Available online at www.sciencedirect.com
ScienceDirect
Physiology & Behavior 93 (2008) 1033 – 1038
PHYSIOLOGY & BEHAVIOR
www.elsevier.com/locate/phb

Successful acquisition of an olfactory discrimination paradigm by South African fur seals, *Arctocephalus pusillus*

Matthias Laska [a,*], Madeleine Svelander [a], Mats Amundin [b]

[a] *IFM Biology, Linköping University, SE-581 83 Linköping, Sweden*
[b] *Kolmårdens Djurpark, SE-618 92 Kolmården, Sweden*

Received 16 August 2007; received in revised form 9 December 2007; accepted 17 January 2008

Abstract

The present study demonstrates that South African fur seals, *Arctocephalus pusillus*, can successfully be trained to discriminate between objects on the basis of odor cues. Using a task based on a food-rewarded two-choice discrimination of simultaneously presented odor stimuli the animals acquired the basic operant conditioning paradigm within 480 to 880 stimulus contacts. Moreover, the fur seals could readily transfer to new S+ and S− stimuli, were capable of distinguishing between fish- and non-fish odors as well as between two fish odors, and were able to remember the reward value of previously learned odor stimuli even after 2- and 15-week breaks. The precision and consistency of the fur seals' performance in tests of discrimination ability and memory demonstrate the suitability of this paradigm for assessing olfactory function in this pinniped.

An across-species comparison of several measures of olfactory learning capabilities such as speed of initial task acquisition and ability to master transfer tasks shows that *A. pusillus* is similar in performance to non-human primates, but inferior to rodents such as mice and rats. The results support the assumption that fur seals may use olfactory cues for social communication and food selection and that the sense of smell may play an hitherto underestimated role in the control of their behavior.
© 2008 Elsevier Inc. All rights reserved.

Keywords: South African fur seals; *Arctocephalus pusillus*; Odor learning; Behavioral testing; Olfactory discrimination; Odor memory

1. Introduction

Marine mammals are traditionally believed to have a poorly developed sense of smell [1]. It is therefore hardly surprising that investigations of sensory perception and processing in this group of animals have so far concentrated on acoustic, visual, and somatosensory function [2,3]. However, the view that olfaction is only minor, if any, importance in marine mammals is exclusively based on an interpretation of neuroanatomical features such as the relative size of olfactory brain structures and not on physiological evidence [4,5]. Furthermore, marine mammals which comprise members of the three orders Sirenia, Carnivora, and Cetacea may differ markedly in their ecology and behavior [6] making generalizing statements as to their sensory capacities more than arguable. Behavioral observations suggest that pinnipeds such as fur seals may use their sense of smell both for social communication as well as for foraging and food selection. South American fur seals, *Arctocephalus australis*, for example, have been reported to rely on vocal cues for long-range localization of pups [7] but appear to use olfactory cues for close-range recognition and acceptance of pups by their mothers [8]. Olfactory recognition of offspring, often accompanied by nuzzling, that is: mutual naso-nasal contact, has also been reported in Antarctic fur seals, *Arctocephalus gazella* [9], South African fur seals, *Arctocephalus pusillus* [10], and harp seals, *Phoca groenlandica* [11]. Female Northern fur seals, *Callorhinus ursinus*, have been described to vigorously sniff at their pups during and immediately after parturition [12], a behavior commonly found in non-aquatic mammals which is thought to aid in building a bond between mother and offspring [13]. Male New Zealand fur seals, *Arctocephalus forsteri*, have been observed to sniff frequently at the perineal and facial regions of females during the breeding season,

* Corresponding author. Tel.: +46 13 28 1240; fax: +46 13 28 1399.
E-mail address: malas@ifm.liu.se (M. Laska).

0031-9384/$ - see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.physbeh.2008.01.019

suggesting an olfactory assessment of the female's reproductive state [14]. Male South American fur seals, *A. australis*, and ringed seals, *Phoca hispida*, have been described to emit a strong odor during the rut which is caused by an enlargement and heightened activity in their sebaceous and apocrine facial glands [15,16]. These secretions are discussed as means of territorial marking and/or attracting females [17,18].

Grey seals, *Halichoerus grypus*, have been observed to appear downwind of an oil slick resulting from another seal surfacing and consuming a captured fish [Arne Fjälling, personal communication]. Similarly, harbour seals, *Phoca vitulina*, have been found to swim on direct routes to their feeding grounds and some authors believe that they may use olfactory cues for spatial orientation and foraging [19,20]. The only published study we found that assessed olfactory performance in a pinniped supports this assumption as it demonstrated harbour seals to have a high olfactory sensitivity for dimethyl sulphide, an odorant which is thought to be indicative of high marine productivity [19].

Despite such observations, there have been few systematic studies of olfactory-guided behavior in marine mammals and, to the best of our knowledge, only one investigation of olfactory performance uses psychophysical procedures so far [19]. It was therefore the aim of the present study to develop a means of reliably assessing olfactory performance, and of odor discrimination and memory capabilities in particular, in a pinniped species, the South African fur seal, *A. pusillus*.

2. Materials and methods

2.1. Subjects

Testing was carried out using three adult females (Flisa, Tinny, and Villma) and one adult male (Jocke) South African fur seals (*A. pusillus*) maintained as part of a group of seven animals at Kolmården Wild Animal Park, Sweden. The group was housed under semi-natural conditions in an 800m^2 outdoor pool with an adjacent house bearing single cages which allowed temporary separation of animals for individual testing. All animals were trained to enter the single cages voluntarily and were completely accustomed to the procedure. Animals were fed with fish and squid twice a day. No food deprivation schedule was adopted. Rather, the food reward given to the animals during the training sessions was part of their two feeding bouts per day.

The experiments reported here comply with the *Guide for the Care and Use of Laboratory Animals* (National Institutes of Health Publication no. 86-23, revised 1985) and also with current Swedish laws.

2.2. The behavioral test

The behavioral test was based on a food-rewarded two-choice instrumental conditioning paradigm. The animals were trained to sniff at two odor sampling ports and then to indicate which of the two options held the rewarded stimulus by poking their nose into the corresponding sampling port. An opaque PVC board (50 cm high × 100 cm wide × 1 cm deep) with two openings (7.5 cm diameter) at equal height and 42 cm apart from each other was mounted at the front side of the test cage in such a way that the openings were 47 cm above the ground. For the presentation of the odor stimuli two HDPE containers with tight-fitting removable lids (Rubbermaid® Cooling Bags, 35 cm high × 35 cm wide × 20 cm deep) were used. Each lid was equipped with a battery-powered ventilator (6 cm diameter) providing an ingoing airflow. A total of 130 holes of 3 mm diameter placed in intervals of even distance forming a filled circle with a diameter of 7.5 cm were drilled in an exact pattern in the middle of one of the front sides of each container serving as an outlet for the airflow provided by the ventilator. The outgoing airflow was adjusted to 8 l/min and a board on the outside of the cage ensured that the containers could be placed with their outlets congruent with the openings of the PVC board. The odor stimuli were placed into opaque HDPE boxes (12 cm high × 20 cm wide × 12 cm deep) without a lid inside the containers. This allowed the airflow provided by the ventilator to reach the surface of the odor stimuli and, at the same time, prevented the animals from using visual cues. A mirror placed on top of the cage allowed the experimenter to observe the animal's behavior without being seen behind the opaque PVC board (Fig. 1).

At the beginning of each trial, the two containers were placed with their outlets towards the odor sampling ports and an animal was allowed to sniff at them as often as it liked. Immediately following the animal's decision (a nose poke into one of the two odor sampling ports), the two containers were removed and, in the case of a correct response (a nose poke into the odor sampling port bearing the rewarded stimulus), the animal was rewarded with a fish or squid. In the case of an incorrect response (a nose poke into the odor sampling port bearing the unrewarded stimulus) no reward was given to the animal.

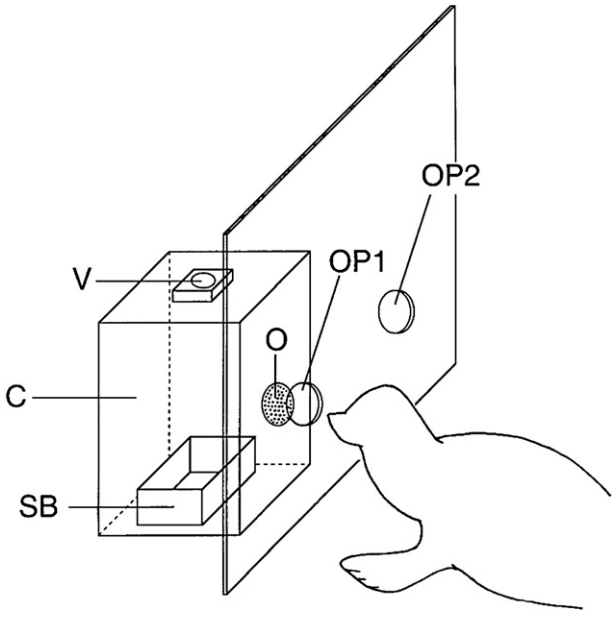

Fig. 1. Schematic drawing of the experimental set-up used to assess olfactory performance in South African fur seals. C: container, V: ventilator for ingoing airflow, SB: stimulus box, O: outlet for outgoing airflow, OP1: odor port 1, OP2: odor port 2. The second, identically built container placed behind odor port 2, is not shown.

Twenty such trials were performed per session and usually two sessions were performed per animal and day. Care was taken to present the rewarded stimulus to the right or the left odor sampling port adopting a pseudorandomized sequence with the limitation that the same option was not used more than three times in a row. At the end of each session, the containers and the boxes bearing the odor stimuli were thoroughly cleaned.

2.3. Odor stimuli

Four capelins (*Mallotus villosus*), one herring (*Clupea harengus*), and one mackerel (*Scomber scombrus*) plus 5ml of salmon oil (Salmopet, Pure Norwegian salmon oil) were used together as rewarded odor stimulus (S+). This mixture is henceforth called "fish odor A". Essential oils of cloves (*Syzygium aromaticum*), black pepper (*Piper nigrum*), and myrtle (*Myrtus communis*) were used separately as unrewarded odor stimuli (S−). Additionally, the same combination of fish used as the rewarded stimulus but without the salmon oil added was used as unrewarded odor stimulus (S−). This mixture is henceforth called "fish odor B". In a final test, two squids (*Ommastrephes argentinus*) were used as rewarded odor stimulus (S+).

2.4. Experimental design

2.4.1. Initial shaping

The first experiment was designed to establish whether South African fur seals can be conditioned to discriminate between objects on the basis of odor. This was assessed by testing their ability to distinguish between fish odor A (used as S+) and clove odor (used as S−).

2.4.2. Stimulus transfer tasks

When the seals had learned to perform the initial discrimination task, we tested their ability to make negative stimulus transfers by replacing cloves odor with black pepper odor, myrtle odor, and fish odor B as the S−, and subsequently a positive stimulus transfer by replacing fish odor A with squid odor as the S+.

2.4.3. Assessment of odor memory

When the seals had mastered the stimulus transfer tasks, we assessed their ability to remember the reward value of both the S+ and the S− by presenting them with the same pair of stimuli after 2-week and 15-week breaks in testing.

2.4.4. Control experiment

To make sure that the animals did not receive any unintentional hint from the experimenter, some control sessions were interspersed at different times of testing. In the control sessions, an assistant baited the containers; the experimenter was thus unaware of their respective contents. Additionally, a series of control trials interspersed between the normal test trials ensured that the animals did not use unwanted olfactory or non-olfactory cues from the experimental set-up for their decisions. To this end, the lids bearing the ventilators as well as the boxes containing the odor stimuli were switched between containers, and the containers themselves assigned to contain either the S+ or the S− were switched during a test session.

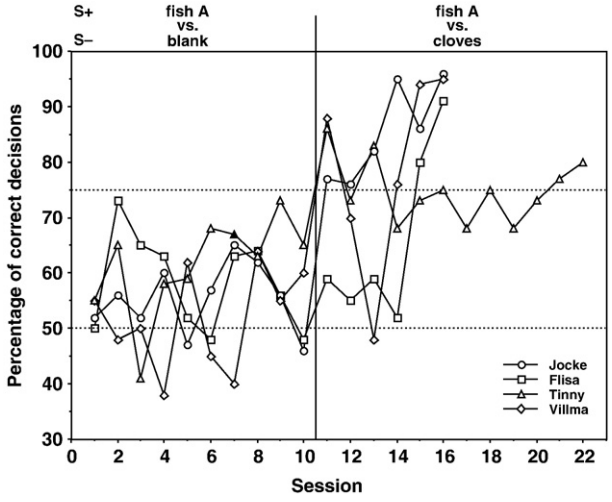

Fig. 2. Performance during initial shaping. Each data point represents the percentage of correct decisions from 20 trials. The four different symbols represent data from each of the four individual animals tested. The horizontal dotted lines indicate chance level (at 50%) and criterion level (at 75%). The vertical line indicates the switch between tasks.

2.5. Data analysis

In the method described here, the animal had two options: (1) to correctly respond to the positive stimulus (hit), and (2) to falsely respond to the negative stimulus (false alarm). The percentage of hits was taken as the measure of performance. For the initial learning task as well as for the transfer and memory tasks, the criterion was set at 75% hits in two consecutive sessions of 20 decisions each (corresponding to $p < 0.01$, binomial test).

3. Results

3.1. Initial shaping

Fig. 2 illustrates the performance of the fur seals during the initial shaping. When presented with fish odor A as the rewarded stimulus and an odorless blank as the unrewarded stimulus, all four animals failed to reach the learning criterion within 10 sessions. Therefore, cloves odor was introduced as S− from session 11 on and within 2 (Jocke), 5 (Villma), 6 (Flisa), and 12 (Tinny) sessions, respectively, all four animals reached the criterion of 75% correct decisions in two consecutive sessions ($p < 0.01$, binomial test). This corresponds to about 480 (Jocke) to 880 (Tinny) stimulus contacts till criterion.

3.2. Stimulus transfer tasks

Fig. 3 summarizes the performance of the animals in the stimulus transfer tasks. Changing the unrewarded stimulus from cloves odor to black pepper odor resulted in a clear although individually different decline in performance in three of the four

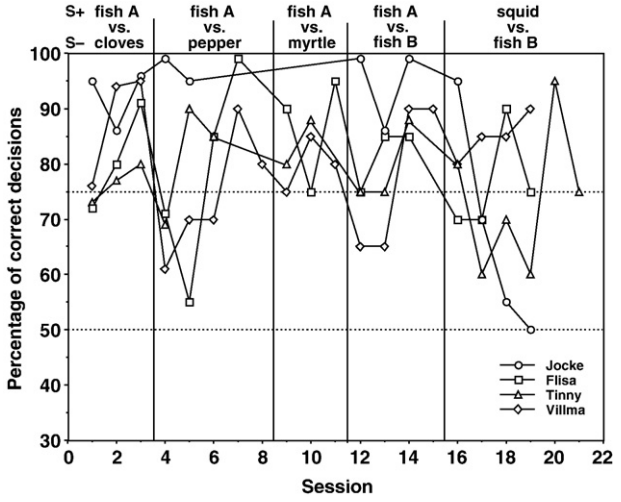

Fig. 3. Performance during the stimulus transfer tasks. Each data point represents the percentage of correct decisions from 20 trials. The four different symbols represent data from each of the four individual animals tested. The horizontal dotted lines indicate chance level (at 50%) and criterion level (at 75%). The vertical lines indicate the switch between tasks.

fur seals. However, all four animals learned the reward value of the new S− and reached criterion within 2 (Jocke), 3 (Flisa and Tinny), and 5 (Villma) sessions, respectively. A subsequent negative stimulus transfer from black pepper odor to myrtle odor had only little effect on performance and was mastered by Flisa, Tinny and Villma within two sessions, that is, the minimum number of sessions necessary to reach criterion. (Note that one animal, Jocke, did not participate in this task). A third negative stimulus transfer from myrtle odor to fish odor B (and from black pepper odor to fish odor B in the case of Jocke) also presented little difficulty to the animals, with three out of four fur seals (Jocke, Flisa, and Tinny) reaching criterion within two sessions, and the fourth animal (Villma) scoring above 75% correct decisions within four sessions. A positive stimulus transfer from fish odor A to squid odor again led to a transient decline in performance. However, three out of four animals finally learned the reward value of the new S+ and reached criterion within 2 (Villma), 4 (Flisa), and 6 (Tinny) sessions, respectively. One animal (Jocke) scored 90% correct decisions in the first session with squid odor but clearly rejected the new S+ in subsequent sessions. This animal is the only one that refuses to eat squid which might explain its failure to reach criterion.

3.3. Assessment of odor memory

Throughout training and testing it was notable that weekend breaks, far from having a detrimental effect on performance, only seemed to increase the animals' interest in the task, and in no case was there any evidence of short term forgetting. As shown in Fig. 4, even breaks of 2 weeks and 15 weeks, respectively, had no negative effect on the individual performance levels of the four fur seals. An analysis of the responses during the very first decisions both after the 2-week and the 15-week retention intervals revealed that all four animals correctly chose the rewarded stimulus immediately and in six out of eight cases they correctly rejected the unrewarded stimulus, suggesting that the good performance of the fur seals was truly due to memory of that specific odor pair and not to a rapid relearning.

3.4. Control experiment

During the control sessions in which the experimenter did not know which container was the baited one, the performance of the fur seals did not differ significantly from their usual performance (data not shown). Thus, it can be concluded that there was no unintentional cue from the experimenter. Additionally, a series of control trials interspersed between the normal test trials ensured that the animals did not use unwanted olfactory or non-olfactory cues from the experimental set-up for their decisions. To this end, the lids bearing the ventilators as well as the boxes containing the odor stimuli were switched between containers, and the containers themselves assigned to contain either the S+ or the S− were switched during a test session. None of these control trials indicated that the animals used anything but the odor stimuli for their decisions (data not shown).

4. Discussion

Although fur seals, as marine mammals in general, are typically regarded as "microsmatic", that is, animals with a poorly developed sense of smell, there is an increasing number of behavioral observations suggesting that olfaction may play a significant part in the regulation of their behavior, including various aspects of their social life [8–12,14–18]. Despite the obvious importance of such studies, the recording of spontaneous preferences or olfactory-related behavior does not allow the accurate assessment of sensory capacities: Firstly, because of the

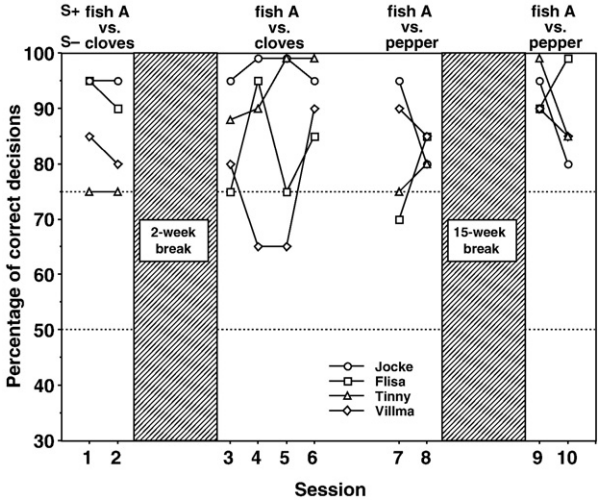

Fig. 4. Performance in the odor memory tasks. Each data point represents the percentage of correct decisions from 20 trials. The four different symbols represent data from each of the four individual animals tested. The horizontal dotted lines indicate chance level (at 50%) and criterion level (at 75%). The shaded bars indicate the retention intervals.

dependence of responding on experience and motivational state of the animals, and secondly, because of difficulties with stimulus standardization and control [21]. However, in order to understand olfactory function and to fully appreciate the role the sense of smell may play in regulating a species' behavior, it is necessary to gain knowledge as to the animals' basic perceptual capacities. It was, therefore, our aim to develop a means of reliably assessing olfactory performance in a pinniped species using a method that was not based on spontaneous preferences or behaviors and that allows for standardization and control of odor stimuli.

The results of the present study demonstrate, for the first time, that South African fur seals can successfully be trained to discriminate between objects on the basis of odor cues. Moreover, the seals could readily transfer to new S+ and S− stimuli, were capable of distinguishing between fish- and non-fish odors as well as between two fish odors, and were able to remember the reward value of previously learned odor stimuli even after 2- and 15-week breaks.

An across-species comparison of performance of the fur seals, as shown in the present study, to that of other species trained on two-odor discrimination tasks using food-rewarded operant conditioning procedures shows that the speed of initial task acquisition (480–880 stimulus contacts till criterion) was comparable to that found with squirrel monkeys, *Saimiri sciureus* [22], and spider monkeys, *Ateles geoffroyi* [23], which needed 450–750 and 660–720 stimulus contacts, respectively, and even slightly superior to pigtail macaques, *Macaca nemestrina* [24], which needed 960–1800 stimulus contacts.

Mice [25], rats [26], and dogs [27], in contrast, have been shown to need less than 150 stimulus contacts to acquire an olfactory discrimination task and thus appear to learn the reward value of odor cues considerably faster than the fur seals, even when taking into consideration that different methods may lead to widely differing results in measures of cognitive performance. These differences, although they should not be taken as absolute measures, suggest that rodents and terrestrial carnivores might be more prepared to use olfactory cues in the initial solving of a learning task compared to marine carnivores such as fur seals. However, the "preparedness" to use a certain sensory modality in cognitive tasks does not necessarily reflect the physiological efficiency of the sensory system involved. In this context it should also be noted that the speed of mastering intramodal stimulus transfer tasks did not generally differ between the fur seals and that reported in mice and rats [25,26].

To the best of our knowledge, only one study so far assessed sensory capabilities in South African fur seals using a two-choice discrimination paradigm [28]. In an experimental set-up similar to the one employed here, five fur seals learned to distinguish between visual stimuli presented simultaneously on wooden plates by making a nose poke onto the plate bearing the rewarded color or black-and-white pattern. Unfortunately, the authors did not report any measures of learning speed for the different discrimination tasks or memory for the visual cues used so that no within-species comparison across sensory modalities is possible.

In the present study, the fur seals showed an excellent performance in a first assessment of their long-term odor memory with no sign of forgetting of the reward values of odor stimuli after 2 weeks and even after 15 weeks (see Fig. 4). This finding is in line with reports from squirrel monkeys [29], spider monkeys [23], and pigtail macaques [30] which also showed excellent retention of the significance of rewarded and unrewarded odor stimuli over periods of time up to 15 weeks. A comparison of the fur seals' long-term memory for odors with that of species presumed to have a particularly keen sense of smell shows that *A. pusillus* does not perform poorer than mice [25], rats [26], gerbils [31], or guinea pigs [32]. This result is in agreement with the often-remarked longevity of olfactory memories [33] which, in turn, may be an evolutionary adaptation to the fact that a variety of biologically meaningful odors occur only seasonally [13,34].

Our finding that the fur seals were not only able to distinguish between pairs of odors which are readily discriminable for humans (e.g. fish odor vs. cloves), but also between a pair of fish odors which only differed from each other in the presence vs. absence of fish oil (see Fig. 3) and which presented some difficulty for humans supports the assumption that the sense of smell may play a role in foraging and food selection by fur seals. This assumption is also supported by a study that demonstrated harbour seals to have a high olfactory sensitivity for dimethyl sulphide, an odorant which is thought to be indicative of high marine productivity [19].

A recent study lends further support to the notion that olfaction may be more important for fur seals than generally believed: based on phylogenetic comparative analyses the authors conclude that "functional differences between pinnipeds and fissipeds appear to have been overstated and may be no greater than those among major fissiped groups" [35]. In line with this conclusion, comparative neuroanatomical studies found that olfactory brain structures of pinnipeds are basically similar to those of fissipeds, and that all species of pinnipeds studied so far possess a vomeronasal organ [6].

Taken together, the results of the present study demonstrate the suitability of the operant conditioning paradigm employed here for assessing olfactory function in *A. pusillus*. They support the assumption that the sense of smell may play an hitherto underestimated role in the control of behavior in this pinniped species. Future studies should systematically explore the discriminative abilities of the fur seals for food-associated and body-borne odors in order to further our understanding of the role of olfactory information for foraging, food selection and social communication in fur seals.

Acknowledgment

We are grateful for the invaluable help of Sunna Edberg and Therese Höglin in collecting data.

References

[1] Brown RE. The marine mammals: orders Cetacea, Pinnipedia, and Sirenia. In: Brown RE, Macdonald DW, editors. Social odours in mammals, vol. 2. Oxford: Clarendon Press; 1985. p. 723–31.

[2] Supin AY, Popov VV, Mass AM. The sensory physiology of aquatic mammals. New York: Springer; 2001.

[3] Thomas JA, Kastelein RA, Supin AY. Marine mammal sensory systems. New York: Plenum Press; 1992.
[4] Fobes JL, Smock CC. Sensory capacities of marine mammals. Psychol Bull 1981;89:288–307.
[5] Lowell WR, Flanigan WF. Marine mammal chemoreception. Mamm Rev 1980;10:53–9.
[6] Hoelzel AR. Marine mammal biology: an evolutionary approach. Durham: Blackwell; 2002.
[7] Insley SJ, Phillips AV, Charrier I. A review of social recognition in pinnipeds. Aquat Mamm 2003;29:181–201.
[8] Phillips AV. Behavioral cues in reunions between mother and pup South American fur seals (*Arctocephalus australis*). J Mammal 2003;84:524–35.
[9] Dobson FS, Jouventin P. How mothers find their pups in a colony of Antarctic fur seals. Behav Processes 2003;61:77–85.
[10] Ross GJB. Nuzzling behaviour in captive Cape fur seals. Int Zoo Yearb 1972;12:183–4.
[11] Kovacs KM. Mother–pup reunions in harp seals, *Phoca groenlandica*: cues for the relocation of pups. Can J Zool 1995;73:843–9.
[12] Bartholomew GA. Mother–young relations and the maturation of pup behaviour in the Alaska fur seal. Anim Behav 1959;7:163–71.
[13] Wyatt TD. Pheromones and animal behaviour: communication by smell and taste. Cambridge: Cambridge University Press; 2003.
[14] Miller EH. Social behaviour between adult male and female New Zealand fur seals, *Arctocephalus forsteri* (Lesson) during the breeding season. Aust J Zool 1974;22:155–73.
[15] Hamilton JR. Scent of Otariids. Nature 1956;177:900.
[16] Hardy MH, Roff E, Smith TG, Ryg M. Facial skin glands of ringed and grey seals, and their possible function as odoriferous organs. Can J Zool 1991;69:189–200.
[17] Ling JK. Functional significance of sweat glands and sebaceous glands in seals. Nature 1965;208:560–2.
[18] Ryg M, Solberg Y, Lydersen C, Smith TG. The scent of rutting male ringed seals (*Phoca hispida*). J Zool 1992;226:681–9.
[19] Kowalewsky S, Dambach M, Mauck B, Dehnhardt G. High olfactory sensitivity for dimethyl sulphide in harbour seals. Biol Lett 2006;2:106–9.
[20] Thompson PM, Miller D. Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina L.*) in the Moray Firth, Scotland. J Appl Ecol 1990;27:492–501.
[21] Passe DH, Walker JC. Odor psychophysics in vertebrates. Neurosci Biobehav Rev 1985;9:431–67.
[22] Laska M, Hudson R. Assessing olfactory performance in a New World primate, *Saimiri sciureus*. Physiol Behav 1993;53:89–95.
[23] Laska M, Hernandez Salazar LT, Rodriguez Luna E. Successful acquisition of an olfactory discrimination paradigm by spider monkeys, *Ateles geoffroyi*. Physiol Behav 2003;78:321–9.
[24] Hübener F, Laska M. A two-choice discrimination method to assess olfactory performance in pigtailed macaques, *Macaca nemestrina*. Physiol Behav 2001;72:511–9.
[25] Bodyak N, Slotnick B. Performance of mice in an automated olfactometer: odor detection, discrimination and odor memory. Chem Senses 1999;24: 637–45.
[26] Slotnick BM, Kufera A, Silberberg A. Olfactory learning and odor memory in the rat. Physiol Behav 1991;50:555–61.
[27] Lubow RE, Kahn M, Frommer R. Information processing of olfactory stimuli by the dog: 1. The acquisition and retention of four odor-pair discriminations. Bull Psychon Soc 1973;1:143–5.
[28] Busch H, Dücker G. Das visuelle Leistungsvermögen der Seebären (*Arctocephalus pusillus und Arctocephalus australis*). Zool Anz 1987;219: 197–224.
[29] Laska M, Alicke T, Hudson R. A study of long-term odor memory in squirrel monkeys. J Comp Psychol 1996;110:125–30.
[30] Hübener F, Laska M. Assessing olfactory performance in an Old World primate, *Macaca nemestrina*. Physiol Behav 1998;64:521–7.
[31] Cheal ML, Klestzick J, Domesick VB. Attention and habituation: odor preferences, long-term memory and multiple sensory cues of novel stimuli. J Comp Physiol Psychol 1982;96:47–60.
[32] Beauchamp GK, Wellington JL. Habituation to individual odors occurs following brief, widely-spaced presentations. Physiol Behav 1984;32: 511–4.
[33] Schab FR, Crowder RG. Memory for odors. Hillsdale, NJ: Lawrence Erlbaum; 1995.
[34] Knudsen JT, Tollsten L, Bergström LG. Floral scents — a checklist of volatile compounds isolated by head-space techniques. Phytochemistry 1993;33:253–80.
[35] Binnida-Emonds ORP, Gittleman JL. Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses. Evolution 2000;54:1011–23.