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Olfactory Discrimination of Aliphatic Odorants in South African Fur Seals (*Arctocephalus pusillus*)

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Using a food-rewarded, two-choice, instrumental conditioning paradigm we assessed the ability of South African fur seals, *Arctocephalus pusillus,* to discriminate between members of five chemical classes of aliphatic odorants presumed to differ in their abundance in the marine chemical environment. We found that the fur seals were able to distinguish between 24 of the 25 odor pairs presented and thus have a well-developed ability to discriminate between structurally related odorants, that aliphatic n-acetic esters were significantly more poorly discriminated by the fur seals than aliphatic n-aldehydes and n-carboxylic acids, and a lack of correlations between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length. These results suggest that the sense of smell may play an important and hitherto underestimated role in regulating the behavior of fur seals. Further, they support the notion that regular connections between the perceived quality of odorants and their molecular structural properties are not a general phenomenon but appear to be odorant class- and species-specific. Our data support the hypothesis that a species' chemical environment may affect its olfactory capabilities.

Keywords: marine chemical environment, pinnipeds, sense of smell, sensory performance

Marine mammals are traditionally considered to have a poorly developed sense of smell (Brown, 1985). However, marine mammals which comprise members of the orders Sirenia, Carnivora, and Cetacea differ markedly in neuroanatomical features such as the relative size of olfactory brain structures (Lowell & Flanigan, 1980) as well as in their ecology and behavior (Hoelzel, 2003) making generalizing statements as to their sensory capacities more than arguable (Supin, Popov, & Mass, 2001). An increasing number of behavioral observations suggest that pinnipeds such as fur seals may use their sense of smell in a variety of behavioral contexts including social communication, foraging, food selection, and reproduction.

South American fur seals, *Arctocephalus australis,* for example, have been reported to use olfactory cues for individual recognition and acceptance of pups by their mothers (Phillips, 2003). Olfactory recognition of offspring, often accompanied by nuzzling, that is: mutual naso-nasal contact, has also been reported in Antarctic fur seals, *Arctocephalus gazella* (Dobson & Jouventin, 2003), South African fur seals, *Arctocephalus pusillus* (Ross, 1972), and harp seals, *Phoca groenlandica* (Kovacs, 1995). 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, suggesting an olfactory assessment of the female's reproductive state (Miller, 1974). Male South American fur seals, *Arctocephalus 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 (Hamilton, 1956; Hardy, Roff, Smith, & Ryg, 1991). These secretions are discussed as a means of territorial marking and/or attracting females (Ling, 1965; Ryg, Solberg, Lydersen, & Smith, 1992).

Gray 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, harbor 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 (Thompson & Miller, 1990; Kowalewsky, Dambach, Mauck, & Dehnhardt, 2006). This assumption is also supported by the finding that harbor seals have a high olfactory sensitivity for dimethyl sulfide, an odorant which is thought to be indicative of high marine productivity (Kowalewsky et al., 2006). In an interesting note, the same odorant has been found to be used for foraging by marine birds such as petrels (Nevitt & Bonadonna, 2005) and, possibly, penguins (Cunningham, Strauss, & Ryan, 2008).

Recent studies suggest that the chemical environment in which an animal develops and lives, or in which a species evolves, may strongly affect its olfactory capabilities (Ayabe-Kanamura et al., 1998; Yee & Wysocki, 2001; Mandairon, Stack, Kiselycznyk, & Linster, 2006). The marine chemical environment differs markedly in its composition of odorants compared to terrestrial environments. It is characterized by an abundance of aliphatic aldehydes, ketones, alcohols and carboxylic acids whereas aliphatic esters are largely lacking (Lindsey, 1990; Josephson, 1991; Cadwallader & Shahidi, 2001; Koep, Hoffman, Dicks, & Slinde, 2007). This should not be surprising given that aliphatic esters which are often described as "fruity" or "flowery" by human observers are among the quantitatively and qualitatively prominent components of fruit

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and flower odors (Maarse, 1991; Burdock, 2005; Knudsen, Eriksson, Gershenzon, & Stahl, 2006) and angiosperms with odor-producing flowers and fruits are not common in the marine environment.

The recent development of a food-rewarded, two-choice, instrumental conditioning paradigm for South African fur seals (Laska, Svelander, & Amundin, 2008) now enables us to assess the olfactory capabilities of this pinniped and to test the hypothesis that the composition of the marine chemical environment affects the olfactory discrimination performance of this species. It was therefore the aim of the present study to assess the ability of *Arctocephalus pusillus* to discriminate between members of five chemical classes of aliphatic odorants presumed to differ in their abundance in the marine chemical environment.

Method

Subjects

Testing was carried out using four adult females (Flisa, Tinny, Sealia, and Villma) and one adult male (Jocke) South African fur seals (*Arctocephalus pusillus*) maintained as part of a group of seven animals at Kolmården Wild Animal Park, Sweden. The group was housed under seminatural conditions in an 800 m^2 outdoor pool with an adjacent house bearing eight cages which allowed temporary separation of animals for individual testing. All animals were trained to enter the individual cages voluntarily and were completely accustomed to the procedure. Animals were born in captivity and fed fish (mackerel, *Scomber scombrus*) and squid (Argentine shortfin squid, *Ommastrephes argentinus*) twice a day. Thus, their daily diet was very similar to the diet reported for free-ranging South African fur seals which comprises up to 70% mackerel and 20% squid, respectively (Mecenero, Roux, Underhill, & Bester, M.N., 2006). 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 APA Ethical Principles, 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.

The Behavioral Test

The behavioral test was based on a food-rewarded, two-choice, instrumental conditioning paradigm. In a previous study (Laska, Svelander, et al., 2008) the animals had learned 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 $\times$ 100 cm wide $\times$ 1 cm thick) 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 high density polyethylene (HDPE) containers with tight-fitting removable lids (Rubbermaid Cooling Bags, 35 cm high $\times$ 35 cm wide $\times$ 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 per minute and a platform on the outside of the cage ensured that the containers could be placed with their outlets congruent with the openings of the PVC board. In order to present the odor stimuli, 1 ml of an odorant was pipetted onto a Petri dish which, in turn, was placed into an opaque HDPE box (12 cm high $\times$ 20 cm wide $\times$ 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 polyvinyl chloride board. A previous study in which the same experimental set-up had been used (Laska, Svelander, et al., 2008) and which included double-blind trials gave no indication that the animals might use unintended cues from the experimenter.

At the beginning of each trial, the two containers were placed with their outlets toward 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. 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 using unperfumed detergent and rinsed with demineralized water. A previous study in which the containers assigned to a given stimulus were occasionally changed between sessions (Laska, Svelander, et al., 2008) gave no indication that potential residues of odorants affected the animals' subsequent choice behavior.

Odor Stimuli

A set of 20 aliphatic odorants was used (see Table 1). All substances were obtained from Sigma-Aldrich (St. Louis, MO), and had a nominal purity of at least 99%. They were diluted using odorless diethyl phthalate (Merck, Darmstadt) as the solvent. The level of dilution was chosen to provide stimuli that were easily detectable and of approximately equal subjective intensity for humans. The rationale for choosing these substances was to assess the discrimination performance of the fur seals for odorants sharing the same functional group but differing in carbon chain length (C4 to C7) and representing five chemical classes presumed to differ in their frequency of occurrence in the marine environment (Josephson, 1991; Burdock, 2005). Furthermore, data on discrimination performance for the same set of stimuli from humans (Laska & Teubner, 1998, 1999; Laska & Hübener, 2001), squirrel monkeys (Laska & Freyer, 1997; Laska & Teubner, 1998; Laska, Trolp, & Teubner, 1999), mice (Laska, Joshi, & Shepherd, 2007; Laska, Rosandher, & Hommen, 2008), and honeybees (Laska,

Table 1
Odorants and Dilutions Used

Odorant	Carbon chain length	Dilution
1-alcohols		
1-butanol	4	1:10
1-pentanol	5	1:10
1-hexanol	6	1:3
1-heptanol	7	1:3
n-aldehydes		
n-butanal	4	1:10
n-pentanal	5	1:10
n-hexanal	6	1:10
n-heptanal	7	1:5
2-ketones		
2-butanone	4	1:10
2-pentanone	5	1:10
2-hexanone	6	1:3
2-heptanone	7	1:3
n-carboxylic acids		
n-butanoic acid	4	1:10
n-pentanoic acid	5	1:10
n-hexanoic acid	6	1:10
n-heptanoic acid	7	1:2
n-acetic esters		
ethyl acetate	4	1:10
n-propyl acetate	5	1:10
n-butyl acetate	6	1:3
n-pentyl acetate	7	1:3

Note. Chemical classes are given in italics.

Galizia, Giurfa, & Menzel, 1999) are at hand allowing across-species comparisons of discrimination performance. Additionally, the essential oil of black pepper (*Piper nigrum*) was used. This odorant had been used in a previous study (Laska, Svelander, et al., 2008) and was thus familiar to the animals.

Experimental Design

For each of the five chemical classes, one odorant (either the C4 or the C7 stimulus) per animal was chosen as the rewarded stimulus (S+) and in an initial phase, each animal was allowed to become familiar with its S+. This was done by using black pepper oil as unrewarded stimulus (S-) in 10 sessions. Black pepper oil had been used as S- in previous experiments and was therefore known to the animals. Once familiarized with the S+, the black pepper oil was exchanged for one of the other odorants of the same chemical class (see Table 1) and each of the critical stimulus combinations (C4 vs. C5, C4 vs. C6, and C4 vs. C7 for animals that had been assigned the C4 stimulus as S+, and C7 vs. C6, C7 vs. C5, and C7 vs. C4 for animals that had been assigned the C7 stimulus as S+) was presented for four sessions. Care was taken that among those animals that were assigned the same S+ (e.g., the C4 stimulus) some began the critical tests with an odorant pair representing the smallest possible difference in carbon chain length (e.g., C4 vs. C5) whereas other animals began with an odorant pair representing the largest possible difference in carbon chain length (e.g., C4 vs. C7). This was done in order to control for possible effects of task order on discrimination performance. If needed, up to two sessions with black pepper oil as S- were implemented between the different test combinations in order to boost the animal's confidence and to refresh its memory for the reward value of the S+. With all animals, the five chemical classes were tested in the following order: n-aldehydes, n-acetic esters, n-carboxylic acids, 2-ketones, and 1-alcohols. With the last three chemical classes, only four of the five animals could be tested as the male (Jocke) was transferred to another zoo.

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 correct decisions was used as the measure of performance and the criterion was set to 67.5% correct in two consecutive sessions of 20 decisions each (corresponding to $p < .05$, two-tailed binomial test). Correlations between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length were evaluated using the Spearman rank correlation coefficient. Comparisons of group performance across tasks were made using the Friedman two-way analysis of variance (ANOVA). When ANOVA detected differences between tasks, this was then followed by pairwise Wilcoxon signed-ranks test for related samples to evaluate which tasks were responsible. Comparisons of performance across individuals were made using the Mann–Whitney *U* test for independent samples.

Results

General Discrimination Performance

Figure 1 summarizes the performance of the fur seals in discriminating between members of the five chemical classes tested. All animals performed significantly above chance level in 24 out of 25 tasks and thus were clearly able to discriminate between most odor pairs. The only odor pair which two animals failed to distinguish above chance involved the discrimination of two n-acetic esters: n-propyl acetate and n-pentyl acetate (odor pair 5–7, lower left panel in Figure 1).

Interindividual Differences in Discrimination Performance

The mean discrimination performance of the individual fur seals across all tasks ranged from 84.0% (95% CI = 75.5, 92.5) for the best-performing animal (Sealia) to 76.5% (95% CI = 65.5, 87.5) for the poorest-performing animal (Tinny) and thus was quite similar between animals. Accordingly, no statistically significant differences in performance between animals were found (Mann–Whitney, $14 \leq U \leq 27$, $-0.36 \leq z \leq -0.08$, $p > .05$ for all pairwise comparisons between individuals).

Training Effects

The mean discrimination performance of the animals across the five sets of experiments (corresponding to the five chemical classes that were tested consecutively) was quite stable. Error rates did not differ systematically as a function of the order of the experiments (Spearman, $r_s = -0.09$, $p > .05$) and thus no training or learning effect was found. This was true at the group level as well as for each of the five individual animals. Similarly, there was

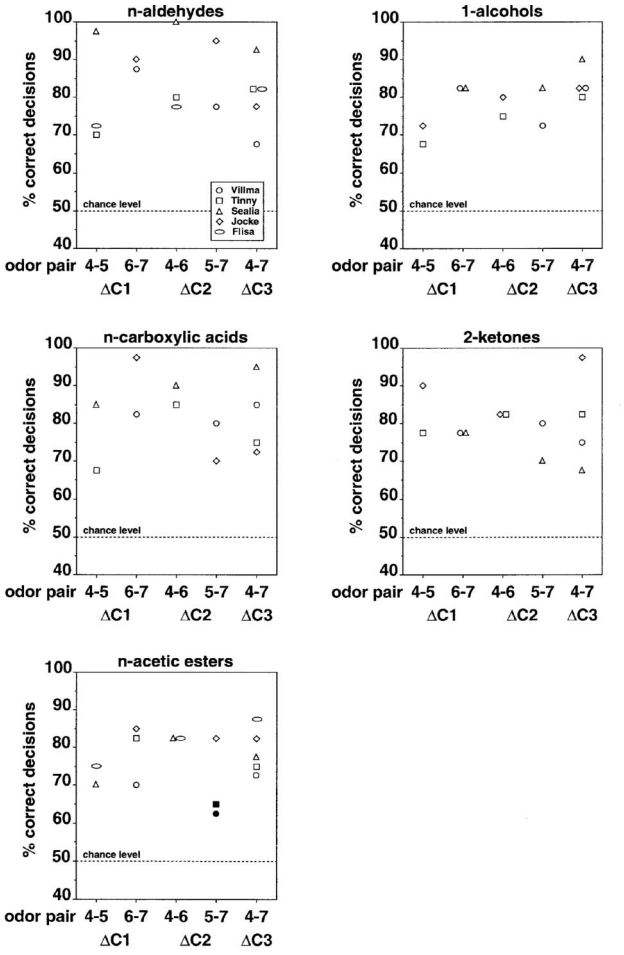

Figure 1. Performance of South African fur seals in discriminating between members of a given homologous series of aliphatic odorants. Each data point represents the percentage of correct decisions from 40 consecutive trials. The different symbols represent data from each of the five individual animals tested (see box in upper left hand panel) and filled symbols indicate odor pairs that were not significantly discriminated above chance (two-tailed binomial test, $p > .05$). Names of odorants corresponding to numbers 4 to 7 are given in Table 1. ΔC1 corresponds to the discrimination of odorants which differ by only one carbon atom, and ΔC2 and ΔC3 to the discrimination of odorants which differ by two and three carbon atoms, respectively. The dotted line indicates the chance level of performance.

no indication that performance of the animals changed systematically within sessions. Error rates did not differ significantly between the beginning and the end of the 20 trials performed per session (Wilcoxon's, $z = -0.13$, $p > .05$) and thus no warming-up or decreasing-attention effects were found. This, too, was true both at the group level as well as for each of the five individual animals.

Comparison of Performance Between Odorant Classes

A repeated measures ANOVA showed that the five chemical classes differed significantly in their discriminability for the fur seals (Friedman, $Chi^2 = 9.74$, $p < .05$). Subsequent pairwise comparisons demonstrated that the n-acetic esters were significantly more difficult to discriminate than the n-aldehydes and the n-carboxylic acids (Wilcoxon's, $z = -2.07$ and -2.33, respectively, $p < .05$, respectively). This is also reflected by the fact that the mean score of correct discriminations across all tasks and animals with a given chemical class was lowest with the n-acetic esters (76.8%; 95% CI = 67.8, 85.8) and highest with the n-aldehydes (83.3%; 95% CI = 75.0, 91.6) and the n-carboxylic acids (82.1%; 95% CI = 71.6, 92.6), with the 2-ketones (80.0%; 95% CI = 67.8, 92.2) and the 1-alcohols (79.2%; 95% CI = 68.8, 89.6) falling in between.

Correlation Between Discrimination Performance and Structural Similarity of Odorants

No statistically significant correlation between discrimination performance and structural similarity in terms of differences in carbon chain length was found in any of the five chemical classes (Spearman, $r_s = -0.09, +0.43, -0.03, -0.03$, and $+0.13$ for the n-aldehydes, 1-alcohols, n-carboxylic acids, 2-ketones and n-acetic esters, respectively; $p > .05$ for all five classes), although a nonsignificant trend toward a positive correlation could be observed with the 1-alcohols (see upper right panel in Figure 1).

Discussion

The results of the present study demonstrate a) that South African fur seals have a well-developed ability to discriminate between structurally related aliphatic odorants, b) that aliphatic n-acetic esters were significantly more poorly discriminated by the fur seals than aliphatic n-aldehydes and n-carboxylic acids, and c) a lack of correlations between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length.

Our finding of a well-developed discrimination ability for structurally related aliphatic odorants is in line with the growing body of evidence suggesting that the sense of smell may play an important and hitherto underestimated role in regulating the behavior of fur seals (Dobson & Jouventin, 2003; Insley, Phillips, & Charrier, 2003; Phillips, 2003; Kowalewsky et al., 2006). This assumption is also supported by a previous study using the same instrumental conditioning paradigm as employed here which demonstrated *Arctocephalus pusillus* to be as fast as mice and rats in mastering intramodal transfer tasks with odor stimuli, and to have an excellent long-term memory for odors which was comparable to that of mice, rats, gerbils and guinea pigs (Laska, Svelander et al., 2008). The notion that the sense of smell may be more important for fur seals than generally believed is further supported by a study that performed phylogenetic comparative analyses from which the authors conclude that "functional differences between pinnipeds (aquatic carnivores) and fissipeds (terrestrial carnivores) appear to have been overstated and may be no greater than those among major fissiped groups" (Binnida-Emonds & Gittleman, 2000). 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 (Hoelzel, 2003).

A comparison of the discrimination performance displayed by the fur seals to that of other species tested previously on the same set of odor pairs demonstrates that this marine mammal does not

perform more poorly than terrestrial species. Humans (Laska & Teubner, 1998, 1999; Laska & Hübener, 2001), squirrel monkeys (Laska & Freyer, 1997; Laska & Teubner, 1998; Laska, Trolp, et al., 1999), and honeybees (Laska, Galizia et al., 1999) failed with three, two, and one of the 25 odor pairs, respectively. Only mice tested on the same stimulus combinations as the fur seals successfully discriminated between all 25 odor pairs (Laska et al., 2007; Laska, Rosandher, et al., 2008). It is interesting to note, however, that none of the four terrestrial species failed with odor pairs involving n-acetic esters and that none of them performed poorer with this class of odorants compared to the other four chemical classes tested.

Our finding that the fur seals performed significantly more poorly in discriminating between aliphatic n-acetic esters than between n-aldehydes and n-carboxylic acids is in line with the idea that the chemical environment in which an animal develops and lives, or in which a species evolves, may strongly affect its olfactory capabilities (Ayabe-Kanamura et al., 1998; Yee & Wysocki, 2001; Mandairon et al., 2006). Given the plethora of odors found in most chemical environments it should not be surprising that none of them has been completely characterized so far with regard to its composition of volatile substances. However, as a first approximation it seems reasonable to consider those parts of a given chemical environment that an animal is likely to be exposed to or to interact with regularly. This is certainly true for food-associated odors and for body-borne odors which, in the case of mammals, often serve important functions in the context of social communication and reproduction. Analyses of the odor composition of fish and squid which comprise the food of fur seals revealed that they are characterized by an apparent lack of aliphatic esters whereas other classes of aliphatic odorants such as aldehydes, alcohols, ketones, and carboxylic acids are abundant and determine their odor quality (Refsgaard, Haahr, & Jensen, 1999; Mansur, Bhadra, Takamura, & Matoba, 2003; Morita, Kubota, & Aishima, 2003). The relative proportions of aliphatic aldehydes, ketones, and carboxylic acids have even been shown to be indicative of the maturity and/or nutritive value of fish (da Cunha Veloso, da Silva, Santos, & de Andrade, 2001; Iverson, Frost, & Lang, 2002; Alinelli et al., 2007) and thus a well-developed ability to discriminate between odorants from these chemical classes appears to be adaptive for fur seals. Similarly, the body odors of fur seals are dominated by a mixture of aliphatic carboxylic acids and are lacking esters (Cadwallader & Shahidi, 2001; Arnould, Nelson, Nichols, & Oosthuizen, 2005; Koep et al., 2007). Thus, here too, the ability to discriminate well between body-borne carboxylic acids appears to be adaptive for fur seals whereas an ability to distinguish between esters is unlikely to be of particular value in this context.

This raises the question as to why the fur seals did not fail with all odor pairs involving n-acetic esters? First, we do not know whether aliphatic esters are indeed more or less absent from the marine chemical environment as our knowledge about its composition is limited. The fact that they are rare in the food and the body-borne odors of fur seals does not exclude the possibility that esters may occur in other parts of the marine chemical environment or in behavioral contexts we have not considered although both possibilities are not very likely. Second, all five chemical classes of odorants employed in the present study comprise comparatively small and flexible molecules which have been shown to interact with a variety of mammalian olfactory receptor types (Johnson & Leon, 2007) which also plausibly explains why all n-acetic esters tested were clearly perceived (although not necessarily discriminated to the same degree) by the fur seals. Third, it should not be forgotten that the ancestors of marine mammals were terrestrial and therefore the fur seals' olfactory system may have retained at least a basic ability to perceive and discriminate between esters.

The idea that the composition of an animal's chemical environment affects its olfactory performance is supported by some other studies. Laska and Galizia (2001) demonstrated that the ability of honeybees to discriminate between enantiomeric odor pairs correlates highly significantly with the frequency of occurrence of these terpenoids in the odors of nectar-bearing flowers. Similarly, Laska and coworkers showed that the ability of frugivorous squirrel monkeys to discriminate between fruit-typical aliphatic esters is markedly better than their ability to distinguish between other classes of aliphatic odorants (Laska & Freyer, 1997; Laska & Teubner, 1998; Laska, Galizia et al., 1999).

Whether such differences in an animal's ability to discriminate between members of different chemical classes are due to ontogenetic factors and thus represent a trait that is only typical for an individual or due to its phylogeny and thus represents a trait that is typical for the species as a whole is difficult to decide. This is particularly true as studies in a variety of species have demonstrated that repeated exposure to odors and associated learning processes may markedly increase olfactory discrimination capabilities (humans: Ayabe-Kanamura et al., 1998; rats: Mandairon et al., 2006; mice: Takiguchi, Okuhara, Kuroda, Kato, & Ohtake, 2008). The fur seals employed in the present study were born and raised in captivity. However, both their daily diet and their enclosure met the behavioral requirements of this marine mammal and were as similar to their natural diet and environment as possible, even including a maritime microclimate as Kolmården Zoo is situated directly on the coast of the Baltic Sea. Thus, we have no reason to believe that exposure to odors that are lacking or underrepresented in the natural environment of the fur seals affected the discrimination performance of our captive animals.

A final aspect of the present study is our finding of a lack of correlations between discrimination performance and structural similarity of odorants in all five chemical classes. This finding is in contrast to studies in humans (Laska & Teubner, 1998, 1999; Laska & Hübener, 2001), squirrel monkeys (Laska & Freyer, 1997; Laska & Teubner, 1998; Laska, Trolp, et al., 1999) and honeybees (Laska, Galizia, et al., 1999) which all displayed such correlations with all five chemical classes. However, mice tested on the same odor pairs as the fur seals showed such correlations only with the n-acetic esters and 2-ketones, but not with the 1-alcohols, n-aldehydes, and n-carboxylic acids, and thus with two of the five chemical classes (Laska, Rosandher, et al., 2008). Thus, the present results lend further support to the notion that regular connections between the perceived quality of odorants and their molecular structural properties are not a general phenomenon but appear to be odorant class- and species-specific.

Taken together, the results of the present study support the assumptions that the sense of smell may play an important and hitherto underestimated role in the control of behavior in fur seals, and that the marine chemical environment may affect the olfactory discrimination capabilities of this pinniped species. Future studies

should aim at determining olfactory detection thresholds in furs seals as not only discrimination performance but also olfactory sensitivity may be correlated with a species' chemical environment.

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