simple approach to testing whether and how well a seal can steer a straight course would be to blindfold the animal while swimming towards a previously seen target location. Recording the movement from above would allow the analysis of whether or by how much the seals would veer. The results of such an experiment could ultimately fulfil the second prerequisite for path integration (see Chapter 1.4).

As a logical consequence and the culmination of experiments on distance estimation and the use of directional information, path integration itself should be tested directly. The path integration experiment could be performed as an open-field experiment, allowing the testing of path integration under natural conditions without spatial limitations. Hereby, the experimental paradigm could be a triangle-completion experiment (for a review, see Etienne and Jeffery 2004). Using triangle completion, the animal would swim two legs of a triangle and, upon hearing a signal, would have to head back to the unmarked starting point. If the seals are able to perform path integration, it would be interesting to compare the seal's performance with the performance of other organisms that have already been tested in path integration experiments. To give an example, in previous path integration experiments, the experimental subjects made systematic errors, as already mentioned (see Chapter 1.4.1). Ultimately, I would assume seals to be able to perform path integration with high precision even when tested under conditions in which sensory cue availability is reduced, as a seal might regularly encounter these conditions and thus be particularly adapted to them.

In the context of landmark orientation and navigation, the seals' preference for specific landmarks could be examined. Similar to our findings, pigeons seem to include only a subset of landmarks in order to find the goal location (Spetch and Mondloch 1993). In the case of pigeons, the experimenters presented visually distinct landmarks to the birds and removed or shifted the landmarks in probe trials. The results show that the landmark that controlled the search behaviour of the pigeons varied from individual to individual (Spetch and Mondloch 1993). With two landmarks present, one close to the goal and another further away, pigeons preferred to shift their search behaviour to the direction of the closer landmark, when both landmarks were moved further away, as did other birds (Cheng 1989, Bennett 1993). Analysing which landmark from a subset controls the search behaviour could thus help explain how seals process the information of landmarks in general and what specifics of a landmark can or cannot contribute towards navigation or orientation.

Landmarks are considered components of cognitive maps. Our experiments on relational landmark use in harbour seals demonstrated that one seal found the midpoint between two landmarks regardless of his familiarity with specific landmark arrays. Some authors hold the ability to represent geometric relations between oneself and other objects in the environment as an essential component of a cognitive map (Kamil and Jones 1997). A cognitive map is a spatial representation of the suspect and its surroundings in relation to the goal and its surroundings (Gallistel and Cramer 1996). An important criterion for the use of a cognitive map is that subjects can find short cuts and travel novel routes between themselves and their destination or goal (Tolman 1948). According to Kitchin (1994), using a cognitive map can influence spatial behaviour, making decisions, wayfinding and orientation, and ultimately might explain some behaviours of animals in the wild. A first study on northern elephant seals (*Mirounga angustirostris*) already indicated the presence of a map in a pinniped species (Beltran et al. 2022). Outside the breeding season, seals are scattered over the Pacific Ocean and travel to places that are often ten thousand kilometres away from the coastline. However, regardless of how far each individual is away from the breeding location, they finally gather at specific beaches right on time to give birth. Tagging the female elephant seals revealed that individuals farthest away start their inward trip earlier than closer females. This behaviour was interpreted as an inertial "map-sense". To gather evidence for a cognitive map underlying the behaviour of harbour seals, who, unlike elephant seals, do not always congregate at the same natal beaches and do not scatter as much as elephant seals, an alternative approach in line with studies including bats could be appropriate (Fenton 2020, Harten et al. 2020, Toledo et al. 2020). New-born animals could be tagged, and their tracks could be analysed. The way in which the pups form relationships between different locations, such as goals, and whether they find shortcuts between the localities could then be examined. If novel shortcuts were documented, the results could then provide initial evidence of the use of cognitive mapping in harbour seals.

Goal localisation with the help of landmarks and distance estimation have been examined separately in this thesis, which is certainly not the case when considering animals in the wild. Here, both mechanisms complement each other. Out in the open ocean, before the coastline or other useful landmarks come into sight, keeping track of the distances covered while swimming helps the seal swim to familiar areas. Within familiar areas, known landmarks can then be used to pinpoint the goal. Distance estimation and path integration are error-prone, as error increases with path length, as does the tendency to deviate from the path (Lappe et al. 2007, Souman et al. 2009, Lappe et al. 2011). However, landmarks nullify accumulated errors and consequently enhance distance estimation and path integration (Etienne 2004). This way, both mechanisms, each enabling the seal to navigate and orientate itself safely in its environment, complement and reinforce each other. In general, complex behaviour is based on numerous mechanisms that enable harbour seals to navigate in their natural environment and find their way "there and back again".

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2. Publications of this Dissertation

2.1. Declaration of the Author Contributions

This thesis is based on three publications involving co-authors. On the following page, I will outline my contribution, and the contributions of the co–authors to the studies, and the resulting publications according to the author contribution sections included in the publications.

Maaß, E., & Hanke, F. D. (2021). Distance estimation in reproduction tasks in a harbor seal (*Phoca vitulina*). *Water*, *13*(7), 938.

Conceptualization, E.M. and F.D.H.; methodology, E.M. and F.D.H.; formal analysis, E.M.; investigation, E.M.; writing—original draft preparation, E.M.; writing—review and editing, E.M. and F.D.H.; visualization, E.M.; supervision, F.D.H.; project administration, E.M.; funding acquisition, E.M. and F.D.H.

Maaß, E., & Hanke, F. D. (2022). How harbour seals (*Phoca vitulina*) encode goals relative to landmarks. Journal of Experimental Biology, 225(5), jeb243870.

Conceptualization, E.M. and F.D.H.; methodology, E.M.; validation, E.M.; formal analysis, E.M.; investigation, E.M.; resources, E.M. and F.D.H.; data curation, E.M.; writing - original draft, E.M.; writing - review and editing, E.M. and F.D.H.; visualization, E.M.; supervision, F.D.H.; project administration, F.D.H.; funding acquisition, E.M. and F.D.H.

Maaß, E., Miersch, L., Pfuhl, G., & Hanke, F. D. (2022). A harbour seal (*Phoca vitulina*) can learn geometrical relationships between landmarks. Journal of Experimental Biology, 225(24), jeb244544.

Conceptualization, E.M. and F.D.H.; methodology, E.M., L.M. and F.D.H.; software: E.M. and L.M.; validation, E.M.; formal analysis, E.M. and G.P.; investigation, E.M.; resources, E.M. and F.D.H.; data curation, E.M.; writing - original draft, E.M.; writing - review and editing, E.M.[1], L.M., G.P., F.D.H.; visualization, E.M.; supervision, F.D.H.; project administration, E.M.; funding acquisition, E.M. and F.D.H.

[1] correction to author contribution of publication: EM had mistakenly not been listed for this category but was strongly involved in reviewing/editing as for the other publications.

2.2. Distance estimation in reproduction tasks in a harbor seal (*Phoca vitulina*)

Maaß, E., & Hanke, F. D. (2021). *Water*, *13*(7), 938.

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Article

Distance Estimation in Reproduction Tasks in a Harbor Seal (*Phoca vitulina*)

Eric Maaß and Frederike D. Hanke *

Institute for Biosciences, Neuroethology, University of Rostock, Albert-Einstein-Str.3, 18059 Rostock, Germany; eric.maass@uni-rostock.de
* Correspondence: frederike.hanke@uni-rostock.de; Tel.: +49-381-666971914

Abstract: Harbor seals commute between haul-out places and feeding grounds close to the shore or in the open ocean, which is considered a low structured environment, at first sight not providing many cues for orientation/navigation. Nevertheless, seals are well-oriented. For returning to a specific location, seals may use both external and internal cues to, for example, perform path integration requiring the integration of distances traveled and angles steered. We herein assessed the seal's ability to estimate distances, previously swum or unknown, in reproduction tasks. Reproduction tasks refer to an experimental paradigm in which the experimental animal is required to swim a specific distance first and subsequently reproduce this distance, with visual cues present or absent. The seal was able to estimate and then reproduce distances (0.5–18.5 m) with the smallest error below 10% of the actual distance, and its precision was higher with distances repeatedly swum compared to its performance with unfamiliar distances. In the absence of visual cues, the seal's performance slightly dropped; however, it was still able to perform the task with an error of 21%. In conclusion, distance estimation may help seals to navigate precisely towards their goals, even if, for example, visual information is not available.

Keywords: pinnipeds; navigation; spatial orientation; distance estimation; distance reproduction

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1. Introduction

The open ocean, in contrast to the coastline or continental shelves, is considered a low-structured habitat. Nevertheless, marine mammals, such as cetaceans and pinnipeds, often travel through the open ocean searching for places where they can forage, rest or reproduce [1–4]. Some marine mammals even return to specific haul-out or birthplaces consistently. Moreover, on their journeys, some species are even able to steer straight courses. Research on humpback whales has revealed the animals' ability to keep a constant course with an accuracy of less than one degree over hundreds of kilometers traveled over many days [1]. Furthermore, pinnipeds, such as elephant seals, can keep a straight course even when submerged, most likely based on visual information obtained at the water surface; the envisaged direction is even maintained after a spiraling descend [5]. Thus, there is evidence that marine mammals are well oriented in their natural environment.

Seeing how well these animals are navigating, the question emerged which sensory information the seals and other marine mammals use for orientation and navigation. Theoretical speculation sprouted over the use of stars or the Earth's magnetic field [6–8]; while the first is based on good preliminary experimental evidence [9,10], magnetoreception has not been documented for seals [11]. In general, previous experiments regarding orientation and navigation in seals almost exclusively focused on cues perceived by the classic sensory systems, such as visual, auditory, chemoreceptive or hydrodynamic cues [12–14]. However, in the marine environment, these cues can be impaired or absent due to environmental factors, such as turbidity [15], bad weather conditions or anthropogenic activities. Under these conditions, a seal could rely on navigation/orientation mechanisms that can be solely based on idiothetic cues, defined as cues derived from self-motion, such as path integration [16–18]. Fundamental to path integration is keeping track of distances covered, and directions steered on the outbound path. This information is then integrated into a homing vector, which leads the organism back to its starting point, for example, its haul-out place. The ability to integrate paths has already been shown in many terrestrial and some semi-terrestrial species [17,19–25]. We consider path integration to be a navigation mechanism very promising to look at in marine mammals in line with Fuiman et al. [26].

In this study, we analyzed if a harbor seal (*Phoca vitulina*) can estimate and reproduce distances in distance reproduction tasks. In a reproduction task, the experimental animal needs to swim a specific, predetermined distance. Afterwards, the animal must continue swimming until it subjectively decides it has reproduced this distance, meaning it has swum the distance another time. The estimation of distances is interesting regarding path integration, but it might also play a role in path return or might generally assist navigation in seals. Distance information can be derived from self-motion cues or cues derived from the classic sensory systems, most notably the visual system [18,27]. Most of our knowledge on distance estimation stems from human subjects. These experiments were often analyzing the influence of the visual system on distance estimation. In these experiments on non-visual distance estimation and reproduction, researchers documented a high accuracy of reproduction with an absolute error of 20–35% of the path length [27] or slightly better. While the subjects veered noticeably, the distances were accurately reproduced. Thus, distance estimation is possible in the absence of vision. In Klatzky et al. [27], the mechanism used by the blindfolded subjects was not determined. However, since then, experiments, including normal and labyrinthine-defective human subjects, have shown that locomotor information and especially the vestibular system, can play a major role during distance estimation [28–30].

Possible mechanisms for distance estimation were also investigated in various animals. Honeybees rely on optic flow [31–35], whereas desert ants gauge distances additionally through a pedometer [36–39]. In mammals other than humans, experiments on distance estimation itself are scarce and, to our knowledge, have only been addressed in rodents, for example, in hamsters in a homing task on the basis of non-visual cues [18,40].

In the study at hand, we investigated distance estimation in a (semi)aquatic animal, the harbor seal. The distance reproduction task (experiment 1) involved a preset distance interval of 0.5–18.5 m length, which the subject had to reproduce subsequently by keeping the same swimming direction. A follow-up experiment (experiment 2) focused on the maximum precision the seal can achieve during a distance reproduction task. Finally (experiment 3), the influence of the visual system on distance reproduction was determined by comparing the seal's performance with and without a blindfold. We discuss our findings in the context of orientation/navigation of seals.

2. Materials and Methods

2.1. Experimental Animal

The experiment was conducted with an adult male, captive-born harbor seal (*Phoca vitulina*) named "Nick" (16 years old at the beginning of the experiments) at the Marine Science Center of the University of Rostock in Warnemünde/Hohe Düne, Germany. The seal had previously participated in many scientific experiments (see, for example, [12,41,42]). Nick was housed with eight other harbor seals, two juvenile California sea lions (*Zalophus californianus*), and an adult South African fur seal (*Arctocephalus pusillus 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 animal received 1–5 kg of fish a day, depending on season and motivation. We performed experiments five days a week.

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2.2. General Experimental Setup

The experimental setup consisted of a belt-system stretched over 43 m (Figure 1). This was the maximum distance that could be covered within the largest enclosure of the Marine Science Center. The belt was painted in intervals of 10 cm using water-resistant paint to be able to use the belt as measuring tape. Although the belt was clamped, the units on the belt and on a calibrated measurement tape only deviated by ±1%.

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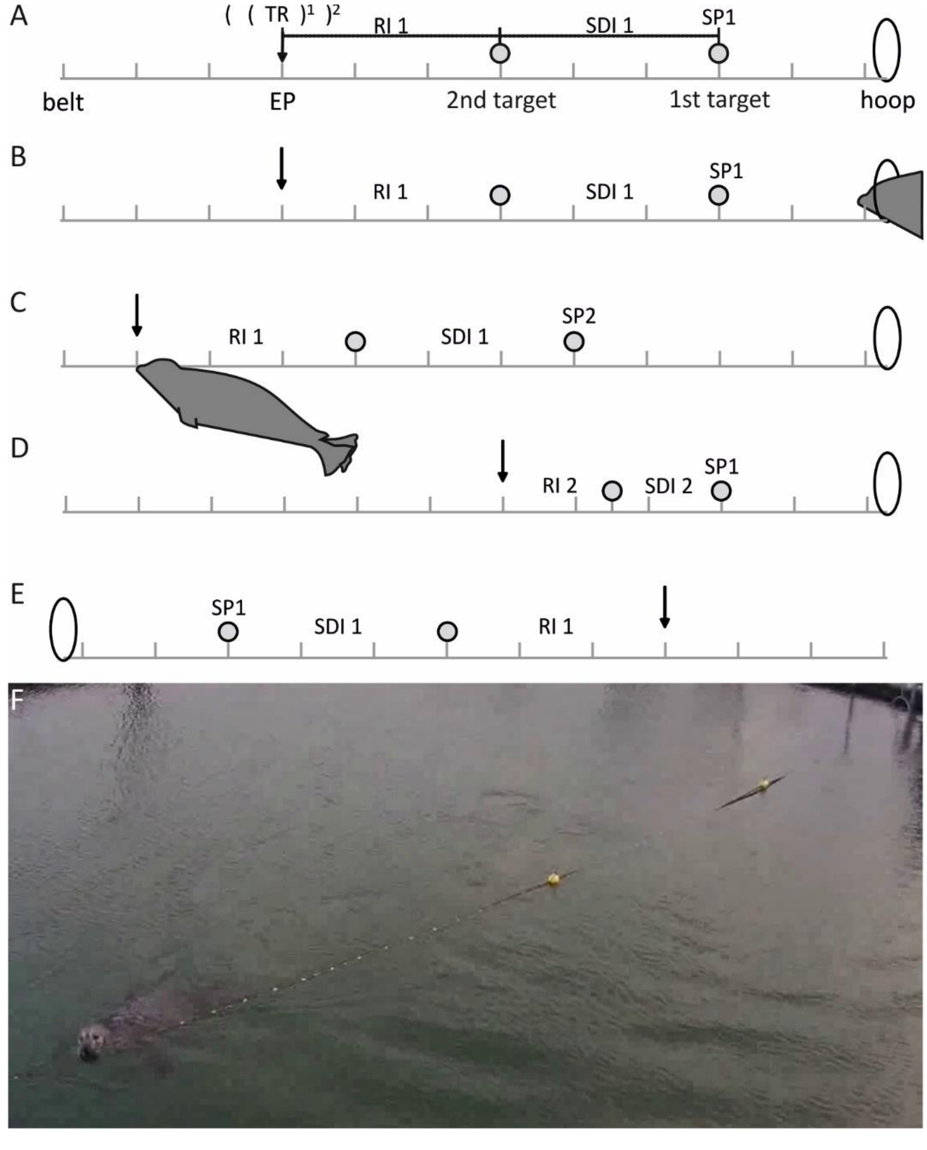

Figure 1. Experimental setup and procedure. (**A**) The basic components of the setup along a belt system are displayed, including a hoop station, in which the seal rested in between trials and two target-balls, the starting point (SP), the standard distance interval (SDI), and the reproduction interval (RI). For differential rewarding, we introduced two tolerance ranges, TR1 and TR2 (see text for explanation). (**B**) The seal started every trial from its hoop station and passed two target-balls marking the SDI along the belt system. It then had to reproduce the distance presented in the SDI in the RI. The seal was indicating the end of the RI by stationing at the belt; this point is defined as the seal's endpoint (EP; black arrow). (**B**,**C**) Throughout the experiment, the SP was varied along the belt and/or (**D**) the distance within the SDI was varied. (**E**) After the testing phases in stages 1 to 4 of experiment 1, we conducted a control session in which the animal had to perform the task in the opposite swimming direction. (**F**) Image of the camera recording the experimental trials. The seal has passed the two target balls, has reproduced the distance presented in the SDI (here: a 3 m distance was presented) and now indicates its decision by resting at the belt.

Figure 1. Experimental setup and procedure. (A) The basic components of the setup along a belt system are displayed, including a hoop station, in which the seal rested in between trials and two target-balls, the starting point (SP), the standard distance interval (SDI), and the reproduction interval (RI). For differential rewarding, we introduced two tolerance ranges, TR1 and TR2 (see text for explanation). (B) The seal started every trial from its hoop station and passed two target-balls, marking the SDI along the belt system. It then had to reproduce the distance presented in the

Two balls were clipped onto the belt that served as the starting point (SP) and endpoint (EP) of the sample distance interval (SDI, see Figure 1). The SP was defined as the distance from the hoop station, in which the seal was resting during the inter-trial interval, to the first target ball. The second target ball also indicated the start of the reproduction interval (RI). Both target balls could be shifted in position along the belt (Figure 1) according to a preset schedule (Table 1). This way, the SDI could be presented at different positions in space defined by the SP. The variation of the position of the SDI and RI along the belt achieved by the variation of the SPs served to minimize the possibility that the seal was learning EPs defined absolutely in space to solve the task instead of estimating/reproducing the distance in the SDI. For the control session, the belt system was clamped from the other side of the enclosure (Figure 1E).

Table 1. Overview of the pretraining (P) and the experimental stages 1–5 of experiment 1. Indicated are the distances presented in the standard distance interval (SDIs in m) from the respective starting points (SPs in m from the hoop station) and the number of trials conducted during the acquisition phase and during the testing phase, as well as the respective tolerance ranges (TR1 and TR2) for the different distances.

		Tolerance Range		Acquisition Phase		Testing Phase	
Stage	**SDI (m)**	**TR1 (m)**	**TR2 (m)**	**SP (m)**	**Number of Trials**	**SP (m)**	**Number of Trials**
P	5	±0.5	±1	1	280		
1	10	±0.5	±1	3	516 [1]		
	5	±0.5	±1	3, 6	444	4, 6, 8, 10, 12, 14	150
2	3	±0.3	±1.0	2, 4, 8	859	4, 6, 8, 10, 12, 14	300
	7	±0.7	±1.5		864		
	(12) [2]	±1.2	±2.4		177		
3	1	±0.1	±0.2	2, 4, 8	643	4, 6, 8, 10, 12, 14	300
	11	±1.1	±2.2				
4	1, 3, 7, 11	see above [3]	see above [3]	2, 4, 8	1646	4, 6, 8, 10, 12, 14	600
5	various [4]	±10%	±20%			various [4]	29

[1] In stage 1, the seal started with an SDI of 10 m, which the seal, however, did not learn to reproduce in 516 trials. Thus, the SDI was changed to 5 m. [2] Stage 2 was initially started with three SDIs. The seal did not reach the learning criterion in 531 trials with the 12 m distance included. Thus, we excluded the 12 m distance and proceeded with only two distances, 3 m and 7 m.[3] The tolerance ranges for the SDIs of stage 4 were chosen as during the previous experimental stages, in which the respective SDI had already been tested. [4] In stage 5, 29 different SPs and distances were presented to the animal. Each combination occurred only once (see Appendix A).

2.3. General Experimental Procedure

Each trial began with the experimenter asking the animal to station in the hoop station (Figure 1). Then the experimenter positioned the target balls and thus laid out the SP/SDI combination of the respective trial with the help of an observer. The observer was situated at an elevated position, from which she/he could oversee the whole experiment.

On verbal command by the experimenter, the seal left the hoop station and started to move alongside the belt to the SP. The seal then proceeded to the second target ball at the end of the SDI. It was then required to reproduce the distance presented in the SDI by swimming further along the belt. A trial ended when the seal stationed at the belt.

The accuracy of reproduction was determined by the observer and was communicated to the experimenter, who could then reward the animal according to its performance. When reading the belt during the experiment, the error of the observer was determined as ±2%. Exact reproduction, meaning that SDI and RI were equal in distance, led to a reward of five pieces of fish. For the purpose of differential rewarding, we introduced two tolerance ranges (TRs; Table 1). Reproduction within the predefined first tolerance range (TR1) led to a reward of three pieces of fish. If the animal reproduced the distance within the predefined second tolerance range (TR2), it received a reward of one piece of fish. In stage 1, the TR1 was set to 1 m, approximately half the body length of the animal, and the TR2 was 10% of the distance (50 cm). In the following experimental stages (stage 2–5), we chose relative percentile TRs (Table 1). The values we picked for both TRs were set in line with values from the literature [27,43]. No reward was given if the seal stopped outside the respective TRs.

The observer filmed the trials with a camera (Rollei Actioncamera 7S Wi-Fi, Hamburg, Germany) for further offline analysis of the animal's movements and behavior.

2.4. Experiment 1

Experiment 1 was divided into five experimental stages. Stages 1–4 of the experiment were subdivided into a phase of acquisition, in which the seal was familiarized with (a) distance(s), a phase of testing, in which the precision of the seal was determined with familiar and unfamiliar SPs, and a control session, in which the experimental procedure was performed in reversed swimming direction. Stage 5 consisted of a phase of testing only.

In the acquisition phase, the seal had to reproduce the distance(s) from various preset SPs. The sessions were composed of 24–36 trials in which we presented distance/SP combinations following a pseudorandom schedule [44].

The acquisition phase was considered to be finished once the animal achieved the learning criterion. To reach the learning criterion, the seal's average precision of reproduction had to fall within TR1 (criterion 1). In addition, the standard deviation had to be smaller than 1 m (criterion 2). These criteria need to be met in two consecutive sessions for the acquisition phase to be completed and for the phase of testing to begin. When the seal had reached the learning criterion, its average precision of reproduction during the session was determined.

During the testing phase, the number of SPs was increased, further avoiding that the animal relied its responses on memorized absolute EPs. The general experimental procedure remained as in the acquisition phase. Each session consisted of 18 to 36 trials, and each distance was tested 25 times from each SP, totaling up to 150 trials per distance.

After each testing phase, except for phase 5, a control session was run. During this control session, the seal performed the experiment from the opposite side of the enclosure. Thus, the animal was in a familiar environment but experienced a new setting/panorama that it had never reproduced the distances from and consequently could not have gathered experience with in the first trial. In the control session, the distance(s) presented and the SPs, as well as the general experimental procedure, were the same as in the respective testing phase (Table 1).

2.4.1. Pretraining

During pretraining (P; Table 1), the seal was familiarized with the reproduction task. It was taught to swim towards the target balls with a 5 m distance presented in the SDI. After passing the second target ball, it had to proceed to a third target ball positioned 5 m away from the second target ball, marking the end of the RI. In one session, 10–23 trials were run. After a total of 280 trials, in which the seal learned this procedure, the third target ball was removed, and stage 1 could be started.

2.4.2. Stage 1

The acquisition phase of stage 1 was started with a 10 m distance presented from an SP at 3 m (Table 1). In each session, 30 trials were conducted. The TR1 was chosen as ±0.5 m. In addition, the TR2 was set at ±1 m from the exact distance of 10 m. In the acquisition phase, the seal did not show any signs of learning for the 10 m distance. We then chose to switch to the 5 m distance the animal had experienced during pretraining in an attempt to facilitate learning; the TRs remained as described. With this distance, we could complete the acquisition phase.

In each session during the testing phase, the seal was asked to reproduce the 5 m distance from six SPs, out of which the seal had only experienced the 3 m-SP previously (Table 1).

Additionally, the seal was asked to reproduce the 5 m distance from these six SPs, however, with reversed swimming direction in a control session consisting of 30 trials.

2.4.3. Stage 2

To test whether the seal could discriminate between distances, the distances 3 m, 7 m, and 12 m were presented during stage 2 of experiment 1. During the acquisition phase of stage 2, the distances were presented from three different SPs (Table 1). The TR1 was set at ±10% of the distance; the TR2 was defined as ±1 m for the 3 m distance, ±1.5 m for the 7 m distance and ±2.4 m for the 12 m distance. In the acquisition phase, the seal easily learned to reproduce the 3 m and 7 m distance but had difficulties in learning to reproduce the 12 m distance. Consequently, we excluded the 12 m distance enabling us to proceed with training.

Once the learning criterion (see stage 1) was fulfilled, the number of SPs was increased to six SPs for the testing phase; four of these SPs were new to the seal.

2.4.4. Stage 3

In the third stage, the question was addressed whether the seal was capable of estimating and reproducing particularly small and long distances. Therefore, the distances of 1 m and 11 m were chosen (Table 1). The TRs in this session were set to ±10% and ±20% of the respective distance. SPs, learning criteria, and testing procedure were the same as in the previous stages.

2.4.5. Stage 4

In stage 4, the seal's ability to reproduce four of the distances (1 m, 3 m, 7 m, 11 m) presented in stages 2 and 3 within one session was assessed. Together with three SPs, 12 different distance/SP-combinations were trained in the acquisition phase. Each combination was tested twice in a session of 24 trials until reaching the learning criterion. During the testing phase, the distances needed to be reproduced from four new and two old SPs as in the previous phases. The TRs in this session were set as in stage 3. Each distance/SP combination was tested once in 24 trials-sessions.

2.4.6. Stage 5

In stage 5 of the experiment, the seal was confronted with one session, in which a new distance was presented in every trial. Moreover, these unknown distances were presented from unknown SPs. Altogether 29 unfamiliar combinations of distances and SPs (see Appendix A) were tested. Here, TRs were set as in stage 3 (Table 1).

2.4.7. Data Analysis

To assess the precision of the animal during the session, we analyzed medium averages of signed and absolute error with Excel 2016 (Microsoft Corporation, Redmond, Washington WA, USA) in line with the analysis of Bigel and Ellard [45]. Additionally, we used IBM SPSS (v.26; International Business Machines Corporation Armonk, New York, NY, USA) for the analysis of variances.

Saliences in the performance in both swimming directions were also studied. In a first-trial-analysis, we compared the performance during the first trials during the control session swum for each distance and SP in reversed swimming direction with the average performance of the animal in the testing phase. This analysis was informative regarding the influence of memorized EPs on the performance in the previous stages of the experiment. The learning of EPs could have influenced the performance of the animal during the testing and acquisition phases, although we drastically reduced this possibility by varying the intervals along the belt, but could not influence its performance in the first trial in reversed swimming direction, as the animal had no previous memory of the EP.

All videos made during data collection by the observer were analyzed with Avidemux (v.2.6; http://fixounet.free.fr/avidemux/ (accessed on 15 May 2017)). We analyzed the swimming speed in the RI by calculating the time elapsing between the animal leaving the second target ball and the animal stopping at the belt at its chosen EP. Since it was not always unambiguous at which frame the seal touched the second target ball or stopped at the belt, we calculated the resulting error in swimming speed, which amounted to ±2%.

In stage 4, with four distances presented, we investigated if the seal used specific motion patterns for reproducing a specific distance. We chose to investigate the movement patterns in stage 4 only since this was the sole stage in which the animal experienced more than two distances over a longer period. After reviewing the videos, we could classify the movements of the seals in every single trial and analyzed how often a specific movement pattern occurred during the reproduction of a specific distance. We performed a Chi^2 test to test if the seal performed better if it moved with a specific motion pattern.

The ethogram consisted of the following movement patterns:

1. "touch–dive–drift"—the animal casually strived the second target ball, performed a flap with its fin and began diving. After diving, the seal surfaced, drifted, and then stopped;
2. "touch–dive–stop"—the animal quickly touched the second target ball with full snout contact and started a dive. After resurfacing, it immediately stopped;
3. "touch–drift"—the animal touched the second target ball with full snout contact and started gliding. During gliding, it performed a turn until it stopped;
4. "touch–stop"—after touching the second target ball, the seal swam continuously at the water surface until stopping entirely;
5. "other"—the seal showed a movement pattern different from points 1–4.

2.5. Experiment 2

In experiment 1, predefined TRs mostly adapted from the literature were used to train the animal. In experiment 2, we wanted to test the precision of reproduction the seal can maximally achieve. Therefore, the seal was trained to reproduce a new distance, which was kept constant during the experiment. It was presented from 24 SPs in a 24 trials-session; these 24 SPs were used throughout experiment 2 in randomized order.

Training started with a preset TR. After reaching the learning criterion, defined as a performance with an absolute error of $\leq$20% achieved in two consecutive sessions, the TR was reduced by 2.5% (9 m distance) or 5% (2 m and 13 m distance). This way, the TR was continuously reduced until the seal was unable to reach the learning criterion within 5–10 sessions. We finally decided to run only five sessions as the seal's performance did not increase over ten sessions; thus, no learning seemed to have taken place neither over five sessions nor over ten sessions. The maximum precision of reproduction was determined for three distances in the following order: 9 m, 2 m, and 13 m.

We used IBM SPSS for the statistical analysis of the data.

2.6. Experiment 3

In experiment 3, the influence of the visual system on the performance of the animal was determined. Hereby, the general procedure was as in the previous experiments. However, now every session included baseline and masked trials. In the baseline trials, the seal was presented with a 4 m distance, which had never been presented to the animal before, from four different SPs: 3 m, 4 m, 5 m, and 6 m. In each session, the distance was presented six times from each SP. Thus, a session included 24 baseline trials.

Within all sessions, masked trials were interspersed in which the seal had to complete the task with a blindfold, a latex mask over its eyes. The animal was highly experienced wearing masks and thus easily adapted to perform the task with a blindfold. With the interspersed masked trials, we could evaluate and compare the precision of reproduction in the baseline trials, in which the seal could rely on all available cues, and the masked trials, in which vision was occluded.

At the beginning of training for experiment 3, the number of masked trials was increased within three sessions from four to the maximum number of eight masked trials within a session. Training continued until the learning criterion was met. The learning criterion was defined as the seal reproducing all baseline trials with an absolute error of

≤20% in two consecutive sessions. Thereafter, testing started in which the number of SPs was increased to six: 2 m, 3 m, 4 m, 5 m, 7 m, and 8 m. During testing, seven sessions were conducted with 18–24 trials. This cumulated in a total of 162 trials, including 108 baseline trials and 54 masked trials.

The performance of the animal was analyzed as in the previous experiment with IBM SPSS. Additionally, we also compared masked and unmasked trials in terms of precision of reproduction.

3. Results

3.1. Experiment 1

3.1.1. Pretraining

The seal had no difficulties in learning the basic experimental procedure. The familiarization with the experimental setup and procedure, meaning that the animal left the hoop station on command, proceeded to the first and second target-ball and finally stopped alongside the belt, took 280 trials (Table 1).

3.1.2. Stage 1

In stage 1 of experiment 1, during the reproduction of a 10 m distance from an SP of 3 m, the seal did not reach the learning criterion within 571 trials (Table 1). Thus, a new distance, 5 m, from the 3 m SP was presented to the seal. After 554 trials of training with this combination, the number of SPs was increased to two. After an additional 60 trials with these two SPs, the seal completed the acquisition phase by reaching the learning criterion (Table 1).

During the testing phase, the seal reproduced the 5 m distance with an overall absolute error of 13.3% (n = 150). The overall signed error was −7%, indicating that the seal tended to undershoot the distance. We found a highly significant effect of the SPs on the accuracy of the seal's reproduction (Kruskal–Wallis test, $p < 0.001$). Hereby, the seal overshot the 5 m distance by +10.1% for the SP closest to the hoop station (4 m) and undershot the distances for all other SPs by −2.6% to −15.6% (Table 2).

Table 2. Overview of the absolute error (AE), the signed error (SE), and the performance in the first trial in opposite swimming direction in the control session (C). Described are medium averages (%) per SP [in m from hoop station]. Each distance for each SP was tested 25 times. The algebraic signs indicated an overshooting (+) or an undershooting (−) of the respective distance. The final column shows the reproduction of every first trial with each distance in the control session (C). Numbers written in italics indicate the first trials of the control session within which the reproduction was outside of both TRs.

Stage	Distance (m)	SP (m)																	
		4			6			8			10			12			14		
		AE (%)	SE (%)	C (m)	AE (%)	SE (%)	C (m)	AE (%)	SE (%)	C (m)	AE (%)	SE (%)	C (m)	AE (%)	SE (%)	C (m)	AE (%)	SE (%)	C (m)
1	5	11.4	+10.1	4.7	10.6	−2.6	6.0	9.9	−7.0	5.3	13.4	−12.2	4.8	14.8	−14.8	4.1	19.7	−15.5	4.0
2	3	13.5	+8.5	3.0	10.4	−1.3	2.5	10.9	+0.7	*3.8*	10.9	+2.8	2.5	15.3	+4.7	*2.6*	18.3	+7.4	2.5
	7	15.7	−5.6	6.6	14.2	+3.7	2.0	13.3	+5.2	7.3	20.7	−2.0	5.5	15.7	−7.7	*4.4*	12.7	−9.5	6.0
3	1	20.0	+11.2	1.2	16.4	−0.4	1.2	23.2	+8.0	1.0	23.2	+7.2	*0.7*	22.0	−1.2	*1.6*	26.8	+8.4	*1.5*
	11	11.3	+7.1	12.3	8.5	+2.4	10.8	10.1	−5.1	8.9	8.6	−4.4	10.2	16.5	−14.2	8.8	19.4	−19.0	9.6
4	1	12.0	−7.2	1.0	9.6	−3.2	0.8	23.2	+7.2	0.8	26.4	+5.6	0.8	43.6	+22.8	0.8	15.2	−10.4	0.8
	3	18.5	+5.2	2.7	15.2	+8.5	2.2	20.5	+8.3	*5.0*	34.0	+24.7	*4.5*	48.3	+28.3	*6.0*	48.4	+29.2	*7.0*
	7	21.8	−15.1	6.8	22.3	−11.2	5.6	22.0	−6.9	6.0	27.4	+3.7	8.4	26.9	+19.0	5.5	28.3	+25.6	6.8
	11	26.7	−18.4	*7.0*	13.1	−5.9	*6.0*	13.7	−9.5	*6.0*	12.1	−10.7	*7.0*	17.0	−17.0	*8.0*	14.8	−12.4	*5.8*

During the control session with changed swimming direction, the seal performed all 30 trials within the preset TR2 and some even within the TR1. Consequently, when analyzing the first trials, no significant difference between the performance of the seal in the testing phase and the first trial of the control session was found (Table 2).

The analysis of the swimming speed revealed that the seal was swimming with an average speed of 0.99 ± 0.03 m/s (n = 149) in the RI. When the seal swam at a different swimming speed, its performance decreased significantly (Kruskal–Wallis test; $p < 0.001$).

3.1.3. Stage 2

The acquisition phase of this stage took 1898 trials (Table 1). In the first 591 trials, we presented three distances to the animal. However, the seal showed no improvement for the reproduction of the 12 m distance and either stopped at approximately 3 m from close SPs or at approximately 7 m from far SPs. We thus decided to dismiss the 12 m distance and continued with the 3 m and the 7 m distance, with which the seal reached the learning criterion after 1307 trials.

In the testing phase, the seal reproduced the 3 m and 7 m distance with an overall absolute error of 13.2% regarding the 3 m distance and with an absolute error of 15.4% regarding the 7 m distance and an overall signed error of −2.7% and +3.8%, respectively (Table 2). Thus, the short distance was undershot; the longer distance was overshot (Mann–Whitney U test; $p < 0.05$). We did not find any correlation between the position of the SP and accuracy for any of the distances during the reproduction. This provides evidence that the reproduction was not influenced by the absolute position of the SDI and RI in space (Kruskal–Wallis test; $p > 0.001$). In line, changing the swimming direction during the control session had no pronounced effect on the performance of the animal, as most trials were performed inside the TRs, except for three distance/SP combinations: 3 m distance/8 m–SP, 3 m distance/2 m–SP, and 7 m distance/12 m–SP (Table 2).

The swimming speeds with which the animal swam during the RI were 0.56 ± 0.10 m/s (n = 162; 3 m distance) and 0.90 ± 0.20 m/s (n = 160; 7 m distance). As in the previous stage, a lower or higher swimming speed significantly decreased the accuracy (Kruskal–Wallis test; $p < 0.001$).

3.1.4. Stage 3

In stage 3 of experiment 1, the seal learned to reproduce the 1 m and 11 m distances within only 643 trials (Table 1). During data collection, the seal's reproduction accuracy for the 1 m and the 11 m distances was characterized by an absolute error of 21.9% and 12.4% and a signed error of +5.5% and −5.5%. In this stage, similar to the previous stages of experiment 1, a highly significant effect of the distance swum on the performance of the animal was found, as the distance of 11 m was reproduced with significantly higher precision than the distance of 1 m (Mann–Whitney U test; $p < 0.001$). The position of the SP affected the performance of the animal for the 11 m distance; when the seal had to reproduce the 11 m distance from an SP close to the hoop station, it often underestimated the distance (Kruskal–Wallis test; $p < 0.001$). Such a trend was not found for the 1 m distance (Kruskal–Wallis test; $p > 0.001$).

The results of the control session indicate that reversing the swimming direction had no significant effect on the performance of the animal (Table 2). Only 3 out of 12 first trials in opposite swimming directions were outside the TRs, one being only slightly, 10 cm, out of the TR2, and two overshooting the TR2 by 60 cm and 50 cm (Table 2). These three trials occurred when the seal reproduced the 1 m distance.

Swimming speed was determined as 0.52 ± 0.18 m/s (n = 159) for the 1 m distance and 0.90 ± 0.13 m/s (n = 159) for the 11 m distance. As in the previous stages, an alteration of the speed caused accuracy to decrease significantly regarding the 11 m distance (Kruskal–Wallis test; $p < 0.05$), but not regarding the 1 m distance (Kruskal–Wallis test; $p > 0.001$).

3.1.5. Stage 4

In stage 4 of experiment 1, the acquisition phase lasted 1646 trials (Table 1).

During the testing phase, the overall absolute errors for the 1 m, 3 m, 7 m, and 11 m distances were 21.7%, 30.8%, 24.8%, and 16.2%, respectively. The overall signed error for the 1 m, 3 m, 7 m, and 11 m distances were +2.5%, +17.4%, +2.5% and −12.3% (Table 2). These signed errors manifested in a significant influence of the distance on the performance of the animal, as it overshot all distances, except for the 11 m distance (Kruskal–Wallis test; $p < 0.001$). We also found a significant influence of the SP on the precision of the reproduction for the 3 m and 7 m distance (Kruskal–Wallis test; $p < 0.05$). When reproducing these distances from an SP close to the hoop station, the seal's precision was higher than when the animal had to reproduce the distances from SPs beyond 8 m.

Focusing on the performance of the seal during the control session, the first trial analysis for stage 4 showed that in 14 out of 24 trials, the seal reproduced the respective distances within the TRs (Table 2). In contrast to the previous stages of experiment 1, we found a significant effect of the swimming speed on the performance of the animals solely for the 11 m distance (Kruskal–Wallis test; $p < 0.001$; swimming speeds: 0.59 ± 0.18 m/s (n = 153; 1 m distance), 0.80 ± 0.20 m/s (n = 153; 3 m distance), 0.94 ± 0.20 m/s (n = 152; 7 m distance), 0.99 ± 0.18 m/s (n = 150; 11 m distance)).

In stage 4 of experiment 1, we also investigated the motion patterns of the animal during reproduction. We found that every distance was reproduced almost exclusively with one specific motion pattern. Regarding three distances, we found that a deviation from the specific motion pattern resulted in a significant decrease in accuracy during the reproduction; the animal favored to use the "touch–stop"-motion pattern for a distance of 1 m (94%; Chi^2 test, $p < 0.05$; $n = 147$), the "touch–drift" movement pattern was associated with the reproduction of the 3 m distance (85%; Chi^2 test, $p < 0.05$; $n = 149$), and the "touch– dive–drift"-movement pattern occurred mainly during the reproduction of the 11 m distance (82%; Chi^2 test, $p < 0.05$; $n = 148$). For the 7 m distance, we did not find a single specific motion pattern. Here, the animal used the "touch–drift" (44%) or the "touch–dive- drift" (42%) motion pattern but did not show a statistically significant preference between the two (Chi^2 test, $p > 0.05$; $n = 145$).

3.1.6. Stage 5

In stage 5 of experiment 1, the seal had to reproduce 29 unknown combinations of distances and SPs (Figure 2). The overall absolute error was 39.2%, and the overall signed error +0.6%. In total, 9 out of 29 trials were inside the given TR2 of ±20%. The medium absolute error for the first eight trials was approximately 65%, whereas the trials thereafter were performed with a medium absolute error of around 30%. Distances longer than 9.5 m were reproduced with higher accuracy (medium absolute error: 27.1%) as distances shorter than 9.5 m, which were reproduced with a medium absolute error of 54.1% (Mann–Whitney U test; $p < 0.05$). Moreover, the seal significantly undershot distances shorter than 9.5 m and overshot distances longer than 9.5 m (Mann–Whitney U test; $p < 0.05$).

Figure 2. Signed error (in%) for the reproduction of each unknown distance in stage 5 of experiment 1. Each combination of distance and SP was tested only once (see Appendix A). Negative values of the signed error describe an undershooting of the distance; positive values describe an overshooting.

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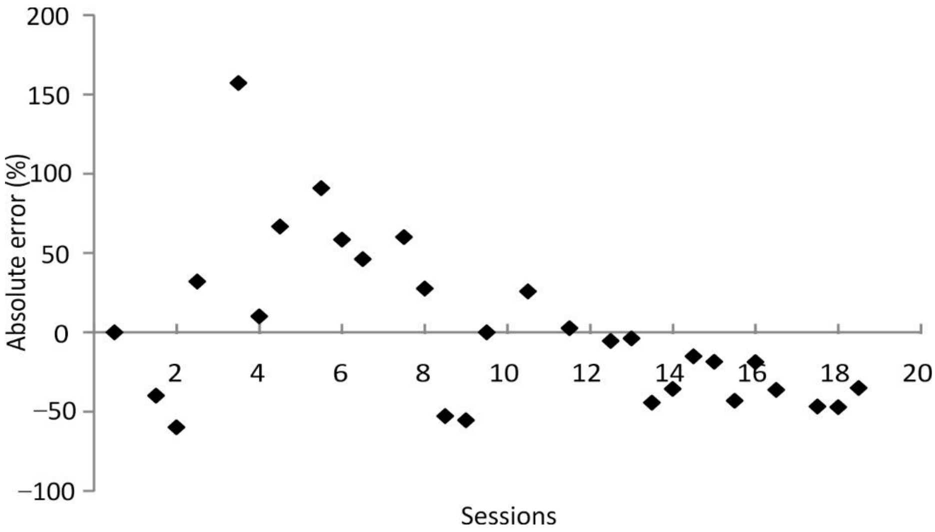
The position of the SP had a significant influence on the performance of the animal; the precision of the animal was higher with SPs up to 8 m from the hoop station and lower for SPs beyond 8 m (Mann–Whitney U test; $p < 0.05$).



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3.2. Experiment 2

In experiment 2, it took the seal 251 trials to reach the learning criterion with a TR of ±20% for the 9 m distance (Figure 3A). In the course of training, the seal managed to reach the learning criterion for two subsequently defined TRs, ±17.5% and ±15%. The average absolute error for the last ten sessions was 12.7%. However, during testing, the

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When training with the 2 m distance, the seal needed 312 trials to reach the learning criterion with a TR of ±20% (Figure 3B). Thereafter, it met the learning criterion for a TR of ±15% as well. In the end, the seal did not reach the learning criterion for a TR of ±10%. The average absolute error for the last 10 sessions was 16.4%, while the absolute minimum error achieved during a session was 9.8%.

During training with a 13 m distance, the trial number to reach the first learning criterion with a TR of ±20% decreased to 120 trials (Figure 3C). Additionally, the seal reached the learning criterion for the two subsequent TRs of ±15% and ±10% as well, before failing to reach the learning criterion for a TR of ±5%. In the last five sessions, the seal showed an overall absolute error of 9.8%. The minimum absolute error per session was 6.7%.

3.3. Experiment 3

In experiment 3, the seal was asked to perform the distance reproduction task with (masked trials) and without visual masking (baseline trials). The learning criterion for the baseline trials was reached after 140 trials. In the testing phase, the seal reproduced the distance during unmasked trials with an average absolute error of 17.2% and during masked trials with an average absolute error of 21.1%. The seal's performance during masked trials was significantly worse than in the baseline trials (Mann–Whitney U test; $p = 0.037$).

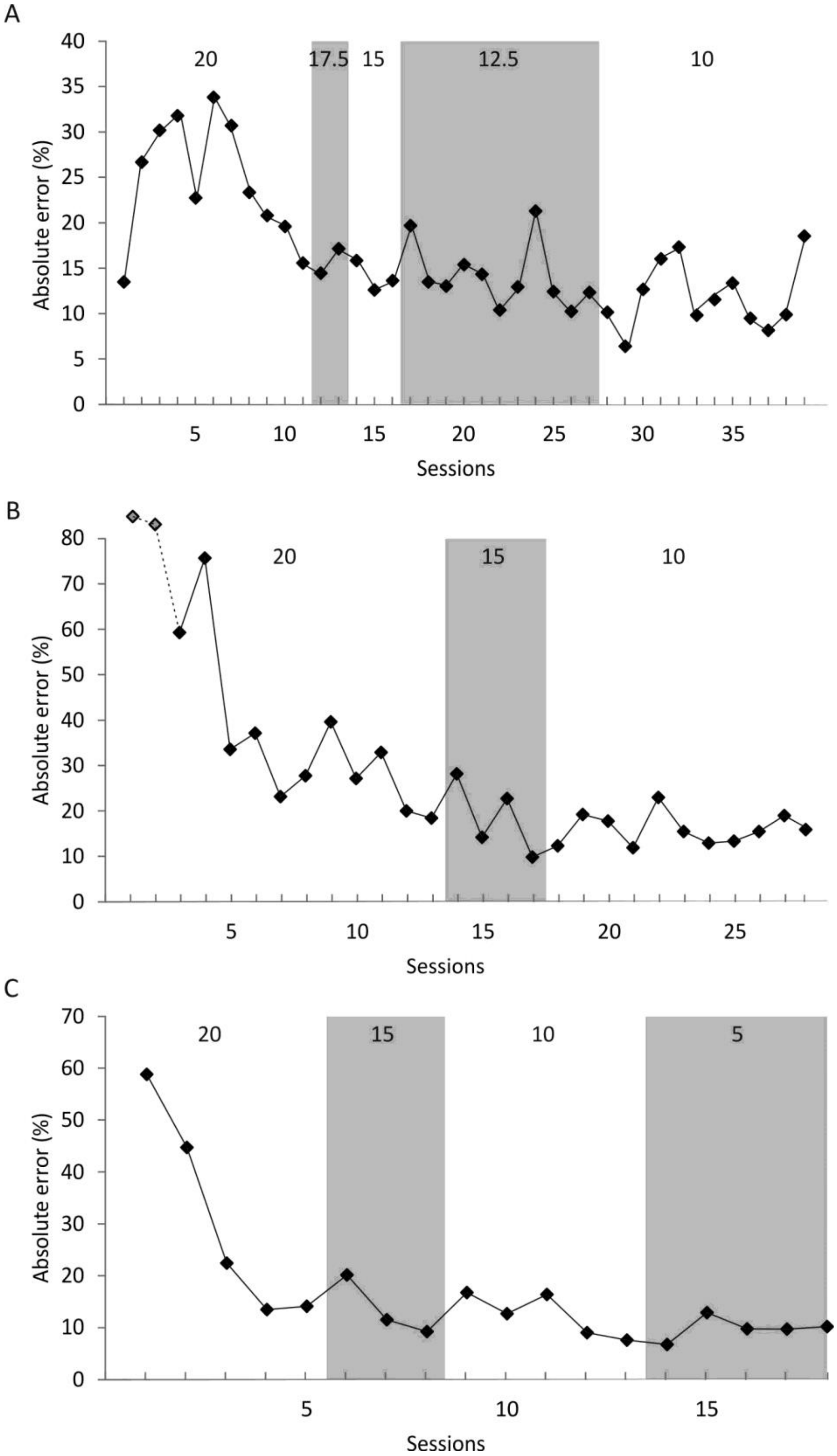

Figure 3. Results of experiment 2. Average absolute error for each session conducted: (**A**) 9 m distance; (**B**) 2 m distance; (**C**) 13 m distance. Every data-point depicts the average absolute error during one session with pseudorandomized SPs. Experimental blocks comprise the performance for the different TR, the seal experienced during the sessions. Due to portrayal issues, we did not illustrate the right scale of the axis for graph B and excluded the to-scale portrayal of the first two values. These values were 360% and 277%.

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4. Discussion

In this study, we analyzed the distance estimation ability of one captive harbor seal, which was available for the extended behavioral experiments. Consequently, the conclusions drawn always need to be considered taking this small sample size as well as the laboratory conditions of our large seawater enclosure, under which the data were obtained, into account and will remain speculative regarding the behavior of wild seals. However, the experimental animal behaves normally and does not have any general deficits, which makes us confident about the reliability of the data concerning this seal individual.

In experiment 1, in phases 1–4, we could show that a harbor seal can learn to estimate and reproduce distances between 1 and 13 m within a predefined range of accuracy. This conclusion is based on the fact that, when presented with two or more distances within one session, the seal could only solve the task if it had derived distance information from the SDI. The use of memorized EPs to solve the task can largely be excluded, as (1) we asked the seal to perform from numerous SPs, (2) the seal was able to perform successfully in most first trials when asked to run the experiment with inversed swimming direction in the control sessions, and (3), over the course of the experiment, one point in space could have been the EP of two SP/SDI combinations, such as 12 m/3 m and 14 m/1 m. Thus, we present the first evidence for distance estimation and reproduction in a marine mammal, the harbor seal. Previously, distance estimation has only been demonstrated in terrestrial animals, such as in insects, gerbils, and humans (see, for example, [18,45–48]). However, as aquatic mammals, harbor seals may also profit from this ability when navigating their environment using, for example, path integration or path return (see Introduction) to find their way back to a location, such as a haul-out place.

In the first stages of experiment 1, the question was addressed, if a harbor seal could learn to reproduce distances in a reproduction task typically used with human subjects. The seal here showed an absolute error between 12% and 31%. This means that not only can the seal learn to reproduce single and multiple distances, but the resulting precision from the experiment also implies that seals could use distance estimation for navigation purposes. Short distances, when seals stay close to shore, could thus be estimated effectively. However, even on a journey covering kilometers, the precision shown in the first phases of experiment 1 would bring the animal close enough towards its goal to then to pinpoint the exact location using, for example, visual cues; for visual cues to be effectively used to, for example, spot a haul-out place rising only 0.1 m above the water surface under good visibility at sea [49,50], the seal would need to get as close as 1.2 km. Additionally, information obtained by other sensory systems can reduce the errors that might accumulate when large distances are traveled or during path integration.

Two interesting phenomena were documented that provide evidence regarding the mechanism of distance estimation in our reproduction tasks. First, the seal used motoric cues to reproduce a distance. All distances, except for one distance, were reproduced with a specific motion pattern, and the accuracy of reproduction was highest if the seal used a specific motion pattern for the reproduction of a specific distance. We consider it unlikely that seals are using specific motion patterns for every single distance traveled in the wild. However, seals might nevertheless use motoric cues to reproduce and maybe to estimate distances in general. Harbor seals could, for example, apply a pedometer comparable to desert ants [37,51]. In seals, this would correspond to counting the number of tail fin flaps, which might be revealed when seals are asked to estimate larger distances. A detailed analysis of GPS recordings in combination with accelerometer tags [52,53] might even enable researchers to determine whether the number of tail fin flaps correlates with the distance swum in wild seals. Second, the seal's performance was highest if it was reproducing a distance with a specific swimming speed. As previously it was documented that harbor seals have an accurate sense of time [54,55], the seal might have kept swimming speed constant, allowing it to use time as a measure for distance. Future studies are required to further elucidate the mechanism of distance estimation in harbor seals. These studies also need to consider ecological factors, such as waves or ocean currents, determining whether seals can perceive and compensate for them or whether these present challenges for using motoric cues or for the determination of swimming speed.

In phase 5 of experiment 1, we asked the seal to reproduce new distances without prior acquisition/learning phase for these distances. The seal's precision noticeably dropped in this stage to an overall error of 39.2%. However, its accuracy was best, with a mean absolute error of 27.1%, when asked to reproduce distances $\geq$10 m, which is comparable to the previous stages that included acquisition phases. On the one hand, the seal might have performed better for distances $\geq$10 m as these are most likely of higher ecological relevance. Seals in their natural habitat are reported to travel distances of dozens of kilometers per day [56]. However, a fine-scale analysis of these trips needs to be done to unravel if these long trips consist of short-distance legs in which distances in the range of the distances or slightly beyond those presented in this study are covered. On the other hand, the seal might have performed worse for distances <10 m as it had already gained extensive experience for distances in this short-range in stages 1–4 of experiment 1. Its previous experience might have negatively affected his performance for distances <10 m in the final phase as it might have tried to fit a solution, such as a motion pattern, for a previously presented distance to a new distance of comparable length. In conclusion, comparing the results of phases 1–4 to the results of phase 5 of experiment 1, repeatedly swimming a specific path/distance increases accuracy, but nevertheless, even when asked to reproduce unknown distances, the seal achieved accuracy in the same range when presented with distances longer than 10 m.

The maximum precision a seal can reach during the reproduction of a repeatedly swum distance was assessed in experiment 2. We found that with specific training to the highest possible precision, the harbor seal's absolute error for distance reproduction could decrease to a precision lower than 10%. The highest accuracy, an absolute error as small as 6.4%, was documented for the 9 m distance. We can thus further stress that the seal's precision when repeatedly swimming a specific distance can be very high. Tagging wild seals has indeed revealed that some seals occasionally choose a specific route repeatedly [57]. Consequently, under these circumstances, they will be able to precisely locate their goal.

The final experiment 3 revealed that the occlusion of vision does not have a major effect on distance reproduction. Instead, (1) the seal quickly transferred the paradigm to the non-visual procedure, (2) even when blindfolded, the distance was reproduced with an error comparable to the errors documented in studies involving human subjects in similar tasks [27,45], and (3) the difference in accuracy when reproducing a distance without a blindfold and with the blindfold was, although significantly different, only 4%. These results most likely mimic that seals frequently encounter conditions in which vision is reduced, such as when active at night or when diving in dark or turbid waters. Future experiments can address the role of other senses during distance estimation. Moreover, in line with our original thought, it would be interesting to examine the seal's ability to estimate and reproduce distances solely based on idiothetic cues and then to put it into the larger context of path integration and orientation/navigation in general.

Throughout the experiment, the seal did not show the same motion pattern in the SDI and the RI; whereas it swam parallel to the belt in the SDI, it included curves or diving phases into the RI. The distance swam during the RI thus deviated from the distance of the SDI. However, the horizontal distance of both intervals matched. Documentation of the horizontal distance to compute a homing vector has been shown for the desert ant, if the ant was foraging in uneven terrain [38,58]. It may be highly adaptive for a harbor seal to also neglect the third dimension, meaning to not include the diving profile into the estimation of traveled distance as its diving pattern and thus distance traveled most likely deviate between the out- and inbound trip. Instead, it would be advantageous to keep track of the horizontal distance, which the seal did during our experiment.

In our study, we also found an influence of the distance on the precision of the animal. The seal was, in general, overshooting short distances and undershooting the reproduction of long distances as previously reported, for example, in humans [59]. The underestimation of long distances has been explained by the amount of information intake exceeding the processing capabilities of the brain [59]. This overflow of information results in a less accurate estimation of the distance; the animal is coming short [60]. An underestimation of a distance can be highly adaptive and has been observed, for example, during path integration [21]. If the animal underestimates the distance of its homing vector, it is not directly brought back to its goal, but its homing vector ends close to its goal. In the familiar terrain close to the goal, the animal can then use, for example, landmarks or the panorama to locate its goal precisely [61]. An interesting future experiment, besides experiments on path integration or path return, could be a visual distance estimation experiment [30], in which the seal must approach a goal, at which a target was presented, before the animal starts to move towards it. Such an experiment would mimic a natural situation, in which the seal was viewing a landmark at the water surface and was approaching it underwater without directly seeing the landmark anymore. These experiments could then be complemented by studies on the use of landmarks.

5. Conclusions

For the first time, we were able to show that a marine mammal can learn to use distance information in reproduction tasks. The captive, experimentally experienced seal could also estimate and reproduce distances largely independent from environmental cues under laboratory conditions. Additionally, we could show that the seal's precision can be compared to that of human subjects, and visual input may not be imminent for distance reproduction. The precision achieved during distance estimation/reproduction would enable the seal to use navigational strategies, such as path integration or path return, especially when covering short absolute distances to prevent the accumulation of errors, but also when traveling larger distances and/or when the information provided by the sensory systems is considered, which are possible strategies used by seals in their challenging habitat.

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Institutional Review Board Statement: The experiments were carried out in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC). According to §8 of the German Animal Welfare Act of 18 May 2006 (BGB I. I S. 1206, 1313), experiments conducted in this study were not subject to approval or notification since they did not cause pain, suffering or injuries to the animals.

Data Availability Statement: All data are available in this manuscript. Detailled raw data are available from the authors on request.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Overview of the SPs (in m from hoop station) and the distances (in m) presented from the SPs tested in stage 5 of experiment 1. All combinations were presented in pseudorandomized order and are only depicted by order of increasing distance for a better overview here.

SP (m from Hoop Station)	Distance (m)
11	0.5
10.5	1.5
12	2
11.5	2.5
14.5	3.5
13	4
12.5	4.5
10	5.5
9.5	6
13.5	6.5
8	7.5
14	8
4.5	8.5
3.5	9
15	9.5
9	10.5
7.5	11.5
8.5	12.5
7	13
5	13.5
6.5	14
4	14.5
5.5	15
2.5	15.5
3	16
2	16.5
1.5	17.5
1	18
0.5	18.5

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

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RESEARCH ARTICLE

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

Eric Maaß and Frederike D. Hanke*

ABSTRACT

Visual landmarks are defined as objects 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, reptiles and terrestrial mammals. The present study aimed to provide insight into how a marine mammal, the harbour seal, encodes 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 the first insight into how a semi-aquatic predator could encode landmark information when swimming along the coastline in search of a goal location.

KEY WORDS: Spatial strategies, Navigation, Orientation, Expansion test, Marine mammal

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 that clearly contrast from the background (Yesiltepe et al., 2021). The use of visual landmarks for goal localization has been documented in multiple species including bees (Cartwright and Collett, 1983), birds (e.g. Cheng, 1989, Cheng and Sherry, 1992, Spetch, 1995), fish (Burt and Macias Garcia, 2003), dogs (Fiset, 2007), rodents (e.g. Cook and Tauro, 1999), turtles (Lopez et al., 2001) and several non-human primates (e.g. MacDonald et al., 2004, Marsh et al., 2011). In contrast, the role of landmarks and landmark orientation has not yet been experimentally studied in marine mammals, 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 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 et al., 2019; Vance et al., 2021). While in the open ocean, landmarks may not be continuously available; however, the coastline offers many landmarks, such as rock formations, sandbanks and anthropogenic structures, that can 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 et al., 1996; Spetch et al., 1997; MacDonald et al., 2004; Potì et al., 2005, 2010; Marsh 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. 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 et al., 2011).

There are at least three different strategies describing how a landmark is used for orientation and navigation (Marsh et al., 2011). In the first strategy, 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 et al., 2001), monkeys (Potì et al., 2005) and human children (MacDonald 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 the 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 et al., 2011). This type of landmark use has been documented in gerbils (Collett et al., 1986), pigeons (Spetch et al., 1996, 1997) and primates (Potì et al., 2005, 2010).

Those organisms that apply a third strategy, the rule-based strategy, operate with the configuration of an entire array of landmarks and

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

*Author for correspondence (frederike.hanke@uni-rostock.de)

F.D.H., 0000-0002-1737-3861

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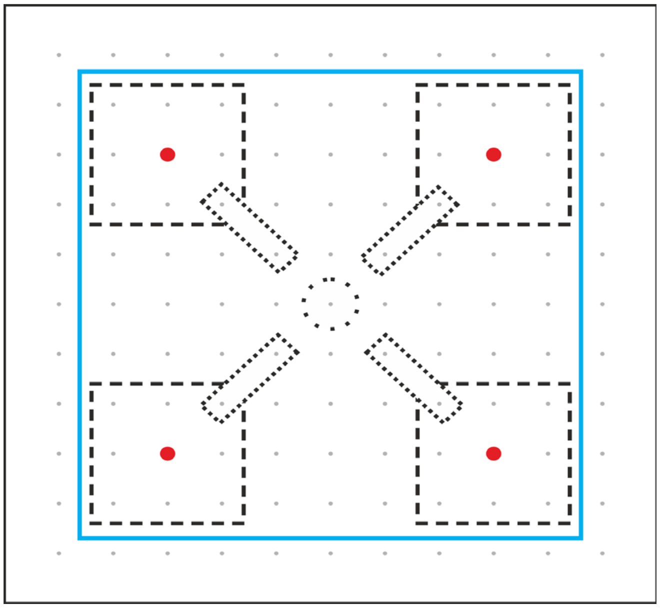

Fig. 1. Search areas predicted by a beacon strategy (squared dashed lines), a rule-based strategy (dotted circle) and a directional vector strategy (dotted rectangles) in an expansion test. Red dots represent the landmarks within a four-landmark array, and the blue line indicates the landmark boundary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

encode the position of the goal in relation to all available landmarks (Fig. 1). So far, only adult humans have been documented to use this strategy ad hoc (MacDonald 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 et al., 2002; Potì 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.

MATERIALS AND METHODS

Experimental animals

The experiment was conducted with three adult male harbour seals (*Phoca vitulina* Linnaeus 1758) named 'Nick' (21 years old; length: 173 cm; mean mass: 121 kg), 'Filou' (14 years old; length: 165 cm; mean mass: 109 kg) and 'Moe' (14 years old; length: 151 cm; mean mass: 91 kg) at the Marine Science Center of the University of Rostock, Germany. All seals had previously participated in numerous different scientific experiments (e.g. Kowalewsky et al., 2006, Schulte-Pelkum et al., 2007, Byl et al., 2016, Niesterok et al., 2017, Krüger 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 3 to 4 days a week. The experiment took place in an enclosure (7×12 m) separated from the main enclosure.

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 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. 2A) that served as the starting point for the animal in each trial. This station

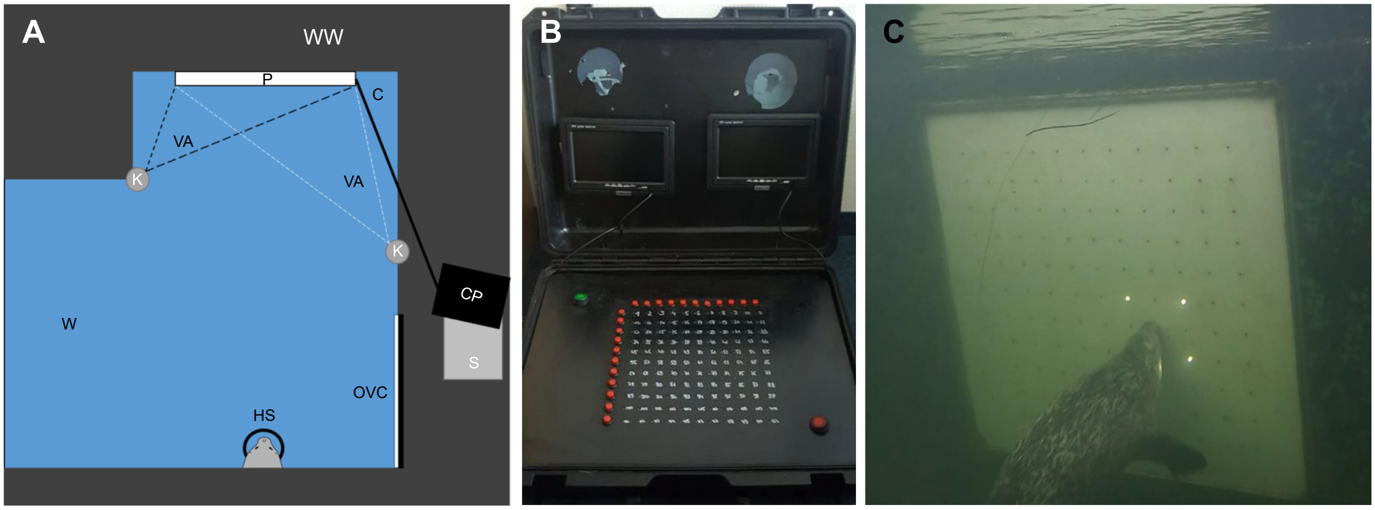

Fig. 2. Experimental setup. (A) Schematic top view of the experimental basin, in which the experiment took place, with the walkway (WW) and the water area (W). The experimenter sat on the walkway (position S) behind an opaque visual cover (OVC) to avoid secondary cueing and set the landmark array with 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 a signal, it swam towards the submerged LED panel (P), indicating with its snout where it assumed the goal was. 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 seal Nick giving a response at the goal location.

was positioned opposite to a 2×2 m integral foam wall (Figs 2A,C and 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 (Figs 2C and 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. 2B) 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 control of 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 away) and right (3 m away) of the LED wall and served to observe the animals' performances, displayed 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. 2C). 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 (Figs 1–3). 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.

Pre-training

Pre-training 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 pre-training, 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 3 s. After successfully completing 10 correct trials per target in succession, trials without an assistant and target ball were

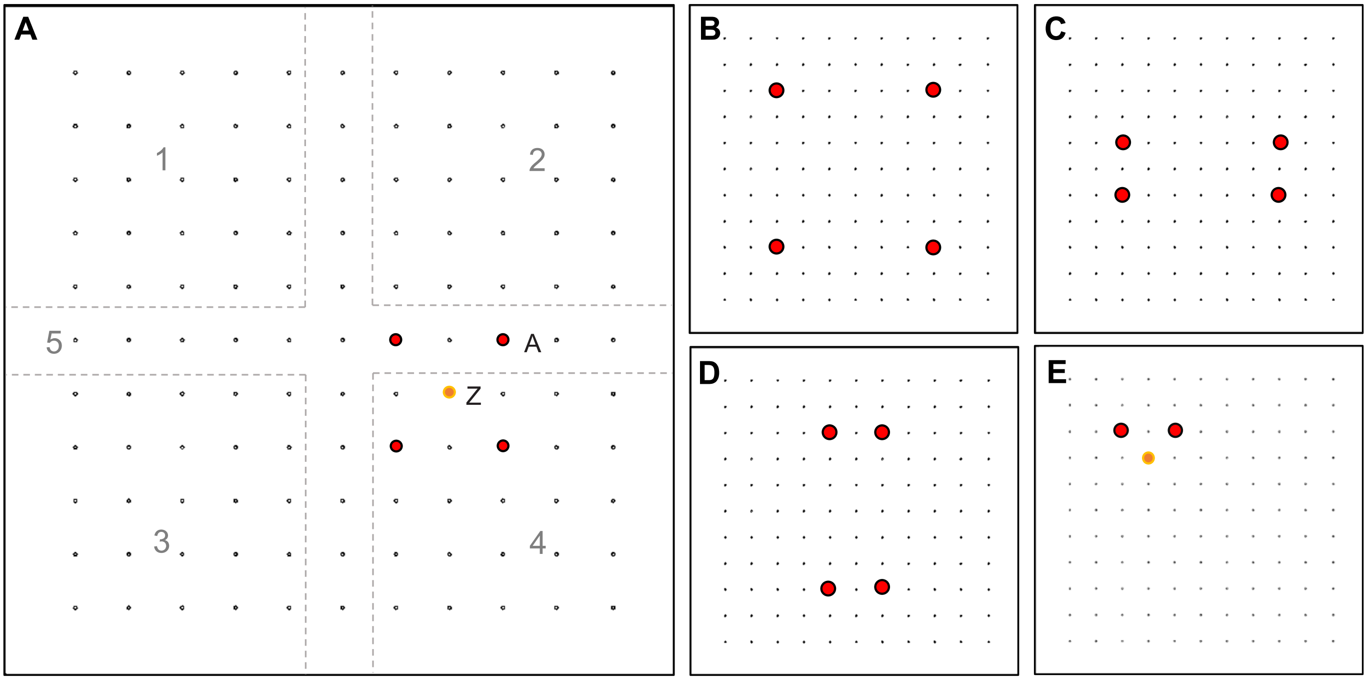

Fig. 3. Landmark array on the LED panel during baseline and test trials in experiment 1 and 2. (A) One-hundred and twenty-one LED lights were attached to a plastic foam wall. In every trial of experiment 1, four LEDs (red dots) were lit and served as landmark array (A). The task of the animal was to 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 Materials and Methods for details. (B–D) 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 two lit LEDs. The goal the animals needed to respond to is marked with a yellow dot; however, during the experiment the goal remained unmarked.

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 assistance and was eager to participate in the training, more trials without assistance were conducted, in comparison with 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 30 cm apart as during baseline trials (Fig. 3B). 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. 3C). In vertical expansion, the two upper and the two lower LEDs kept their position, but those two pairs were moved 90 cm apart vertically (Fig. 3D).

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-trial 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. 3E). 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. 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, WA, USA) and IBM SPSS (v.26; International Business Machines Corporation Armonk, NY, USA). During analysis, we focused 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 (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 that of Marsh et al. (2011). According to their analysis, the three landmark-based strategies predict specific hypothetical goal-locations, with corresponding peak search areas. Because Marsh and colleagues could not differentiate between the beacon strategy and the directional vector strategy owing to an overlap of the hypothetical goal locations, we redefined the goal locations to clearly separate them for the beacon and the directional vector strategies (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 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 1725 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 directional vector strategy more than expected by chance (binomial test: $P<0.05$; Fig. 4, Table 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 focusing 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

Table 1. Number of searches in the expansion test trials of experiments 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)

			Hypothetical goal locations			
Experiment	Subject	Expansion	Beacon	Vector	Rule-based	Other
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
2	Filou	Horizontal	*12*	*18*	0	0
	Moe	Horizontal	*12*	*18*	0	0
	Nick	Horizontal	*19*	*10*	0	1

Numbers written in italics indicate percentages higher than expected by chance (α=0.05). Note that the chance level was different for each of the landmark strategies in the two experiments (see Materials and Methods, Data analysis). 'Other' defines any position chosen by the seals not in line with the goal locations predicted by the beacon, vector or rule-based strategy.

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, in contrast, favoured two different positions, one defined by the training vector, and one defined by a length of 15 cm with an angle of 45 deg 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 his responses to the upper half of the wall, even Moe mainly directed his 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, all seals prioritised their searches in the regions predicted by the vector and beacon strategies more than expected by chance (binomial test: $P<0.05$; Fig. 5, Table 1). No search was ever in line with rule-based searching, i.e. 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. 5A), 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 landmarks; 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 deg counter-clockwise to the training vector with a length of 21 cm and a vector 45 deg clockwise to the training vector with a length of 15 cm with almost the same frequency (Fig. 5A). Nick again, as in experiment 1, favoured the training vector and the vector 45 deg 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. 5B). In contrast, Moe's and Nick's responses were distributed over locations defined by the training vector and by a vector pointing to the LED directly underneath the landmark. Both animals responded with the training vector in 50% of the trials (Fig. 5B).

DISCUSSION

In this study, it was determined how harbour seals encode positional information in respect to landmarks. The seals learnt the experimental paradigm within 746–1725 trials. For comparison, orangutans needed several thousand trials to acquire the basic task in a comparable study (Marsh 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 non-human primates and gerbils, among others (Collett et al., 1986; MacDonald et al., 2004; Potì et al., 2005, 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 behaviours; 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

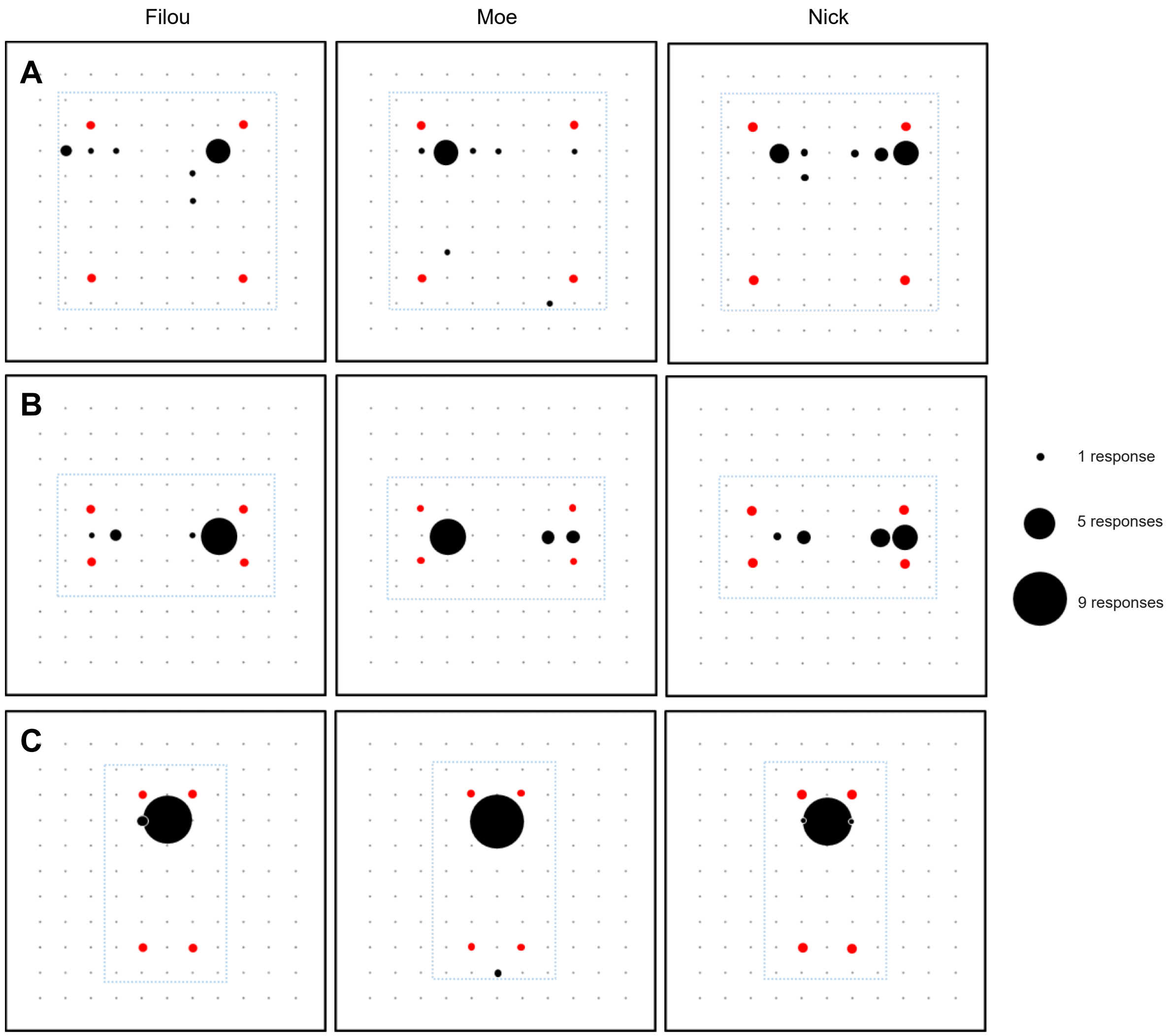

Fig. 4. Response behaviour of seals Filou (left), Moe (center) and Nick (right) in respect to different types of expansion of the four-landmark array (experiment 1). (A) Diagonal expansion, (B) horizontal expansion and (C) vertical expansion. Black circles represent the responses of the seals with the 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 in the key. Conventions as in Figs 1 and 3; the array is always shown in the middle of the LED wall, although its position was varied across the LED wall over trials.

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 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, and 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 aforementioned 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). Owing to their dorsal eye position, harbour seals have a large dorsal, but only a small ventral, visual field (see Fig. S1). 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

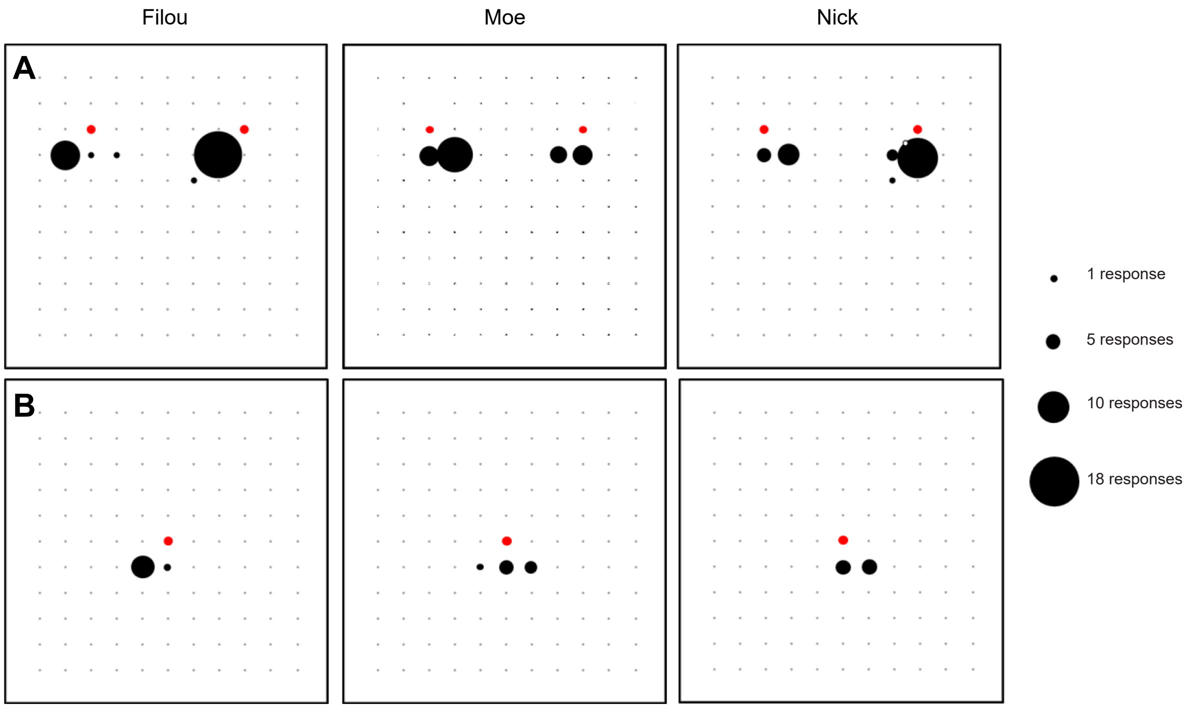

Fig. 5. Response behaviour of seals Filou (left), Moe (center) and Nick (right). Data are shown for the expansion trials of (A) experiment 2A and (B) experiment 2B. Results are visualized as in Fig. 4 and the conventions of all other figures. Please note that in experiment 2A, each seal performed 30 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.

strategy increased in experiment 2 in comparison to experiment 1; 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 the goal versus the 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 has already been documented for human children and capuchin monkeys, for example (MacDonald et al., 2004; Potì 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 et al., 1996, 1997; MacDonald 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 et al., 1997; Potì 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 et al., 2002; Spetch et al., 2003; Potì 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 showed 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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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: E.M., F.D.H.; Methodology: E.M.; Validation: E.M.; Formal analysis: E.M.; Investigation: E.M.; Resources: E.M., F.D.H.; Data curation: E.M.; Writing - original draft: E.M.; Writing - review & editing: E.M., F.D.H.; Visualization: E.M.; Supervision: F.D.H.; Project administration: F.D.H.; Funding acquisition: E.M., F.D.H.

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Supplementary Material for the Manuscript

HOW HARBOUR SEALS (*PHOCA VITULINA*) ENCODE GOALS RELATIVE TO LANDMARKS

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*Author of correspondence:

Frederike D. Hanke, University of Rostock, Institute for Biosciences, Neuroethology, Albert-Einstein-Str. 3, 18059 Rostock, Germany, frederike.hanke@uni-rostock.de

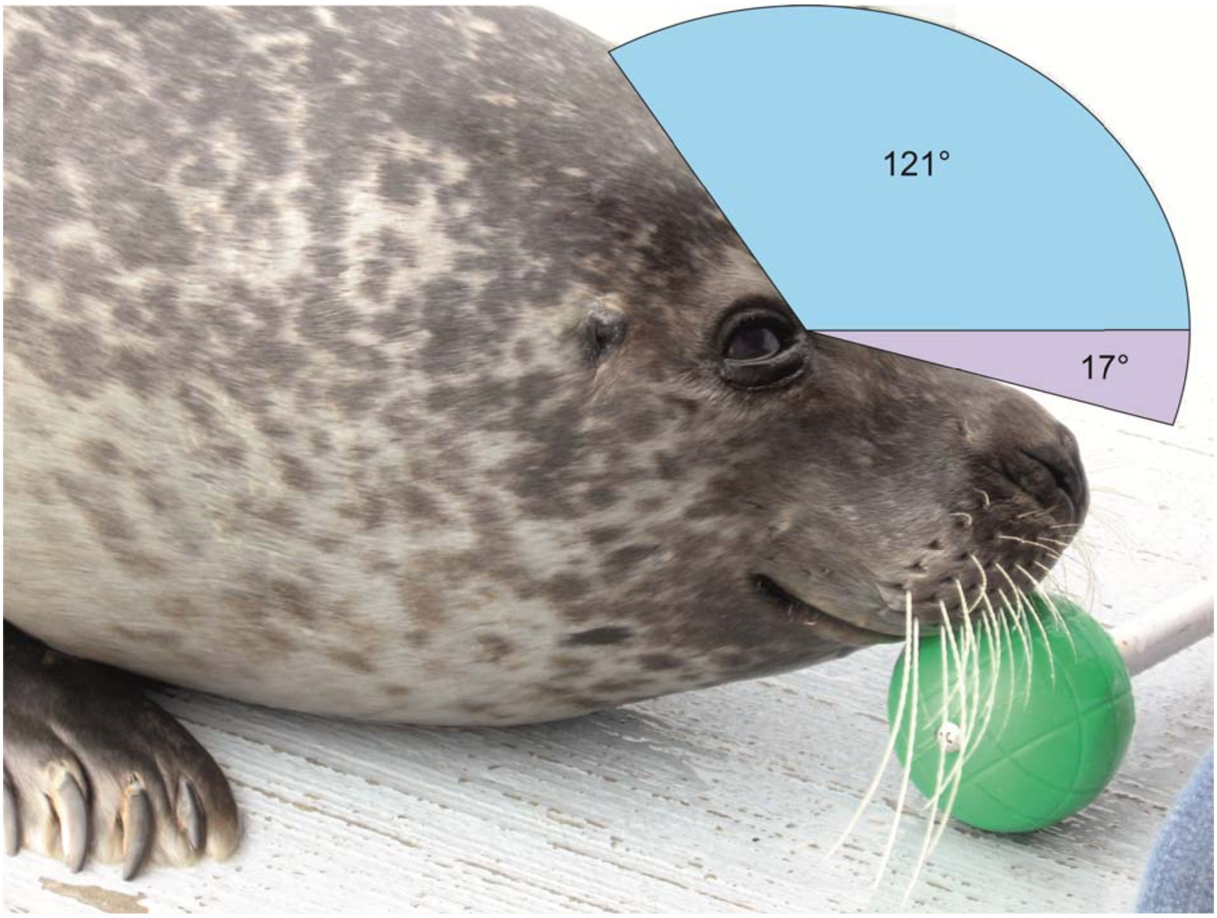

Fig. S1. Dynamic visual field of a harbor seal. Ha bor seals have a large dorsal but only small ventral dynamic visual field. When eye movements are prohibited, the dorsal visual field is still extending over 69 deg. The ventral visual field is reduced to 12 deg without eye movements (data taken from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

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

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RESEARCH ARTICLE

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

Eric Maaß[1], Lars Miersch[1], Gerit Pfuhl[2] and Frederike D. Hanke[1,*]

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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[1]University of Rostock, Institute for Biosciences, Neuroethology, Albert-Einstein-Str. 3, 18059 Rostock, Germany. [2]Norwegian University of Science and Technology, Postbox 8900 Torgarden, 7491 Trondheim, Norway.

*Author for correspondence (frederike.hanke@uni-rostock.de)

G.P., 0000-0002-3271-6447; F.D.H., 0000-0002-1737-3861

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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

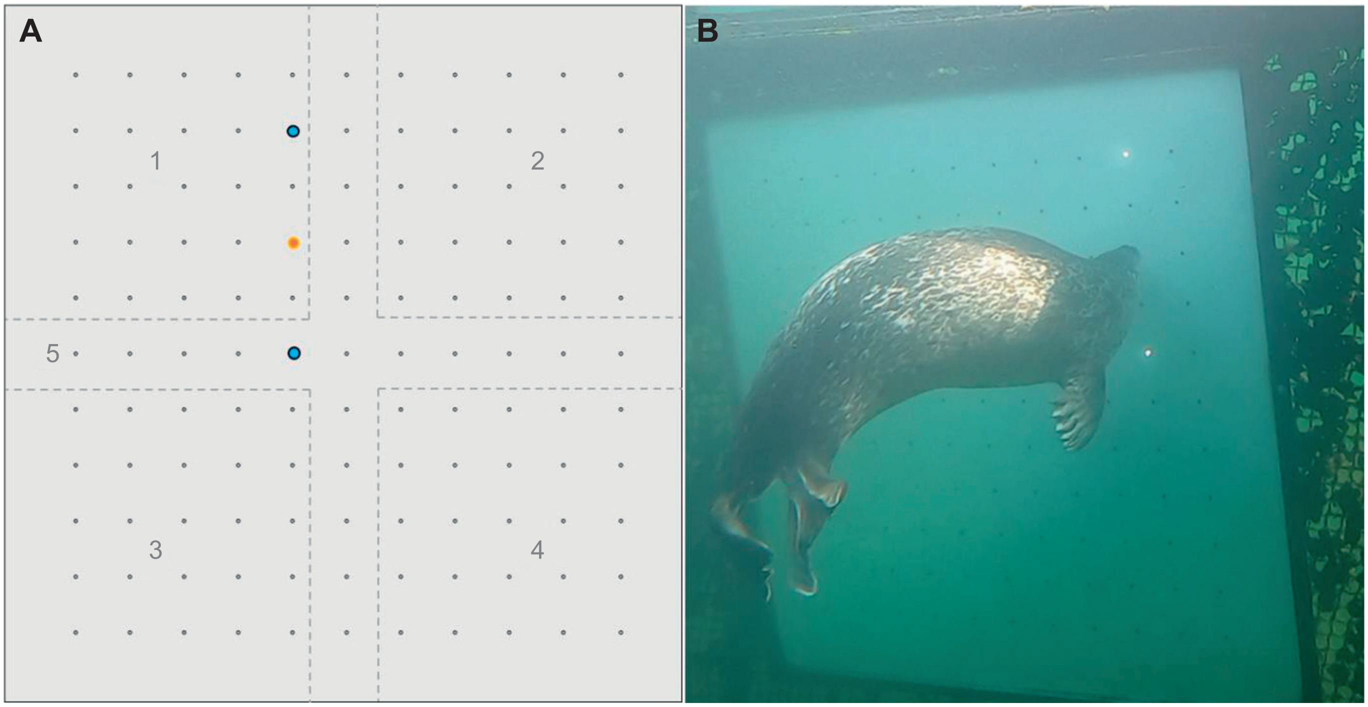

Fig. 1. Experimental setup from the seal’s point of view and *in situ* as well as the seal’s response behaviour when making a correct response to the middle of the two-LED landmark array. (A) On a plastic foam wall, we fixed 121 LED lights. In every trial, two LEDs (blue dots) were lit and served as 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

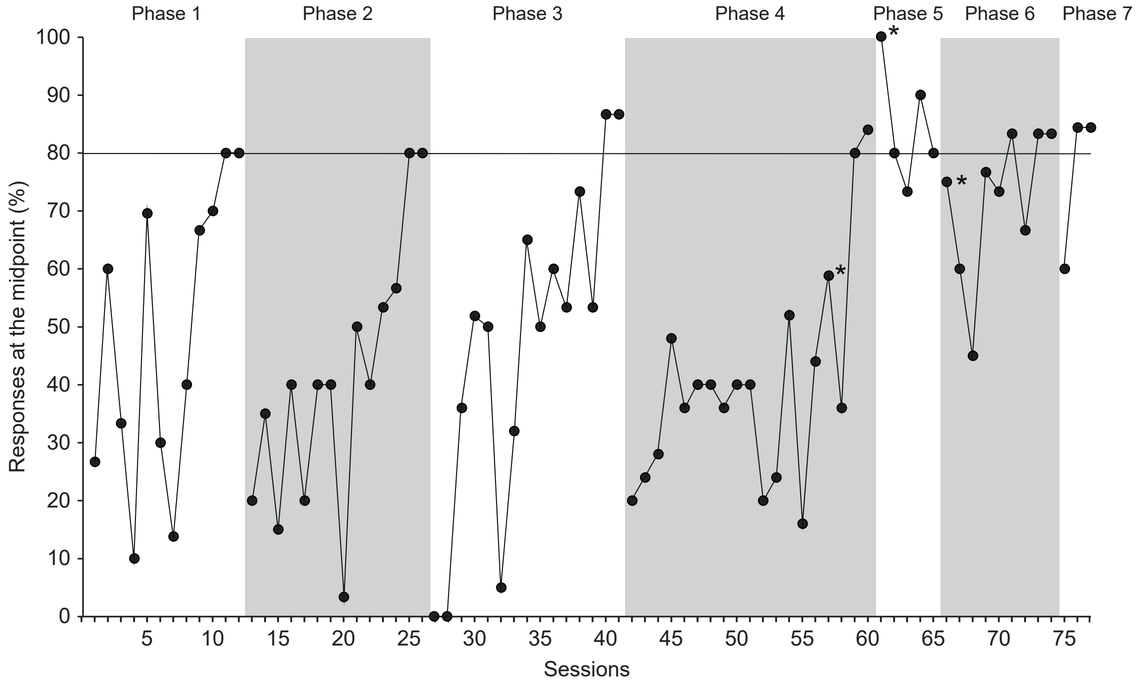

Fig. 2. Learning curve of the training phase of the experiment. Percentages of responses at the midpoint for each session during training phases 1–7. Each session was composed of 20–30 trials. The black horizontal line indicates the learning criterion that the animal had to reach, which was defined as 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

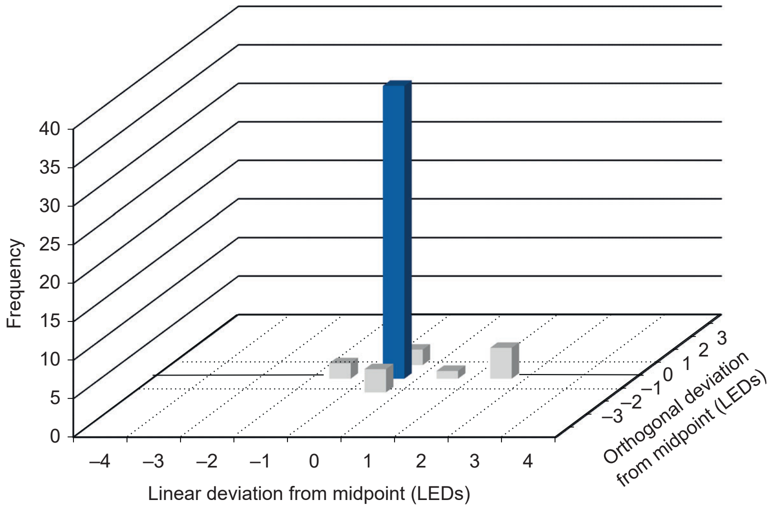

Fig. 3. The seal's search behaviour summarised for all test trials (*N*=50) over all two-LED landmark array configurations. The absolute frequency of responses at a specific position relative to the midpoint (at the origin of the coordinate system). To depict the error in deviation from the midpoint 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.

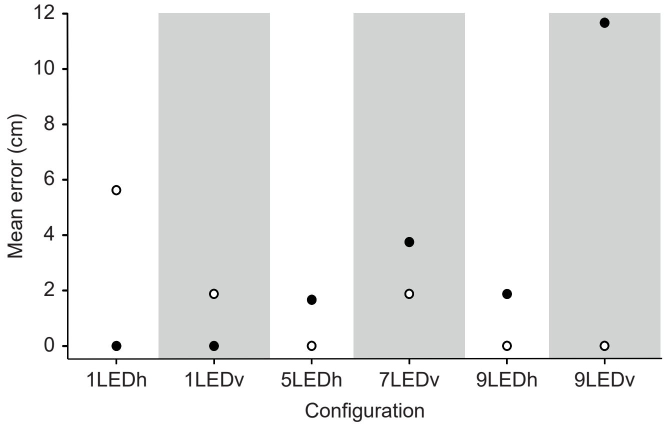

Fig. 4. Mean linear (filled circles) and orthogonal error (open circles) for each configuration presented in the testing phase (note that the distance between two LEDs on the LED panel was 15 cm). The errors occurring as a response to vertical configurations are highlighted with a grey background. Each 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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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: E.M., F.D.H.; Methodology: E.M., L.M., F.D.H.; Software: E.M., L.M.; Validation: E.M.; Formal analysis: E.M., G.P.; Investigation: E.M.; Resources: E.M., F.D.H.; Data curation: E.M.; Writing - original draft: E.M.; Writing - review & editing: L.M., G.P., F.D.H.; Visualization: E.M.; Supervision: F.D.H.; Project administration: E.M.; Funding acquisition: E.M., F.D.H.

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Data availability
The original data files and videos can be found at https://osf.io/54vfa/.

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Supplementary Material for the Manuscript

A HARBOUR SEAL (*PHOCA VITULINA*) CAN LEARN GEOMETRICAL RELATIONSHIPS BETWEEN LANDMARKS

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*Author of correspondence:

Frederike D. Hanke, University of Rostock, Institute for Biosciences, Neuroethology, Albert-Einstein-Str. 3, 18059 Rostock, Germany, frederike.hanke@uni-rostock.de

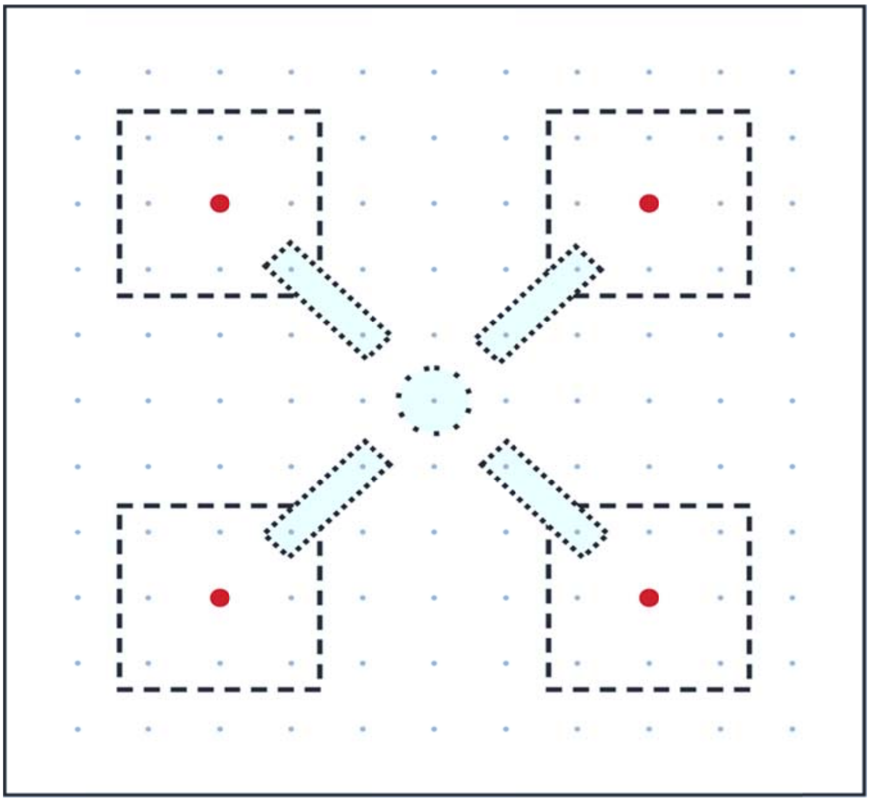

Fig.S1. Predicted search areas after expanding a landmark array consisting of four landmarks (red dots). The search areas in line with a beacon strategy (squared dashed line), a rule-based strategy (dotted circle) and a directional vector strategy (dotted rectangles) are shown (modified after Marsh et al., 2011; Potì et al., 2010).

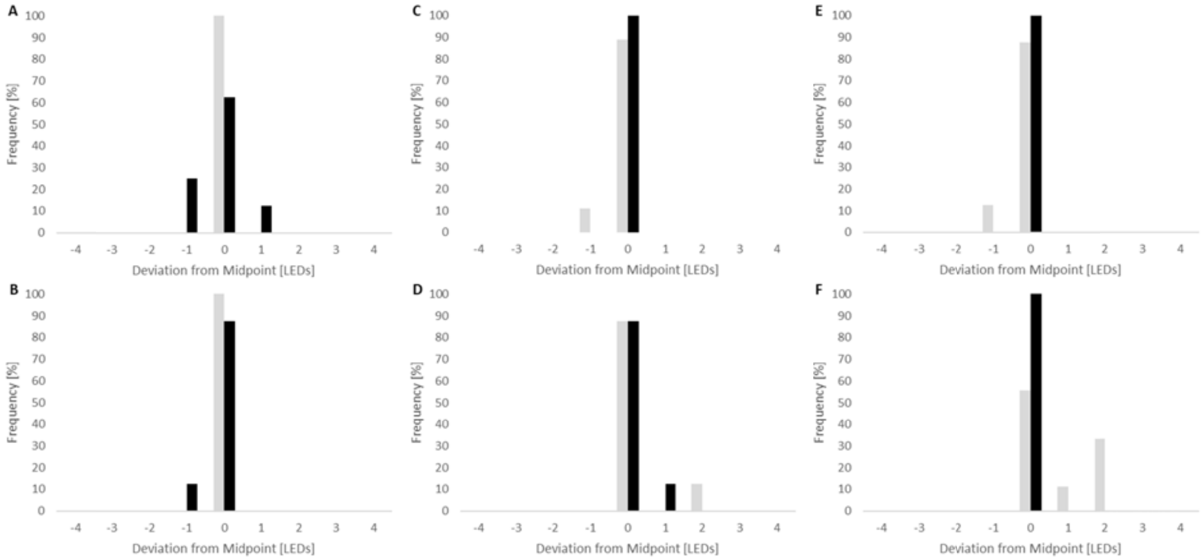

Fig. S2. Search behaviour of the seal during the test trials of the experiment for each configuration separately. A shows the 1LEDh configuration (N = 8), B the 1LEDv configuration (N = 8), C the 5LEDh configuration (N = 9), D the 7LEDv configuration (N = 8), E the 9LEDh configuration (N =8) and F the 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).

	Configurations											
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

				Wald Test			95% Confidence interval	
	Estimate	Standard Error	z	Wald Statistic	df	p	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 absolute size 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

3. Danksagung

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Danke

4. Statement of Authorship/ Selbständigkeitserklärung

I hereby solemnly declare that I produced the present Doctoral Thesis independently without external assistance, and that no other than the listed sources of information and references were used, and that the passages taken literally and with regard to the contents from these sources are clearly indicated as such.

Ich versichere hiermit an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt und ohne fremde Hilfe verfasst habe. Ich habe keine außer den von mir angegebenen Hilfsmitteln und Quellen verwendet und die den benutzten Werken inhaltlich und wörtlich entnommenen Stellen als solche kenntlich gemacht habe.

Rostock, den 14.08.2023

Eric Maaß

Eric Maaß

Address:	Knud-Rasmussen-Str. 10, 18106 Rostock
Date of birth:	09.08.1990 in Berlin
Mail:	eric.maass@uni-rostock.de
Nationality:	German

Educational Path

2015 - 2023 **Ph.D. candidate (Dr. rer. nat.)**

University of Rostock

- Institute for Biosciences, Neuroethology
- Thesis Topic: *Spatial Orientation in Harbour Seals*

2016 - 2019 **Ph.D.-Scholarship of the Deutsche Bundesstiftung Umwelt**

2013 – 2015 **Master of Science**

University of Rostock

- Area of Study: Marine Biology
- Thesis Topic: *Distance Reproduction in Harbour Seals*
- Grade: 1.7

2010 – 2013 **Bachelor of Science**

Christian-Albrechts-University Kiel

- Area of Study: Biology
- Thesis Topic: *Alarmstoffe: Interaktionen von Fischen mit dem Edelkrebs (Astacus astacus)*
- Grade: 1.9

2003 – 2010 **Abitur**

Wilhelm-von-Siemens-Gymnasium Berlin-Marzahn

- Grade: 1.9

Practical Experience

since 2023 **Research Assistant**

Federal Maritime and Hydrographic Agency of Germany

2022-2023 **Associate Head of Department**

State Office for Environment, Nature Conservation and Geology Mecklenburg-Vorpommern

2019 – 2021 **Research Assistant**

Marine Science Center Rostock Hohe Düne

Further Knowledge

Languages:	German – first language English – fluent (Certificate C1)

Publications

Maaß, E., & Hanke, F. D. (2021). Distance estimation in reproduction tasks in a harbor seal (*Phoca vitulina*). *Water*, *13*(7), 938.

Maaß, E., & Hanke, F. D. (2022). How harbour seals (*Phoca vitulina*) encode goals relative to landmarks. Journal of Experimental Biology, 225(5), jeb243870.

Maaß, E., Miersch, L., Pfuhl, G., & Hanke, F. D. (2022). A harbour seal (*Phoca vitulina*) can learn geometrical relationships between landmarks. Journal of Experimental Biology, 225(24), jeb244544.

Conference Proceedings

Maaß, E., Dehnhardt, G., & Hanke (2016) Distance reproduction in harbor seals. Deutsche Zoologische Gesellschaft, Kiel, Germany, September 14-17, 2016.

Maaß, E., Hanke, F. D.; Dehnhardt, G.; Are we there yet? Distance estimation in a harbour seal. Forschungscamp, Rostock, Germany, November 23, 2017.

Maaß, E., Hanke, F. D.; Dehnhardt, G.; Are we there yet? Distance estimation in a harbour seal; Society of Marine Mammals, 22nd Biennial Conference, Halifax, Nova Scotia, Canada October 23-27, 2017

Maaß, E., Hanke, F. D.; Dehnhardt, G.; Distance estimation in a harbour seal; **World Marine Mammal Conference, 2019** Barcelona, Spain 9-12 December

Participation

Society of Marine Mammals, 22nd Biennial Conference, 2017 Halifax, Nova Scotia, Canada 23-27 October

World Marine Mammal Conference, 2019, co-hosted with the European Cetacean Society Barcelona, Spain 9-12 December