Chem. Senses 29: 101–109, 2004 DOI: 10.1093/chemse/bjh010

Olfactory Sensitivity for Carboxylic Acids in Spider Monkeys and Pigtail Macaques

Matthias Laska[1], Alexandra Wieser[1], Rosa Mariela Rivas Bautista[2] and Laura Teresa Hernandez Salazar[2]

[1]Department of Medical Psychology, University of Munich Medical School, Goethestr. 31, D-80336 Munich, Germany and [2]Instituto de Neuro-Etologia, Universidad Veracruzana, Xalapa, Mexico

Correspondence to be sent to: Matthias Laska, Department of Medical Psychology, University of Munich Medical School, Goethestr. 31, D-80336 Munich, Germany. e-mail: laska@imp.med.uni-muenchen.de

Abstract

Using a conditioning paradigm, the olfactory sensitivity of four spider monkeys and four pigtail macaques for a homologous series of carboxylic acids (*n*-propionic acid to *n*-heptanoic acid) was investigated. With only few exceptions, the animals of both species significantly discriminated concentrations <1 p.p.m. from the odorless solvent and in several cases individual monkeys even demonstrated thresholds <1 p.p.b. The results showed (i) both primate species to have a well-developed olfactory sensitivity for carboxylic acids, which for some substances matches or even is markedly better than that of species such as the rat or the dog and (ii) a significant correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the carboxylic acids in both species tested. These findings lend further support to the growing body of evidence suggesting that between-species comparisons of the number of functional olfactory receptor genes or of neuroanatomical features are poor predictors of olfactory performance, and that general labels such as 'microsmat' or 'macrosmat'—which usually are based on allometric comparisons of olfactory brain structures—are inadequate to describe a species' olfactory capabilities.

Key words: carboxylic acids, detection thresholds, nonhuman primates, olfactory sensitivity

Introduction

Recent genetic studies have demonstrated that the mammalian genome is coding for approximately 1000 different types of olfactory receptors (Issel-Tarver and Rine, 1997; Young and Trask, 2002). Further, it has been reported that the proportion of functional olfactory receptor (OR) genes may be markedly reduced in some mammalian species. Humans, for example, are said to have only ~350 functional OR genes, with the rest being pseudogenes which are presumed not be transcribed into proteins, and Old World primates such as macaques are supposed to have only 700 functional genes coding for olfactory receptors, whereas New World primates such as the spider monkey are said to have the full repertoire of ~1000 functional OR genes (Glusman *et al.*, 2001; Rouquier *et al.*, 2000). This led the authors of such genetic studies to conclude that the reduction in the number of functional OR genes in humans and Old World primates should explain the 'greatly reduced sense of smell in primates compared to other mammals such as dogs or rodents' (Rouquier *et al.*, 2000). However, physiological evidence supporting a positive correlation between the number of functional OR genes and olfactory performance is largely lacking.

The view that primates are 'visual' animals with a poorly developed sense of smell has a long-standing tradition (King and Fobes, 1974; Walker and Jennings, 1991) which is mainly, if not exclusively, based on an interpretation of neuroanatomical features such as the relative size of olfactory brain structures or the absolute size of olfactory epithelia (Stephan *et al.*, 1988; Brown, 2001). However, here too, physiological evidence supporting a positive correlation between allometric measures of neuroanatomical features and olfactory performance is largely lacking (De Winter and Oxnard, 2001; Schoenemann, 2001).

Laska and Hudson (1993a) introduced a new testing paradigm which, for the first time, allowed the assessment of olfactory performance in a nonhuman primate species using psychophysical methods. Subsequent studies demonstrated that squirrel monkeys possess highly developed olfactory discrimination abilities for structurally related monomolecular substances (Laska and Freyer, 1997; Laska and

Teubner, 1998; Laska *et al.*, 1999a,b), artificial odor mixtures (Laska and Hudson, 1993b) as well as for conspecific urine odors (Laska and Hudson, 1995). Further, these studies showed that *Saimiri sciureus* has an excellent long-term memory for odors (Laska *et al.*, 1996), a well-developed olfactory sensitivity for carboxylic acids (Laska *et al.*, 2000), acetic esters (Laska and Seibt, 2002a), aliphatic alcohols (Laska and Seibt, 2002b) and aldehydes (Laska *et al.*, 2003b) and is capable of rapid odor learning (Laska and Hudson, 1993a).

Laska and co-workers adapted this method to the species-specific needs of two other primate species, the spider monkey and the pigtail macaque and demonstrated that squirrel monkeys are not the only primate species with surprisingly well-developed olfactory capabilities (Hübener and Laska, 2001; Laska *et al.*, 2003a). Further, their behavioral paradigm allows us to reliably compare olfactory performance between primate species differing both in their number of functional OR genes and in the relative size of their olfactory brain structures.

Therefore, the aims of the present study are twofold: first, to gain further insight into the basic perceptual capacities of nonhuman primates by determining olfactory detection thresholds in spider monkeys and pigtail macaques for a set of monomolecular odorants and, secondly, to assess whether the number of functional OR genes or neuroanatomical features are reliable predictors of olfactory performance by comparing the detection threshold values of the two primate species tested here with each other and to those of human subjects and other mammals. The use of a homologous series of carboxylic acids allowed us to additionally address the question whether structural features of stimulus molecules such as carbon chain length affect detectability in a regular manner.

Materials and methods

Animals

Testing was carried out using four adult female spider monkeys (*Ateles geoffroyi*) and three male and one female pigtail macaques (*Macaca nemestrina*). The spider monkeys were maintained as part of a breeding colony at the Parque de la Flora y Fauna Silvestre Tropical, Catemaco, Veracruz, Mexico and the pigtail macaques were maintained as a social group at the Department of Medical Psychology at the University of Munich Medical School. All animals had served as subjects in previous olfactory experiments (Laska *et al.*, 2003b; Hernandez Salazar *et al.*, 2003) and were completely familiar with the basic test procedure. The animals of both species were housed in large group enclosures with adjacent single cages which could be closed by sliding doors to allow the temporary separation of animals for individual testing. The animals were trained to enter their test cage voluntarily and remained in visual and auditory contact with the rest of their social group during testing. Animals were fed fresh fruit and vegetables, with *ad libitum* access to water.

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 German and Mexican laws.

Behavioral test

Both spider monkeys and pigtail macaques were tested using a two-choice instrumental conditioning paradigm (Hübener and Laska, 2001; Laska *et al.*, 2003a). Two cube-shaped open PVC containers (side length 5.5 cm) were attached to a metal bar (50 cm long and 6 cm wide) at a distance of 22 cm. Each container was equipped with a hinged metallic lid, hanging 2 cm down the front of the container. From the center of the front part of the lid, a pin of 3 cm length extended towards the animal and served as a lever to open the lid. A clip on top of each lid held an absorbent paper strip (70 × 10 mm) impregnated with 10 µl of an odorant signalling either that the container held a Kellogg's Honey Loop® food reward (S+) or that it did not (S–). The odorized paper strips extended 5 cm into the test cage when the apparatus was attached to the front of the cage.

When a monkey tried to open a container without prior sniffing, the experimenter held a chain connected to the lid tight so that the animal could not move the lid. After the olfactory investigation had taken place, the chain was loosend and the animal could open the container.

In each test trial, each monkey sniffed at both options for as often as it liked and then decided to open one of the two boxes. After each decision, the apparatus was removed from the mesh and—out of sight of the test animal—was prepared for the next trial by baiting the container bearing the S+ again and adopting a pseudorandomized sequence of presentations of the S+ on the left or on the right side. Ten such trials were conducted per animal and session and usually three sessions were conducted per day.

Olfactory detection thresholds were determined by testing the animals' ability to discriminate between an absorbent paper strip scented with increasing dilutions of an odorant used as S+ and the alternative paper strip scented with the odorless solvent alone used as S–. Starting with a dilution of 1:100, each odorant was successively presented in 10-fold dilution steps for three sessions each until an animal failed to significantly discriminate the odorant from the solvent. Subsequently, this descending staircase procedure was repeated for three more sessions per dilution step. Finally, intermediate dilutions were tested in order to determine the threshold value more exactly. If, for example, an animal significantly discriminated a 1:10 000 dilution from the solvent, but failed to do so with a 1:100 000 dilution, then the animal was presented with a 1:30 000 dilution. To prevent the more challenging conditions leading to extinction or to a decline in the animals' motivation, these were always followed by a return to an easy control task. This

consisted of the discrimination between a 100-fold dilution of the S+ and the odorless solvent as S–.

Odorants

A set of five odorants was used: *n*-propionic acid, *n*-butanoic acid, *n*-pentanoic acid, *n*-hexanoic acid and *n*-heptanoic acid. The rationale for choosing these substances was to assess the monkeys' sensitivity for odorants representing members of a homologous series of aliphatic compounds, that is, substances sharing the same functional group but differing in carbon chain length, allowing us to assess the impact of this structural feature on detectability. Further, carboxylic acids have been shown to comprise the main components of body-borne odors (Flood, 1985) and, in particular, of primate vaginal odors (Matsumoto-Oda *et al.*, 2003) and thus are believed to be behaviorally relevant for both species tested in the context of olfactory social communication.

All substances were obtained from Merck (Darmstadt, Germany) and had a nominal purity of at least 99%. They were diluted using odorless diethyl phthalate (Merck) as the solvent. The order of presentation of odorants did not follow the sequence mentioned above, but was pseudo-randomized between animals.

Data analysis

In the method described here, the animal had two options: (i) to correctly open the container which carries the positive stimulus (hit) and (ii) to falsely open the container which carries the negative stimulus (false alarm). For each individual animal, the percentage of hits from the best three consecutive sessions per dilution step, comprising at total of 30 decisions, was calculated and taken as the measure of performance.

Significance levels were determined by calculating binomial *z*-scores corrected for continuity (Siegel and Castellan, 1988) from the number of correct and false responses for each individual and condition. All tests were two-tailed and the alpha level was set at 0.05.

Correlations between olfactory threshold values and carbon chain length of the substances tested were calculated using both the Spearman rank-correlation test and second order polynomial regression analysis.

Across-species comparisons of performance were performed using the Mann–Whitney test for independent samples.

Results

Spider monkeys

Figure 1 shows the performance of the spider monkeys in discriminating between various dilutions of a given odorant and the odorless solvent. All four animals significantly distinguished dilutions as low as $1{:}3 \times 10^5$ *n*-propionic acid, $1{:}3 \times 10^6$ *n*-butanoic acid, $1{:}3 \times 10^5$ *n*-pentanoic acid, $1{:}3 \times 10^6$ *n*-hexanoic acid and $1{:}3 \times 10^6$ *n*-heptanoic acid from the solvent (binomial test, $P < 0.05$), with single individuals even scoring better.

The individual spider monkeys demonstrated very similar threshold values and with two of the five odorants (*n*-butanoic acid and *n*-heptanoic acid) they differed only by a dilution factor of ten between the highest- and the lowest-scoring animal. In the case of *n*-propionic acid, *n*-pentanoic acid and *n*-hexanoic acid they even showed identical threshold values.

Figure 2 shows the olfactory detection threshold values (expressed as vapour phase concentrations) of the spider monkeys as a function of carbon chain length of the carboxylic acids tested. When applying linear correlational statistics to the data, a significant negative correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the carboxylic acids was found (Spearman, $r_s = -0.58$, $P < 0.02$).

Table 1 summarizes the threshold dilutions for both the best- and the poorest-performing spider monkeys and shows various measures of corresponding vapour phase concentrations (Weast, 1987) allowing readers to easily compare the data obtained in the present study to those reported by other authors using one of these convertible measures. All threshold dilutions correspond to vapour phase concentrations <1 p.p.m. and in several cases the animals were even able to detect concentrations <1 p.p.b.

Pigtail macaques

Figure 3 shows the performance of the pigtail macaques in discriminating between various dilutions of a given odorant and the odorless solvent. All four animals significantly distinguished dilutions as low as $1{:}1 \times 10^4$ *n*-propionic acid, $1{:}1 \times 10^7$ *n*-butanoic acid, $1{:}3 \times 10^5$ *n*-pentanoic acid, $1{:}1 \times 10^4$ *n*-hexanoic acid and 1:300 *n*-heptanoic acid from the solvent (binomial test, $P < 0.05$), with single individuals even scoring better.

The individual pigtail macaques demonstrated very similar threshold values and with three of the five odorants they differed only by a dilution factor of three (*n*-propionic acid) or ten (*n*-hexanoic acid and *n*-heptanoic acid) between the highest- and the lowest-scoring animals. The largest difference in sensitivity for a given odorant between individuals comprised a dilution factor of 33 and was found with *n*-pentanoic acid.

Figure 4 shows the olfactory detection threshold values (expressed as vapour phase concentrations) of the pigtail macaques as a function of carbon chain length of the carboxylic acids tested. When applying linear correlational statistics to the data, no significant correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the carboxylic acids was found (Spearman, $r_s = +0.24$, $P > 0.05$). However, when removing the threshold values for the substance with the shortest carbon chain tested, i.e. *n*-propionic acid, from the calcula-

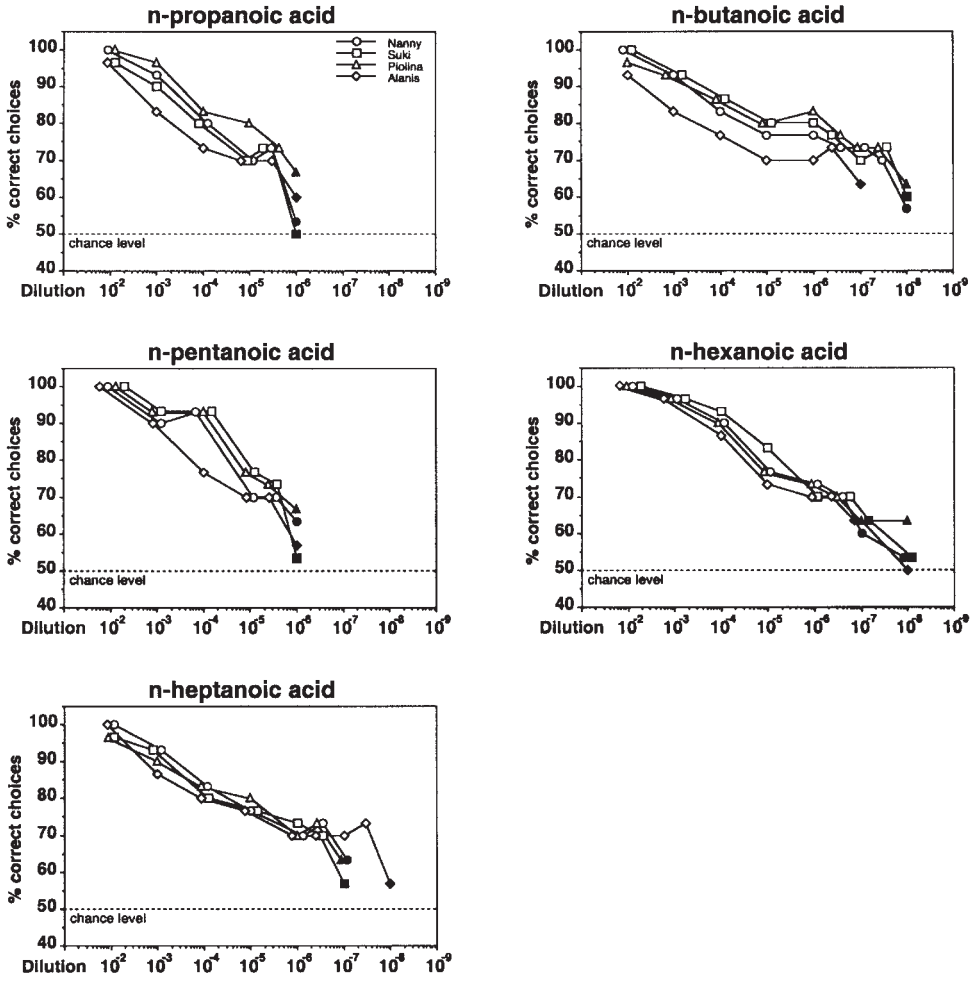

Figure 1 Performance of four spider monkeys in discriminating between various dilutions of a given odorant and the odorless solvent. Each data point represents the percentage of correct choices from 30 decisions. Filled symbols indicate dilutions that were not discriminated above chance level (binomial test, $P > 0.05$).

tions, a statistically significant positive correlation was found (Spearman, $r_s = +0.93$, $P < 0.01$). Thus, the correlation between olfactory detection thresholds of the pigtail macaques and carbon chain length of the carboxylic acid tested can best be described as a U-shaped function (second order polynomial regression, $r = 0.74$, $P < 0.01$).

Table 2 summarizes the threshold dilutions for both the best- and the poorest-performing pigtail macaques and shows various measures of corresponding vapour phase concentrations (Weast, 1987). With only few exceptions, the threshold dilutions correspond to vapour phase concentrations <1 p.p.m., and in several cases the animals were even able to detect concentrations <1 p.p.b.

Discussion

The results of this study demonstrate, for the first time, that spider monkeys and pigtail macaques have a well-developed olfactory sensitivity for monomolecular odorants belonging to the class of carboxylic acids. Further, they show a signifi-

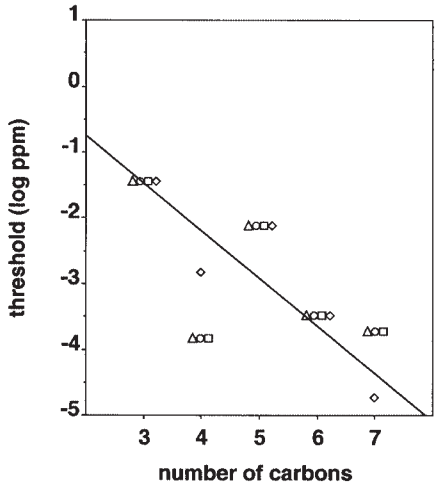

Figure 2 Olfactory detection threshold values (expressed as vapour phase concentrations) of the spider monkeys as a function of carbon chain length of the carboxylic acids tested. The solid line indicates the regression with the best goodness-of-fit according to the Spearman rank-correlation test.

Table 1 Olfactory detection threshold values in *Ateles geoffroyi*

	Dilution	Molecules/cm^3	p.p.m.	Log p.p.m.	mol/l	Log mol/l
n-propionic acid	$1{:}3 \times 10^5$	9.7×10^{11}	0.036	–1.44	1.6×10^{-9}	–8.79
n-butanoic acid	$1{:}3 \times 10^6$	4.0×10^{10}	0.0015	–2.83	6.6×10^{-11}	–10.18
	$1{:}3 \times 10^7$	4.0×10^9	0.00015	–3.83	6.6×10^{-12}	–11.18
n-pentanoic acid	$1{:}3 \times 10^5$	2.0×10^{11}	0.0074	–2.12	3.3×10^{-10}	–9.48
n-hexanoic acid	$1{:}3 \times 10^6$	9.0×10^9	0.0003	–3.48	1.5×10^{-11}	–10.83
n-heptanoic acid	$1{:}3 \times 10^6$	5.0×10^9	0.0002	–3.73	8.3×10^{-12}	–11.08
	$1{:}3 \times 10^7$	5.0×10^8	0.00002	–4.73	8.3×10^{-13}	–12.08

With each stimulus, the upper line represents the lowest concentration that the poorest-performing animal was able to detect, and the lower line represents the lowest concentration that the best-performing animal was able to detect.

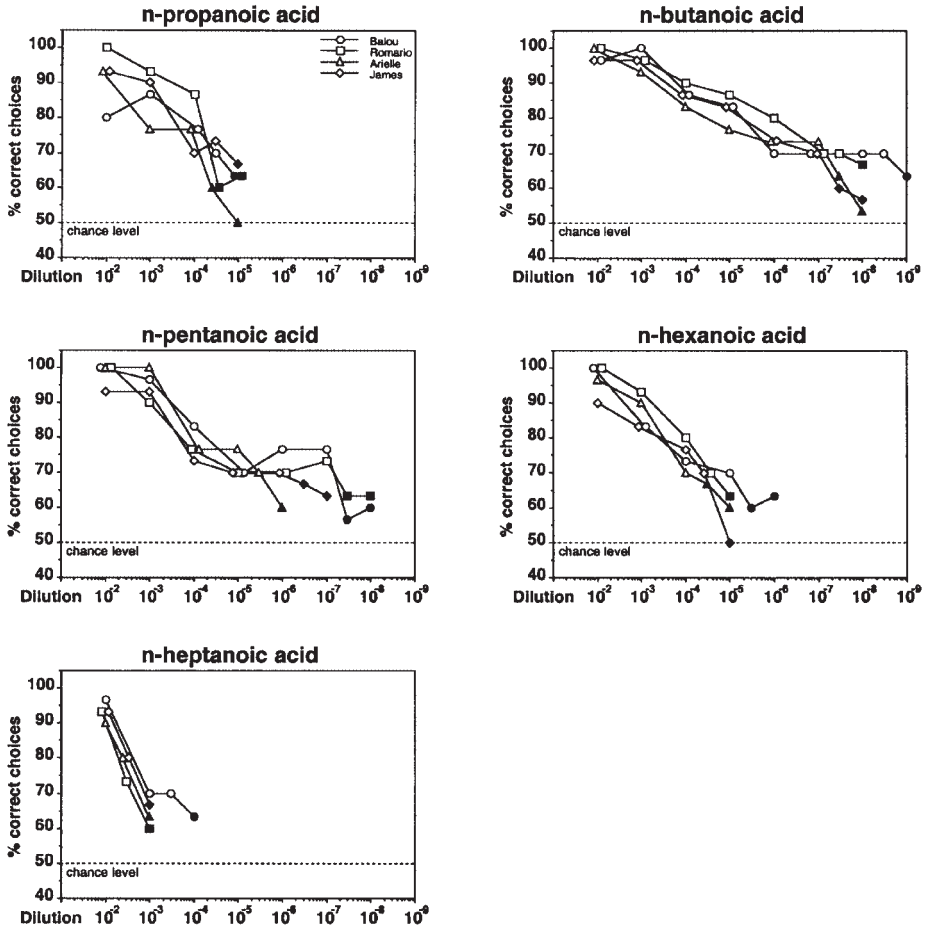

Figure 3 Performance of four pigtail macaques in discriminating between various dilutions of a given odorant and the odorless solvent. Each data point represents the percentage of correct choices from 30 decisions. Filled symbols indicate dilutions that were not discriminated above chance level (binomial test, $P > 0.05$).

cant correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the substances tested. This correlation was linear and had a negative slope with the spider monkeys, and was U-shaped, i.e. non-linear with the pigtail macaques.

Although only four animals per species were tested, the results appear robust as interindividual variability was remarkably low and generally smaller than the range reported in studies on human olfactory sensitivity, that is, within three orders of magnitude (Stevens *et al.*, 1988). In

fact, for the majority of substances tested there was even only a factor of three or ten between the threshold values of the highest- and the lowest-scoring animal. Further, with all substances tested, the animals' performance with the lowest concentrations presented dropped to chance level, suggesting that the statistically significant discrimination between higher concentrations of an odorant and the odorless diluent was indeed based on olfactory perception and not on other cues.

Figure 5 compares the olfactory detection threshold values obtained with the spider monkeys and the pigtail mcaques for the substances tested to those from other mammalian species. Although such across-species comparisons should be considered with caution as different methods may lead to widely differing results, it seems admissible to state that *Ateles geoffroyi* and *Macaca nemestrina* are far from being considered 'microsmatic', i.e. species with a poorly developed sense of smell. With *n*-propionic acid and *n*-pentanoic acid, both spider monkeys and pigtail macaques demonstrated olfactory threshold values that are at least one order of magnitude lower than those of the rat (Passe and Walker, 1985), which is traditionally regarded as 'macrosmatic', i.e. a species with a highly developed sense of smell. Similarly, the sensitivity of the spider monkey for *n*-hexanoic acid and for *n*-heptanoic acid, and the sensitivity of the pigtail macaque for *n*-butanoic acid and for *n*-pentanoic acid was found to be markedly higher than that of the dog (Passe and Walker, 1985), another species usually considered as 'macrosmatic'. This is remarkable considering that the relative size of the rat's or the dog's brain structures devoted to processing olfactory information is considerably larger than that of any primate species (Stephan *et al.*, 1988).

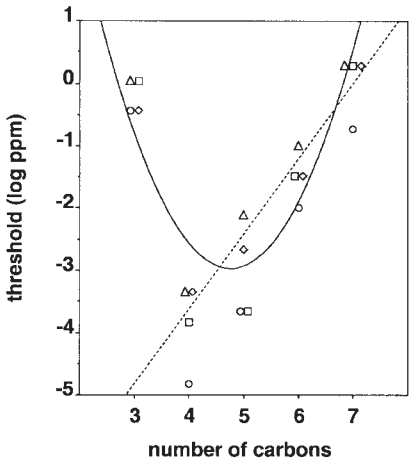

Figure 4 Olfactory detection threshold values (expressed as vapour phase concentrations) of the pigtail macaques as a function of carbon chain length of the carboxylic acids tested. The solid line indicates the regression with the best goodness-of-fit according to second order polynomial regression analysis, and the dashed line indicates the regression with the best goodness-of-fit according to the Spearman rank-correlation test when the data for n-propionic acid are removed from the calculations.

It should be mentioned that all animal data shown in Figure 5 are taken from studies that employed instrumental conditioning paradigms (and not spontaneous preference or habituation/dishabituation paradigms) and it is commonly agreed that such methods provide the best approximation of an animal's sensory capabilities (Hastings, 2003).

A comparison of the olfactory performance between the two primate species tested here—using the same conditioning paradigm—shows that neither is generally more sensitive than the other (Mann–Whitney *U*-test, $P > 0.05$) but rather that the two species differ in their respective patterns of performance across the substances tested (cf. Figures 2 and 4). This is remarkable considering that the pigtail macaque has been shown to have a markedly smaller

Table 2 Olfactory detection threshold values in *Macaca nemestrina*

	Dilution	Molecules/cm^3	p.p.m.	Log p.p.m.	mol/l	Log mol/l
n-propionic acid	$1{:}1 \times 10^4$	2.9×10^{13}	1.07	0.03	4.8×10^{-8}	–7.32
	$1{:}3 \times 10^4$	9.7×10^{12}	0.36	–0.44	1.6×10^{-8}	–7.79
n-butanoic acid	$1{:}1 \times 0^7$	1.2×10^{10}	0.0004	–3.35	2.0×10^{-11}	–10.70
	$1{:}3 \times 10^8$	4.0×10^8	0.000015	–4.83	6.6×10^{-13}	–12.18
n-pentanoic acid	$1{:}3 \times 10^5$	2.0×10^{11}	0.0074	–2.12	3.3×10^{-10}	–9.48
	$1{:}1 \times 10^7$	5.9×10^9	0.00022	–3.66	9.8×10^{-12}	–11.01
n-hexanoic acid	$1{:}1 \times 10^4$	2.7×10^{12}	0.10	–1.00	4.5×10^{-9}	–8.35
	$1{:}1 \times 10^5$	2.7×10^{11}	0.010	–2.00	4.5×10^{-10}	–9.35
n-heptanoic acid	$1{:}3 \times 10^2$	5.0×10^{13}	1.85	0.27	8.3×10^{-8}	–7.08
	$1{:}3 \times 10^3$	5.0×10^{12}	0.185	–0.73	8.3×10^{-9}	–8.08

With each stimulus, the upper line represents the lowest concentration that the poorest-performing animal was able to detect, and the lower line represents the lowest concentration that the best-performing animal was able to detect.

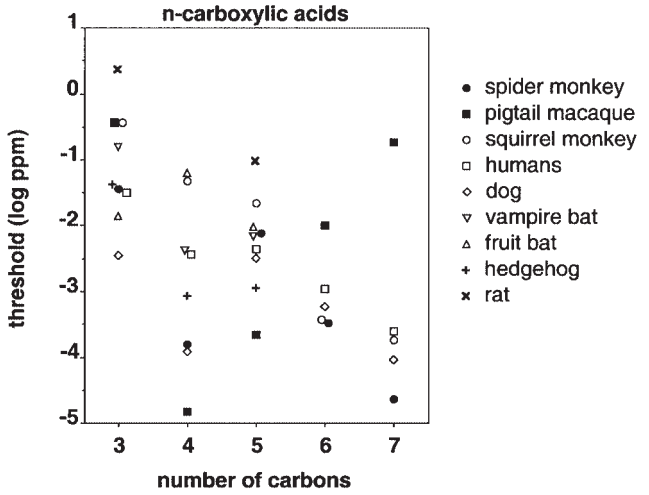

Figure 5 Comparison of the olfactory detection threshold values (expressed as vapour phase concentrations) of the spider monkeys and the pigtail macaques for carboxylic acids to those of other mammalian species. Human data are from Devos *et al.* (1990); animal data are from Passe and Walker (1985), Laska (1990) and Laska *et al.* (2000). Data points of all animal species represent the lowest individual threshold value reported. Data points of the human subjects represent mean values.

relative size of olfactory brain structures compared to the spider monkey (Stephan *et al.*, 1988). Similarly, Old World primates such as the pigtail macaque have recently been shown to have only 700 functional genes coding for olfactory receptors whereas New World primates such as the spider monkey are said to have the full repertoire of ~1000 functional OR genes typically found in mammals (Rouquier *et al.*, 2000).

Interestingly, human subjects—that are known to have even smaller olfactory brain structures relative to overall brain size than monkeys (Stephan *et al.*, 1988) and to have an even more reduced number of only ~350 functional OR genes (Glusman *et al.*, 2001)—do not generally show higher olfactory detection thresholds for carboxylic acids compared to nonhuman primates (cf. Figure 5). This leads us to conclude that between-species comparisons of the number of functional olfactory receptor genes or of neuroanatomical features are poor predictors of olfactory performance. This idea is also supported by earlier studies that reported spider monkeys, squirrel monkeys and pigtail macaques to show an olfactory sensitivity for acetic esters (Laska and Seibt, 2002a; Hernandez Salazar *et al.*, 2003) and aliphatic alcohols (Laska and Seibt, 2002b) that is not generally inferior to and in several cases even clearly better than that of the mouse, the rabbit, the rat, or the dog, all species believed to have a very keen sense of smell.

The second main finding of the present study, a significant correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the carboxylic acids in both species tested, is also in line with earlier studies on olfactory sensitivity for homologous series of substances in both human and nonhuman primates. With regard to the carboxylic acids tested here, both squirrel monkeys (Laska *et al.*, 2000) and human subjects (Cometto-Muniz *et al.*, 1998) have been reported to show a negative correlation between threshold values and carbon chain length. Similarly, either linear or U-shaped correlations between olfactory sensitivity and this structural property of odorant molecules have been reported for acetic esters, aliphatic alcohols and aldehydes in squirrel monkeys, pigtail macaques and human subjects (Cometto-Muniz and Cain, 1991; Cometto-Muniz *et al.*, 1998; Laska and Seibt, 2002a,b; Laska *et al.*, 2003b) and for acetic esters in spider monkeys (Hernandez Salazar *et al.*, 2003). This suggests that regular associations between olfactory sensitivity and carbon chain length of aliphatic odorants may not be restricted to the substance class and species tested here, but may represent a more general phenomenon.

Carbon chain length of odorant molecules has been shown to be an important determinant of the specificity of interaction between stimulus and receptor (Kaluza and Breer, 2000) as well as of the chemotopic organization and thus of odor quality coding within the olfactory bulb (Johnson and Leon, 2000). However, with regard to differences in sensitivity for members of a homologous series of substances at the organismal level it should be considered that the quantitative distribution of individual receptor types, each responding selectively to a limited range of carbon chain lengths and functional groups (Mori and Yoshihara, 1995; Araneda *et al.*, 2000), may differ between species. This may plausibly explain why one species may show a linear correlation between sensitivity and carbon chain length of a given class of substances whereas another species may show a nonlinear, e.g. U-shaped correlation, or may show no correlation at all. A heightened expression of a given receptor type with a specific molecular receptive range may also explain phenomena such as the markedly higher sensitivity of the pigtail macaques for *n*-butanoic acid compared to its neighbour in the homologous series, *n*-propionic acid (cf. Figure 4). A possible reason underlying such phenomena is that repeated exposure to a given odorant—perhaps due to its high abundance in the odorous environment of or its biological significance for an animal—may induce an increased expression of a corresponding receptor type (Yee and Wysocki, 2001).

In conclusion, the results of the present study provide further evidence of a well-developed olfactory sensitivity in two nonhuman primate species, the spider monkey and the pigtail macaque. These findings lend additional support to the notion that general labels such as 'microsmat' or 'macrosmat'–which usually are based either on allometric comparisons of olfactory brain structures or on the number of functional olfactory receptor genes—are inadequate to describe a species' olfactory capabilities.

Acknowledgements

Financial support by the Deutsche Forschungsgemeinschaft (La 635/10-2) and the Volkswagen Foundation (I/77 391) is gratefully acknowledged. L.T.H.S. was awarded a grant (No. 124786) by the Conacyt Mexico.

References

Araneda, R.C., Kini, A.D. and **Firestein, S.** (2000) *The molecular receptive range of an odorant receptor.* Nat. Neurosci., 3, 1248–1255.

Brown, W.M. (2001) *Natural selection of mammalian brain components.* Trends Ecol. Evol., 16, 471–473.

Cometto-Muniz, J.E. and **Cain, W.S.** (1991) *Nasal pungency, odor, and eye irritation thresholds for homologous acetates.* Pharmacol. Biochem. Behav., 39, 983–989.

Cometto-Muniz, J.E., Cain, W.S. and **Abraham, M.H.** (1998) *Nasal pungency and odor of homologous aldehydes and carboxylic acids.* Exp. Brain Res., 118, 180–188.

Devos, M., Patte, F., Rouault, J., Laffort, P. and **van Gemert, L.J.** (eds) (1990) Standardized Human Olfactory Thresholds. IRL Press, Oxford.

De Winter, W. and **Oxnard, C.E.** (2001) *Evolutionary radiations and convergences in the structural organization of mammalian brains*. Nature, 409, 710–714.

Flood, P. (1985) *Sources of significant smells : the skin and other organs.* In Brown, R.E. and MacDonald, D.W. (eds), Social Odours in Mammals. Clarendon Press, Oxford, pp. 19–36.

Glusman, G., Yanai, I., Rubin, I. and **Lancet, D.** (2001) *The complete human olfactory subgenome.* Genome Res., 11, 685–702.

Hastings, L. (2003) *Psychophysical evaluaton of olfaction in nonhuman mammals.* In Doty, R.L. (ed.), Handbook of Olfaction and Gustation, 2nd edn. Marcel Dekker, New York, pp. 385–401.

Hernandez Salazar, L.T., Laska, M. and **Rodriguez Luna, E.** (2003) *Olfactory sensitivity for aliphatic esters in spider monkeys,* Ateles geoffroyi. Behav. Neurosci., 117, 1142–1149.

Hübener, F. and **Laska, M.** (2001) *A two-choice discrimination method to assess olfactory performance in pigtailed macaques,* Macaca nemestrina. Physiol. Behav., 72, 511–519.

Issel-Tarver, L. and **Rine, J.** (1997) *The evolution of mammalian olfactory receptor genes.* Genetics, 145, 185–195.

Johnson, B.A. and **Leon, M.** (2000) *Odorant molecular length: one aspect of the olfactory code.* J. Comp. Neurol., 426, 330–338.

Kaluza, J.F. and **Breer, H.** (2000) *Responsiveness of olfactory neurons to distinct aliphatic aldehydes*. J. Exp. Biol., 203, 927–933.

King, J.E. and **Fobes, J.L.** (1974) *Evolutionary changes in primate sensory capacities.* J. Hum. Evol., 3, 435–443.

Laska, M. (1990) *Olfactory sensitivity to food odor components in the short-tailed fruit bat,* Carollia perspicillata. J. Comp. Physiol. A, 166, 395–399.

Laska, M. and **Freyer, D.** (1997) *Olfactory discrimination ability for aliphatic esters in squirrel monkeys and humans*. Chem. Senses, 22, 457–465.

Laska, M. and **Hudson, R.** (1993a) *Assessing olfactory performance in a New World primate,* Saimiri sciureus. Physiol. Behav., 53, 89–95.

Laska, M. and **Hudson, R.** (1993b) *Discriminating parts from the whole: determinants of odor mixture perception in squirrel monkeys,* Saimiri sciureus. J. Comp. Physiol. A, 173, 249–256.

Laska, M. and **Hudson, R.** (1995) *Ability of female squirrel monkeys (Saimiri sciureus) to discriminate between conspecific urine odours*. Ethology, 99, 39–52.

Laska, M. and **Seibt, A.** (2002a) *Olfactory sensitivity for aliphatic esters in squirrel monkeys and pigtail macaques*. Behav. Brain Res., 134, 165–174.

Laska, M. and **Seibt, A.** (2002b) *Olfactory sensitivity for aliphatic alcohols in squirrel monkeys and pigtail macaques*. J. Exp. Biol., 205, 1633–1643.

Laska, M. and **Teubner, P.** (1998) *Odor structure-activity relationships of carboxylic acids correspond between squirrel monkeys and humans*. Am. J. Physiol., 274, R1639–R1645.

Laska, M., Alicke, T. and **Hudson, R.** (1996) *A study of long-term odor memory in squirrel monkeys,* Saimiri sciureus. J. Comp. Psychol., 110, 125–130.

Laska, M., Liesen, A. and **Teubner, P.** (1999a) *Enantioselectivity of odor perception in squirrel monkeys and humans.* Am. J. Physiol., 277, R1098–R1103.

Laska, M., Trolp, S. and **Teubner, P.** (1999b) *Odor structure–activity relationships correspond between human and non-human primates*. Behav. Neurosci., 113, 998–1007.

Laska, M., Seibt, A. and **Weber, A.** (2000) *'Microsmatic' primates revisited—olfactory sensitivity in the squirrel monkey*. Chem. Senses, 25, 47–53.

Laska, M., Hernandez Salazar, L.T. and **Rodriguez Luna, E.** (2003a) *Successful acquisition of an olfactory discrimination paradigm by spider monkeys (Ateles geoffroyi).* Physiol. Behav., 78, 321–329.

Laska, M., Hofmann, M. and **Simon, Y.** (2003b) *Olfactory sensitivity for aliphatic aldehydes in squirrel monkeys and pigtail macaques.* J. Comp. Physiol. A, 189, 263–271.

Matsumoto-Oda, A., Oda, R., Hayashi, Y., Murakami, H., Maeda, N., Kumazaki, K., Shimizu, K. and **Matsuzawa, T.** (2003) *Vaginal fatty acids produced by chimpanzees during menstrual cycles.* Folia Primatol., 74, 75–79.

Mori, K. and **Yoshihara, Y.** (1995) *Molecular recognition and olfactory processing in the mammalian olfactory system*. Prog. Neurobiol., 45, 585–619.

Passe, D.H. and **Walker, J.C.** (1985) *Odor psychophysics in vertebrates.* Neurosci. Biobehav. Rev., 9, 431–467.

Rouquier, S., Blancher, A. and **Giorgi, D.** (2000) *The olfactory receptor gene repertoire in primates and mouse: evidence for reduction of the functional fraction in primates*. Proc. Natl Acad. Sci. USA, 97, 2870–2874.

Schoenemann, P.T. (2001) *Brain scaling, behavioral ability and human evolution.* Behav. Brain Sci., 24, 293–295.

Siegel, S. and **Castellan, N.J.** (1988) Nonparametric Statistics for the Behavioral Sciences. McGraw Hill, New York.

Stephan, H., Baron, G. and **Frahm, H.D.** (1988) *Comparative size of brains and brain structures*. In Steklis, H. and Erwin, J. (eds.), Comparative Primate Biology, Vol. 4. Alan R. Liss, New York, pp. 1–38.

Stevens, J.C., Cain, W.S. and **Burke, R.J.** (1988) *Variability of olfactory thresholds.* Chem. Senses, 13, 643–653.

Walker, J.C. and **Jennings, R.A.** (1991) *Comparison of odor perception in humans and animals*. In Laing, D.G., Doty, R.L. and Breipohl, W. (eds), The Human Sense of Smell. Springer, Berlin, pp. 261–280.

Weast, R.C. (1987) Handbook of Chemistry and Physics, 68th edn, CRC Press, Boca Raton, FL.

Yee, K.K. and **Wysocki, C.J.** (2001) *Odorant exposure increases olfactory sensitivity: olfactory epithelium is implicated.* Physiol. Behav., 72, 705–711.

Young, J.M. and **Trask, B.J.** (2002) *The sense of smell: genomics of vertebrate odorant receptors.* Hum. Mol. Genet., 11, 1153–1160.

Accepted November 25, 2003