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‘Microsmatic’ Primates Revisited: Olfactory Sensitivity in the Squirrel Monkey

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Abstract

Using a conditioning paradigm, the olfactory sensitivity of three squirrel monkeys to nine odorants representing different chemical classes as well as members of a homologous series of substances was investigated. The animals significantly discriminated dilutions as low as 1:10 000 *n*-propionic acid, 1:30 000 *n*-butanoic acid and *n*-pentanoic acid, 1:100 000 *n*-hexanoic acid, 1:1Mio *n*-heptanoic acid, 1:30 000 1-pentanol, 1:300 000 1,8-cineole, 1:1Mio *n*-heptanal and 1:30Mio amyl acetate from the near-odorless solvent, with single individuals scoring even slightly better. The results showed (i) the squirrel monkey to have an unexpectedly high olfactory sensitivity, which for some substances matches or even is better than that of species such as the rat or the dog, and (ii) a significant negative correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of carboxylic acids. These findings support the assumptions that olfaction may play a significant and hitherto underestimated role in the regulation of primate behavior, and that the concept of primates as primarily visual and ‘microsmatic’ animals needs to be revised.

Introduction

Primates are typically regarded as visual animals and it is therefore hardly surprising that investigations of primate sensory perception and processing have so far concentrated on this modality. Although considerable attention has also been given to acoustic and somatosensory function, olfaction has been traditionally considered of only minor importance. However, it is becoming increasingly clear from studies of both human and non-human primates that olfaction may, in fact, play a significant part in the regulation of a wide variety of primate behaviors.

In addition to its more obvious role in food identification and selection (Ueno, 1994; Bolen and Green, 1997), there is now evidence from a number of primate species for olfactory involvement in social behaviors such as the establishment and maintenance of rank (Kappeler, 1998), territorial defence (Mertl-Millhollen, 1986), identification of sexual partners (Heymann, 1998), recognition of group members (Epple *et al.*, 1993) and communication of reproductive status (Smith and Abbott, 1998).

This is particularly true for the prosimians and New World monkeys, many of which possess odor-producing skin glands (Epple, 1986) and demonstrate conspicuous marking behaviors (Epple, 1985). In the squirrel monkey, *Saimiri sciureus*, for example, hand-washing with urine (Candland *et al.*, 1980), nasal rubbing and sneezing (Schwartz and Rosenblum, 1980), back rubbing (Hennessy *et al.*, 1978) and anogenital inspection (Ploog *et al.*, 1963) all appear to be associated with olfactory communication, and olfactory recognition of mothers by infants has also been demonstrated (Kaplan *et al.*, 1977).

Despite such observations, there have been only few systematic studies of olfactory-guided behavior in non-human primates (Boinski, 1992), and even fewer investigations of olfactory performance using psychophysical procedures. However, if we wish to understand olfactory function and appreciate the role odor cues may play in regulating a species’ behavior, it is necessary to have a knowledge of the animal’s basic perceptual capacities.

Laska and Hudson (1993a) introduced a new testing paradigm which, for the first time, allowed the assessment of olfactory performance in a non-human primate species using psychophysical methods. The test was designed to simulate olfactory-guided foraging behavior and was based on the discrimination of simultaneously presented odorants in a food-rewarded conditioning paradigm (Hudson *et al.*, 1992). 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), artificial odor mixtures (Laska and Hudson, 1993b) and conspecific urine odors (Laska and Hudson, 1995). Further, these studies showed that *S. sciureus* has an excellent long-term memory for odors (Laska *et al.*, 1996) and is capable of rapid odor learning (Laska and Hudson, 1993a).

These findings call into question the still widely held belief that simian primates in general have only a poorly developed sense of smell, and concomitantly that this sensory modality is of little behavioral relevance to members of this suborder of mammals.

In order to gain further insight into the basic perceptual capacities of non-human primates, it was therefore the aim of the present study to assess the olfactory sensitivity of squirrel monkeys by determining olfactory detection thresholds for an array of monomolecular odorants. Initially, we have chosen substances that represent five different chemical classes and for which comparative data from humans and, at least for some odorants, from other mammalian species are at hand.

Materials and methods

Animals

Testing was carried out using one adult male and two adult female squirrel monkeys (*S. sciureus*), maintained as part of an established breeding colony. All animals had served as subjects in previous olfactory experiments and were completely familiar with the basic test procedure (Hudson *et al.*, 1992; Laska *et al.*, 1996; Laska and Freyer, 1997; Laska and Hudson, 1993a,b, 1995; Laska and Teubner, 1998). The colony was housed in a double enclosure comprising a 23 m^3 home cage joined to a 7 m^3 test cage by two tunnels which could be closed by sliding doors to allow the temporary separation of animals for individual testing. Animals were provided with marmoset pellets (Ssniff®, Soest, Germany), fresh fruit, vegetables and water *ad libitum*.

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 laws.

Behavioral test

In a task designed to simulate olfactory-guided foraging, opaque 1.5 ml Eppendorf® flip-top reagent cups were fitted with absorbent paper strips (35 × 7 mm; Sugi, Kettenbach, Germany) impregnated with 10 µl of an odorant signalling either that they contained a peanut food reward (S+) or that they did not (S–). The odor strips were attached to the vials by cutting a slit in each strip and slipping it over the flip-up lid which was connected to the vial by a narrow band. Eighteen such cups, nine positive and nine negative, were inserted in pseudorandom order in holes along the horizontal bars of a climbing frame in such a way that some effort was required for the animals to remove them. The frame was mounted to one of the enclosure walls, and consisted of a 2.5 m vertical pole (40 mm diameter) fitted with seven cross-bars (20 mm diameter) 30 cm apart, the middle three of which extended 50 cm to either side and were equipped with conically bored holes to hold the cups (Hudson *et al.*, 1992).

In each test trial, each monkey was allowed 1 min to harvest as many baited cups from the frame as possible. Five such trials were conducted per animal per session and usually two sessions were conducted per day at least 1 h apart. Peanut rewards were negligible with respect to satiation of the animals. Cups were used only once and the odorized strips were prepared fresh at the start of each session.

Olfactory detection thresholds were determined by testing the animals' ability to discriminate between cups scented with increasing dilutions of an odorant used as S+, and those scented with the near-odorless solvent alone used as S–. Starting with a dilution of 1:100, each odorant was successively presented in 10-fold dilution steps for two sessions until an animal failed to significantly discriminate the odorant from the solvent. Subsequently, this descending staircase procedure was repeated for two 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. All experimental conditions were conducted for a total of four sessions, i.e. 20 × 1 min trials. 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—or, in the case of the intermediate dilutions, interspersed with—an easy control task for two sessions. This consisted of the discrimination between a 100-fold dilution of the S+ and a 50-fold dilution of anethole, a substance that is highly familiar to the animals as S– and readily discriminable from all substances used as S+.

Odorants

A set of nine odorants was used: *n*-propionic acid, *n*-butanoic acid, *n*-pentanoic acid, *n*-hexanoic acid, *n*-heptanoic acid, 1-pentanol, *n*-heptanal, amyl acetate and 1,8-cineole. The rationale for choosing these substances was to assess the monkeys' sensitivity for odorants representing different chemical classes (an alcohol, an aldehyde, an ester and a terpene respectively) as well as members of a homologous series of compounds (carboxylic acids). Furthermore, these substances are believed to differ in their degree of biological relevance to squirrel monkeys (cf. Discussion). All substances were obtained from Merck (Darmstadt, Germany) and had a nominal purity of at least 99%. They were diluted using near-odorless diethyl phthalate (Merck) as the solvent.

Data analysis

For each individual, the percentage of correct choices from the best two sessions per dilution step, that is from 10 × 1 min trials comprising a total of at least 60 decisions, was calculated. Correct choices consisted both in animals correctly rejecting negative cups by failing to open or remove them, and in identifying positive cups by removing and opening them to obtain the food reward. Conversely, errors consisted in animals opening or removing negative cups, or failing to remove and open positive cups.

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 0.01. All data are reported as means ± SD.

Results

Figure 1 shows the performance of the squirrel monkeys in discriminating between various dilutions of a given odorant and the near-odorless solvent. All three animals significantly distinguished dilutions as low as 1:10 000 *n*-propionic acid, 1:30 000 *n*-butanoic acid and *n*-pentanoic acid, 1:100 000 *n*-hexanoic acid, 1:1Mio *n*-heptanoic acid, 1:30 000 1-pentanol, 1:300 000 1,8-cineole, 1:1Mio *n*-heptanal and 1:30Mio amyl acetate from the solvent (binomial test, $P < 0.01$), with single individuals even scoring slightly better.

With the exception of *n*-hexanoic acid and 1,8-cineole, all three monkeys demonstrated very similar threshold values for a given substance and differed only by a dilution factor of three, if at all, between the highest- and the lowest-scoring animal.

A significant negative correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the carboxylic acids was found (Spearman, $r_s = -0.95$, $P < 0.001$).

Table 1 summarizes the threshold dilutions for both the best- and the poorest-performing animals, and shows various measures of corresponding vapour phase concentrations (Weast, 1987). With the exception of *n*-propionic acid, all threshold dilutions correspond to vapour phase concentrations below 1 p.p.m., and in the case of *n*-heptanoic acid and amyl acetate even to concentrations below 1 p.p.b.

Discussion

The results of this study demonstrate, for the first time, that squirrel monkeys have a well-developed and, in some cases, unexpectedly high olfactory sensitivity for monomolecular odorants. These findings are in line with earlier studies using the same methodology that reported squirrel monkeys to have an excellent olfactory discrimination ability for structurally related odorants (Laska and Freyer, 1997; Laska and Teubner, 1998; Laska *et al.*, 1999b), for artificial odor mixtures (Laska and Hudson, 1993b) and for conspecific urine odors (Laska and Hudson, 1995), and thus lend further support to the assumption that olfaction may play a significant and hitherto underestimated role in the regulation of behavior in this primate species.

Although only three animals were tested, the results appear robust as interindividual variability was remarkably low, and for the majority of substances tested there was only a factor of three between the threshold values of the highest- and the lowest-scoring animal. Further, with all nine substances, 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 pure diluent was indeed based on odor perception and not on other cues.

Figure 2 compares the olfactory threshold values obtained with the squirrel monkeys for amyl acetate, 1-pentanol, 1,8-cineole and *n*-heptanal to those from other mammalian species. Although such cross-species comparisons should be considered with caution as different methodologies may lead to widely differing results—as can be seen with the threshold values depicted for amyl acetate in the rat—it seems admissible to state that *S. sciureus* is far from being considered a 'microsmat', i.e. a species with a poorly developed sense of smell. With amyl acetate, for example, the squirrel monkeys demonstrated olfactory threshold values that are at least two orders of magnitude lower than those of the rat and the dog, both of which are traditionally regarded as 'macrosmatic' animals, i.e. species with a highly developed sense of smell. With 1,8-cineole, the monkeys' threshold values are even more than three log units lower than those of the rat, and with 1-pentanol the rats' sensitivity is just a factor of three higher than that of the best-performing monkey. With the exception of amyl acetate, for which the monkeys appear to be considerably more sensitive than humans, the threshold values of human and non-human primates for the other substances were quite similar, i.e. in the same order of magnitude.

Figure 3 compares the olfactory threshold values of the squirrel monkeys for carboxylic acids to those of other mammalian species. Here again, the sensitivity of *S. sciureus* is far from being inferior to that of the rat but, rather, is slightly higher. Olfactory detection threshold values of the dog for propionic acid, butanoic acid, and pentanoic acid, on the other hand, are several orders of magnitude lower than those of the monkeys. However, this marked difference in sensitivity tends to become smaller with longer-chained members of this homologous series of substances, e.g. hexanoic acid and heptanoic acid, for which both species demonstrate similar detection thresholds.

It should be mentioned that the threshold values of the dog for carboxylic acids as depicted in Figure 3 are taken from the study by Moulton *et al.* (Moulton *et al.*, 1960). An earlier study by Neuhaus (Neuhaus, 1953) reported even lower values in a single animal and thereby established the dog's reputation as a 'macrosmat', whereas a study by Ashton *et al.* (Ashton *et al.*, 1957) found the dog's sensitivity

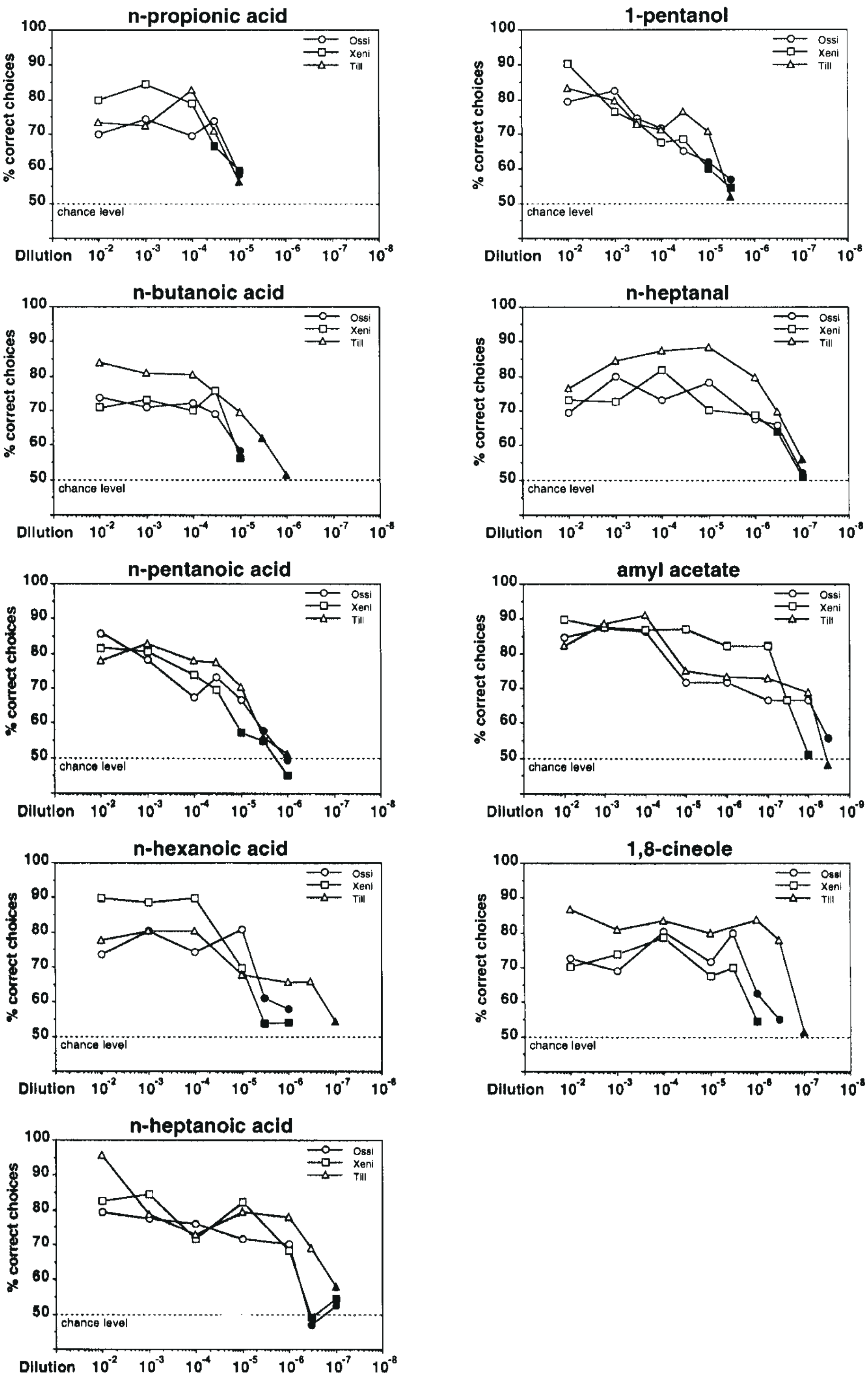

Figure 1 Performance of three squirrel monkeys in discriminating between various dilutions of a given odorant and the near-odorless solvent. Each data point represents the percentage of correct choices from 10 × 1 min trials comprising a total of at least 60 decisions. Filled symbols indicate dilutions that were not discriminated above chance level (binomial test, $P > 0.01$). Note different abscissa for amyl acetate.

for the same carboxylic acids to be more than six log units poorer than reported by Moulton.

Further, this graph illustrates a significant negative correlation between threshold values of the squirrel monkeys and carbon chain length of the carboxylic acids. The same regular association between olfactory sensitivity and this molecular property of the odorants has been found in human subjects (Cometto-Muniz *et al.*, 1998) (cf. Figure 3).

Table 1 Olfactory detection threshold values in *Saimiri sciureus* expressed in various measures of vapor phase concentrations

	Dilution	mol/cm^3	p.p.m.	Log p.p.m.	M	Log M
n-Propionic acid	1:10 000	2.9×10^{13}	1.08	0.036	4.8×10^{-8}	−7.31
	1.30 000	9.8×10^{12}	0.36	−0.44	1.6×10^{-8}	−7.79
n-Butanoic acid	1:30 000	4.4×10^{12}	0.16	−0.79	7.0×10^{-9}	−8.14
	1:100 000	1.3×10^{12}	0.05	−1.31	2.2×10^{-9}	−8.66
n-Pentanoic acid	1:30 000	2.0×10^{12}	0.07	−1.14	3.3×10^{-9}	−8.48
	1:100 000	5.9×10^{11}	0.02	−1.66	9.8×10^{-10}	−9.01
n-Hexanoic acid	1:100 000	3.1×10^{11}	0.01	−1.94	5.1×10^{-10}	−9.29
	1:3Mio	1.0×10^{10}	0.0004	−3.42	1.7×10^{-11}	−10.77
n-Heptanoic acid	1:1Mio	1.5×10^{10}	0.0005	−3.26	2.5×10^{-11}	−10.61
	1:3Mio	4.9×10^{9}	0.0002	−3.74	8.2×10^{-12}	−11.08
1-Pentanol	1:30 000	1.0×10^{13}	0.39	−0.41	1.7×10^{-8}	−7.76
	1:100 000	3.2×10^{12}	0.12	−0.93	5.0×10^{-9}	−8.30
n-Heptanal	1:1Mio	1.9×10^{11}	0.007	−2.15	3.1×10^{-10}	−9.50
	1:3Mio	6.3×10^{10}	0.002	−2.63	1.0×10^{-10}	−9.98
Amyl acetate	30Mio	9.8×10^{9}	0.0004	−3.44	1.6×10^{-11}	−10.79
	100Mio	2.9×10^{9}	0.0001	−3.96	4.9×10^{-12}	−11.31
1,8-Cineole	1:300 000	2.8×10^{11}	0.01	−1.98	4.7×10^{-10}	−9.33
	1:3Mio	2.8×10^{10}	0.001	−2.98	4.7×10^{-11}	−10.33

With each stimulus, the upper line represents the lowest concentration that all three animals were able to detect and the lower line represents the lowest concentration that the best-performing animal was able to detect. M, mol/l.

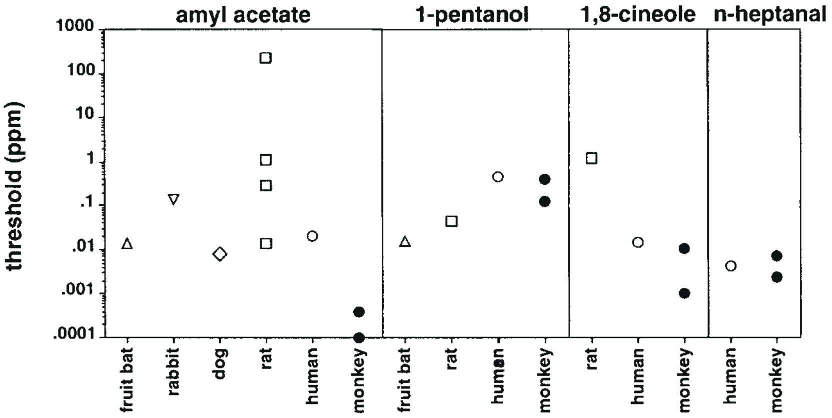

Figure 2 Comparison of the olfactory threshold values (expressed as vapour phase concentrations) of the squirrel monkeys for amyl acetate, 1-pentanol, 1,8-cineole and *n*-heptanal to those of other mammalian species. Data points for amyl acetate and rat illustrate threshold values obtained with different methodologies. The two data points for the squirrel monkeys represent the threshold values of the best- and the poorest-performing animal respectively. Human data (Devos *et al.*, 1990); animal data (Passe and Walker, 1985; Laska, 1990).

Other species such as the dog, the hedgehog, the vampire bat and the fruit bat, for which threshold values from at least three carboxylic acids are at hand, do not show such a monotonous function.

Cross-species comparisons of olfactory performance raise the question as to possible reasons which might account for the observed similarities and (sometimes marked) differences in olfactory sensitivity for a given substance. Likewise, within-species comparisons of olfactory performance should be discussed with regard to possible explanations for differences in sensitivity between substances.

It seems appropriate to assume that the efficiency of a sensory system reflects an evolutionary adaptation of a species to its ecological niche. Whereas this idea is widely recognized and well supported by numerous examples in the visual and auditory modalities (Dusenbery, 1992), surprisingly few authors to date have considered olfactory performance from this point of view. Rather, there is a long-standing tradition of assigning species with general labels such as 'microsmat' or 'macrosmat'. This classification, however, is usually based on neuroanatomical features suggesting either a pivotal or a negligible role of the sense of

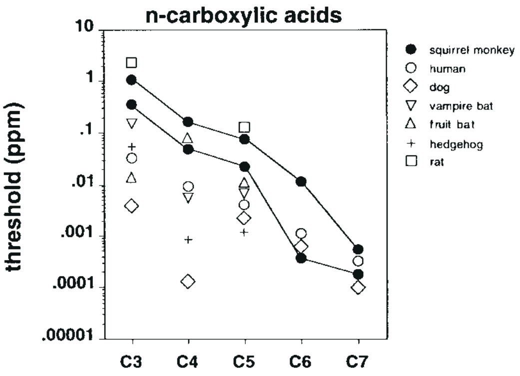

Figure 3 Comparison of the olfactory threshold values (expressed as vapour phase concentrations) of the squirrel monkeys for carboxylic acids to those of other mammalian species. The abscissa refers to carbon chain length of the substances (from C3: propionic acid to C7: heptanoic acid). The two data points for the squirrel monkeys represent the threshold values of the best- and the poorest-performing animal respectively. Human data (Devos *et al.*, 1990); animal data (Passe and Walker, 1985; Laska, 1990).

smell in a given species, and only rarely on experimental assessments of olfactory performance. Our finding of a well-developed olfactory sensitivity in the squirrel monkey is yet another example showing that allometric comparisons of olfactory brain structure volumes or of the absolute size of olfactory epithelia are poor predictors of chemosensory performance. There is no doubt that the relative size of the rat's brain structures devoted to processing olfactory information and the absolute size of the rat's olfactory epithelium are both considerably larger than those of the squirrel monkey (Stephan *et al.*, 1988). Our data, however, clearly show that such comparisons of neuroanatomical structures do not allow us to draw general conclusions as to olfactory sensitivity of any two species.

Considering that even for the most intensively studied species of non-human mammals measurements of olfactory sensitivity or discrimination abilities are so far usually restricted to little more than a handful of substances (Walker and Jennings, 1991), it is obvious that the assignment of general labels such as 'microsmat' or 'macrosmat' to any species is at least premature and does not take into account the vast complexity of our natural odor world and the diversity of contexts in which the sense of smell may be crucial for an animal. Therefore, we argue that these terms should no longer be used.

In order to explain similarities or differences in olfactory performance between or within species, it might be more promising to consider whether given odorants or classes of odorants might differ in their degree of behavioral relevance for a species.

Carnivorous, insectivorous or sanguivorous species such as the dog, the hedgehog or the vampire bat have been found to be much more sensitive to short-chained carboxylic acids than the squirrel monkey (cf. Figure 3). This class of odorants comprises the main components of body-borne prey odors (Flood, 1985) and thus are believed to be highly relevant for species feeding on animal prey but presumably are less important for the mainly frugivorous squirrel monkey. The latter, in contrast, has been found to be considerably more sensitive to amyl acetate and 1,8-cineole than the aforementioned species (cf. Figure 2). This, too, appears to make sense in terms of an evolutionary adaptation to optimal foraging as these substances are known to be components of a wide variety of fruit odors (Knudsen *et al.*, 1993) and thus are likely to be more relevant for a species feeding on fruit than for a carnivore.

Despite the obvious role which the sense of smell plays in finding and selecting food in many species, it should be emphasized that dietary specialization is only one of presumably numerous factors that make up the ecological niche of a species and which are likely also to affect its pattern of olfactory sensitivity and discrimination ability. To identify such factors and their impact on measures of olfactory performance warrants further study.

Finally, there is no reason to believe that squirrel monkeys are special in their olfactory capabilities in comparison with other primates. Recent findings in the pigtail macaque using the same behavioral paradigm as employed here suggest that this Old World primate also has a keen sense of smell (Hübener and Laska, 1998). Our finding that for the majority of substances tested human subjects demonstrated threshold values similar to those of the squirrel monkeys lends additional support to the notion that *S. sciureus* is not likely to be exceptional among primates with regard to its olfactory performance.

In conclusion, the results of the present study provide first evidence of an unexpectedly high olfactory sensitivity in a non-human primate species, the squirrel monkey. These findings support the assumption that olfaction may play an important role in the regulation of this species' behavior. Further, they suggest that between-species comparisons of neuroanatomical features are a poor predictor of olfactory performance and that general labels such as 'microsmat' and 'macrosmat' are inadequate to describe a species' olfactory capabilities. An ecological view of such capabilities which attempts to correlate sensory performance with behavioral relevance of odor stimuli might offer a promising approach in appraising the significance of the sense of smell for a particular species.

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