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Olfactory sensitivity for aliphatic alcohols in squirrel monkeys and pigtail macaques

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Summary

The view that primates are microsmatic animals is based mainly on an interpretation of neuroanatomical features, whereas physiological evidence of a poorly developed sense of smell in this order of mammals is largely lacking. Using a conditioning paradigm, we therefore assessed the olfactory sensitivity of three squirrel monkeys (*Saimiri sciureus*) and of four pigtail macaques (*Macaca nemestrina*) for a homologous series of aliphatic alcohols (ethanol to 1-octanol) and isomeric forms of some of these substances. In the majority of cases, the animals of both species significantly discriminated concentrations below 1 part per million from the odourless solvent, and with 1-hexanol individual monkeys even demonstrated thresholds below 10 parts per billion. The results showed (i) that both primate species have a well-developed olfactory sensitivity for aliphatic alcohols, which for the majority of substances matches or even is better than that of species such as the rat, (ii) that both species generally show very similar olfactory detection thresholds for aliphatic alcohols, and (iii) that a significant negative correlation between perceptibility in terms of olfactory detection threshold and carbon chain length of both the aliphatic 1- and 2-alcohols exists in both species. These findings support the idea that across-species comparisons of neuroanatomical features are a poor predictor of olfactory performance and that general labels such as 'microsmat' or 'macrosmat', which are usually based on allometric comparisons of olfactory brain structures, are inadequate to describe the olfactory capabilities of a species. Further, our findings suggest that olfaction may play an important and hitherto underestimated role in the regulation of behaviour in the species tested.

Key words: olfactory sensitivity, detection threshold, non-human primate, aliphatic alcohol, squirrel monkey, *Saimiri sciureus*, pigtail macaque, *Macaca nemestrina*.

Introduction

A traditional view purports that primates are 'visual' animals with a poorly developed sense of smell (King and Fobes, 1974; Walker and Jennings, 1991; Farbman, 1992; Rouquier et al., 2000). This view 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, physiological evidence supporting a positive correlation between allometric measures of neuroanatomical features and olfactory performance is largely lacking (De Winter and Oxnard, 2000; Schoenemann, 2001).

In recent years, an increasing number of behavioural observations call into question the still widely held belief that olfaction is of only little, if any, behavioural relevance to primates and concomitantly that members of this order of mammals have generally only poor olfactory capabilities. There is now evidence from a number of primate species for olfactory involvement in the identification and selection of food (Bolen and Green, 1997; Ueno, 1994) and in social behaviours 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). Despite such observations, experimental investigations of olfactory performance in non-human primates have been sparse.

Laska and Hudson (1993a) introduced a new testing paradigm which, for the first time, allowed the olfactory performance of a non-human primate species to be assessed 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), for artificial odour mixtures (Laska and Hudson, 1993b) and for conspecific urine odours (Laska and Hudson, 1995). Further, these studies showed that *Saimiri sciureus* has an excellent long-term memory for odours (Laska et al., 1996), a well-developed

olfactory sensitivity for aliphatic carboxylic acids (Laska et al., 2000) and acetic esters (Laska and Seibt, 2002) and is capable of rapid odour learning (Laska and Hudson, 1993a).

Hübener and Laska (1998, 2001) adapted this method to the species-specific needs of another primate species, the pigtail macaque, and demonstrated that squirrel monkeys are not the only primate species with surprisingly well-developed olfactory capabilities. Further, their behavioural paradigm allows us to compare olfactory performance reliably between two primate species.

The aims of the present study are twofold: (i) to gain further insight into the basic perceptual capacities of non-human primates by determining olfactory detection thresholds in squirrel monkeys and pigtail macaques for an array of monomolecular odorants; and (ii) to assess whether neuroanatomical features are reliable predictors of olfactory performance by comparing the detection thresholds of the two primate species tested here with those of other mammals.

We have chosen aliphatic alcohols as odour stimuli because this class of substance is presumed to indicate a fruit's degree of ripeness and is thus likely to be behaviourally relevant for frugivorous primates and because comparative data from humans and, at least for the majority of odorants, from other mammalian species are available. Further, the use of a homologous series of alcohols and some isomeric forms allowed us also to address the question of whether structural features of stimulus molecules such as carbon chain length or the position of a functional group affect detectability in a predictable manner.

Materials and methods

Animals

Testing was carried out using two adult male and one adult female squirrel monkeys (*Saimiri sciureus*) and three adult male and one adult female pigtail macaques (*Macaca nemestrina*), maintained as parts of two established breeding colonies. All animals had served as subjects in previous olfactory experiments and were completely familiar with the basic test procedure (Hudson et al., 1992; Hübener and Laska, 1998, 2001; Laska and Freyer, 1997; Laska and Hudson, 1993a,b, 1995; Laska and Teubner, 1998; Laska et al., 1996, 1999a,b, 2000). The colonies were housed in separate rooms on a 12 h:12 h light:dark cycle at 22–24 °C and >75 % relative humidity. Each room held a double enclosure comprising a spacious home cage joined to a smaller test cage that could be closed by a sliding door 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. All animals were provided with primate chow (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.

Behavioural tests

The squirrel monkeys were tested using a multiple-choice instrumental conditioning paradigm (Hudson et al., 1992). Opaque 1.5 ml Eppendorf flip-top reagent cups were fitted with absorbent paper strips (35 mm×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 odour 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 on one of the enclosure walls at a distance of 10 cm 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.

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. Cups were used only once, and the odourized strips were prepared fresh at the start of each session.

The pigtail macaques were tested using a two-choice instrumental conditioning paradigm (Hübener and Laska, 2001). Two cube-shaped open polyvinyl chloride 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 that could be opened only by drawing a metallic pin from a hole extending horizontally through the overlapping lid and the front side of a container. A clip on top of each lid held an absorbent paper strip (70 mm×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 odourized paper strips extended 5 cm into the test cage when the apparatus was attached to the front of the cage.

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 three sessions were usually conducted per day.

It is important to note that the mode of stimulus presentation (10 µl of odorant on an absorbent paper strip) was identical with squirrel monkeys and pigtail macaques.

For both species, olfactory detection thresholds were determined by testing the animals' ability to discriminate between manipulation objects scented with increasing dilutions of an odorant used as S+ and those scented with the odourless solvent alone used as S–. Starting with a dilution of 1:100, each

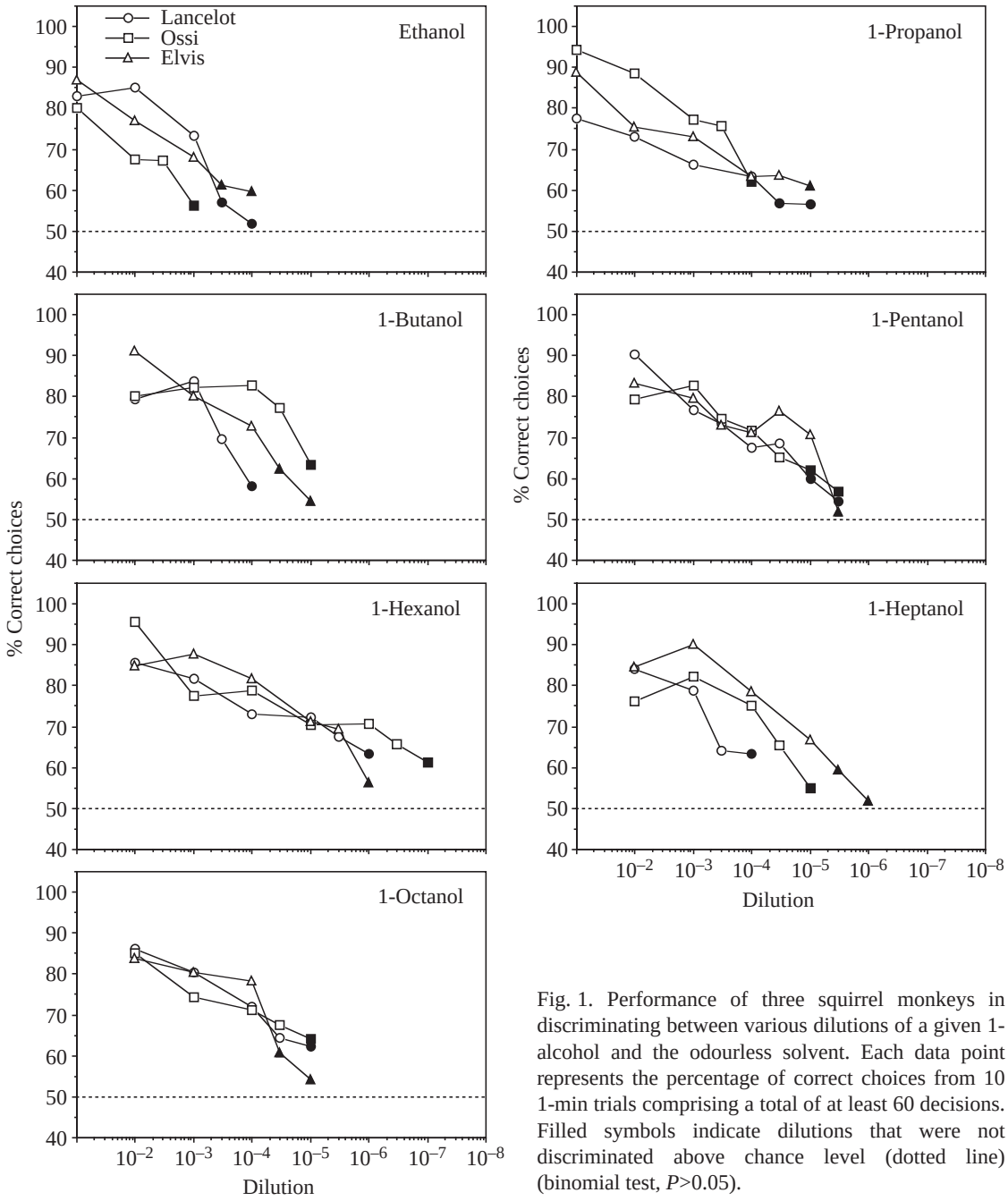

Fig. 1. Performance of three squirrel monkeys in discriminating between various dilutions of a given 1-alcohol and the odourless solvent. Each data point represents the percentage of correct choices from 10 1-min trials comprising a total of at least 60 decisions. Filled symbols indicate dilutions that were not discriminated above chance level (dotted line) (binomial test, $P>0.05$).

odorant was successively presented in 10-fold dilution steps, for two sessions with the squirrel monkeys and for three sessions with the pigtail macaques, until an animal failed to discriminate significantly the odorant from the solvent. Subsequently, this descending staircase procedure was repeated for two (for squirrel monkeys) or three (for pigtail macaques) more sessions per dilution step. Finally, intermediate dilutions were tested 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, or in the case of the intermediate dilutions, interspersed with, an easy control task. This consisted of the discrimination between a 100-fold dilution of the S+ and the odourless solvent as S–.

Odorants

A set of 11 odorants was used: ethanol, 1-propanol, 1-butanol, 1-pentanol, 1-hexanol, 1-heptanol, 1-octanol, 2-propanol, 2-butanol, 2-pentanol and 3-pentanol. The rationale for choosing these substances was to assesss the monkeys'

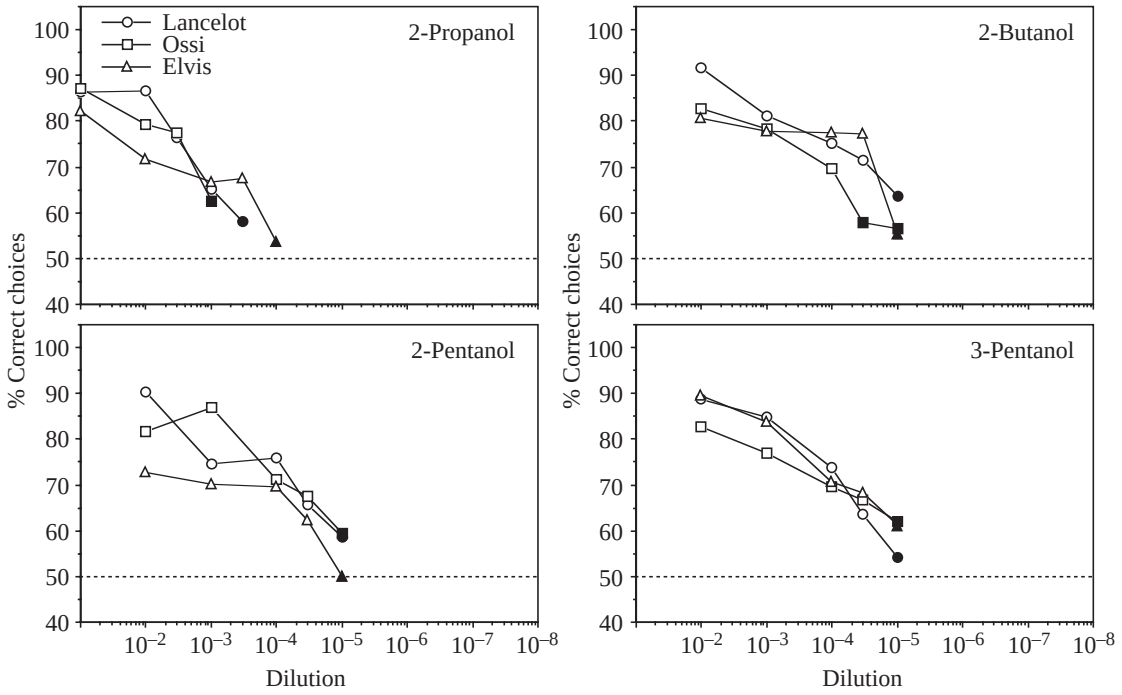

Fig. 2. Performance of three squirrel monkeys in discriminating between various dilutions of a given isomeric alcohol and the odourless solvent. Each data point represents the percentage of correct choices from 10 1-min trials comprising a total of at least 60 decisions. Filled symbols indicate dilutions that were not discriminated above chance level (dotted line) (binomial test, $P>0.05$).

sensitivity for odorants representing members of a homologous series of aliphatic compounds, i.e. substances sharing the same functional group but differing in carbon chain length, and for isomeric forms of some of these compounds, i.e. substances sharing the same carbon chain length and type of functional group but differing in the position of their oxygen moiety, allowing us to assess the impact of both structural features on detectability. All substances were obtained from Merck (Darmstadt) and had a nominal purity of at least 99 %. They were diluted using odourless diethyl phthalate (Merck) as the solvent.

Data analysis

For each squirrel monkey, the percentage of correct choices from the best two sessions per dilution step, i.e. from 10 1-min trials comprising a total of at least 60 decisions, was calculated. Similarly, for each pigtail macaque, the percentage of correct choices from the best three sessions per dilution step, comprising a total of 30 decisions, was calculated.

Correct choices consisted both of animals correctly rejecting negative manipulation objects by failing to open them and identifying positive manipulation objects by opening them to obtain the food reward. Conversely, errors consisted of animals opening negative manipulation objects or failing to open positive manipulation objects.

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.

Results

Squirrel monkeys

Fig. 1 shows the performance of the squirrel monkeys in discriminating between various dilutions of a given aliphatic alcohol with a terminal functional group and the odourless solvent. All three animals significantly distinguished dilutions as low as 1:300 ethanol, 1:3000 1-propanol, 1:3000 1-butanol, 1:30 000 1-pentanol, 1:300 000 1-hexanol, 1:3000 1-heptanol and 1:10 000 1-octanol from the solvent (binomial test, $P<0.05$), with some individuals scoring even better.

Fig. 2 shows the performance of the squirrel monkeys in discriminating between various dilutions of a given aliphatic alcohol with a non-terminal functional group and the odourless solvent. All three animals significantly distinguished dilutions as low as 1:300 2-propanol, 1:10 000 2-butanol, 1:30 000 2-pentanol and 1:30 000 3-pentanol from the solvent (binomial test, $P<0.05$), with some individuals scoring even better.

The individual squirrel monkeys demonstrated very similar threshold values and usually differed only by a dilution factor of three or ten between the highest- and the lowest-scoring animal. In the case of 2-pentanol and 3-pentanol, they even showed identical threshold values. The largest difference in sensitivity for a given odorant between individuals comprised a dilution factor of 33 and was found with 1-heptanol.

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

		Vapour phase concentration				
Stimulus	Dilution	(molecules cm^{-3})	(p.p.m.)	log (p.p.m.)	(mol l^{-1})	log (mol l^{-1})
Ethanol	1:300	1.0×10^{16}	368.55	2.57	1.7×10^{-5}	–4.78
	1:1000	3.0×10^{15}	110.56	2.04	5.0×10^{-6}	–5.30
1-Propanol	1:3000	4.8×10^{14}	17.85	1.25	8.0×10^{-7}	–6.10
	1:30 000	4.8×10^{13}	1.78	0.25	8.0×10^{-8}	–7.10
1-Butanol	1:3000	2.3×10^{14}	8.65	0.94	3.9×10^{-7}	–6.41
	1:30 000	2.3×10^{13}	0.86	–0.06	3.9×10^{-8}	–7.41
1-Pentanol	1:30 000	1.1×10^{13}	0.40	–0.38	1.9×10^{-8}	–7.73
	1:100 000	3.4×10^{12}	0.13	–0.90	5.6×10^{-9}	–8.25
1-Hexanol	1:300 000	5.4×10^{11}	0.019	–1.70	8.9×10^{-10}	–9.05
	$1:3\times10^{6}$	5.4×10^{10}	0.0019	–2.70	8.9×10^{-11}	–10.05
1-Heptanol	1:3000	2.8×10^{13}	1.05	0.02	4.7×10^{-8}	–7.33
	1:100 000	8.5×10^{11}	0.032	–1.50	1.4×10^{-9}	–8.85
1-Octanol	1:10 000	3.9×10^{12}	0.14	–0.85	6.4×10^{-9}	–8.19
	1:30 000	1.3×10^{12}	0.048	–1.32	2.1×10^{-9}	–8.67
2-Propanol	1:300	8.6×10^{15}	318.80	2.50	1.4×10^{-5}	–4.84
	1:3000	8.6×10^{14}	31.88	1.50	1.4×10^{-6}	–5.84
2-Butanol	1:10 000	1.3×10^{14}	4.98	0.70	2.2×10^{-7}	–6.65
	1:30 000	4.5×10^{13}	1.66	0.22	7.4×10^{-8}	–7.13
2-Pentanol	1:30 000	2.6×10^{12}	0.10	–1.01	4.4×10^{-9}	–8.36
	1:30 000	2.6×10^{12}	0.10	–1.01	4.4×10^{-9}	–8.36
3-Pentanol	1:30 000	2.5×10^{13}	0.93	–0.03	4.2×10^{-8}	–7.38
	1:30 000	2.5×10^{13}	0.93	–0.03	4.2×10^{-8}	–7.38

For each stimulus, the upper value gives the lowest concentration that all three animals were able to detect and the lower value gives the lowest concentration that the best-performing animal was able to detect.

p.p.m. parts per million.

A significant negative correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the 1-alcohols was found (Spearman, r_s=–0.81, P<0.01; Fig. 3). This correlation was even highly significant when the threshold values for the two substances with the longest carbon chain tested, i.e. 1-heptanol and 1-octanol, were removed from the calculations (Spearman, r_s=–0.95, P<0.001). A corresponding significant correlation was also found with the three 2-alcohols tested (Spearman, r_s=–0.97, P<0.01; Fig. 3).

Table 1 summarizes the threshold dilutions for both the best- and the poorest-performing squirrel monkeys and shows various measures of corresponding vapour phase concentrations (Weast, 1987). In the majority of cases, threshold dilutions correspond to vapour phase concentrations below 1 part per million, and with 1-hexanol the best-scoring animal was even able to detect a concentration of 2 parts per billion.

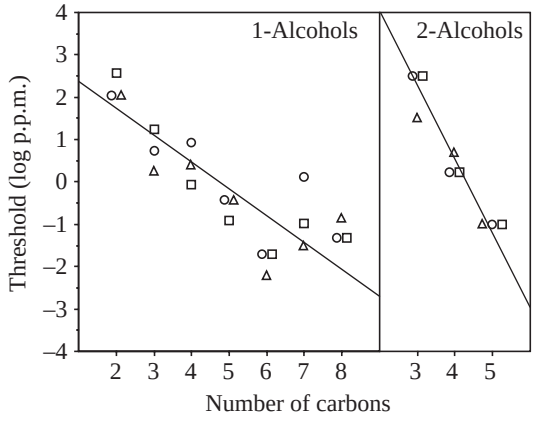

Fig. 3. Olfactory detection threshold values (expressed as vapour phase concentrations) of the three squirrel monkeys as a function of carbon chain length of the aliphatic alcohols tested.

Pigtail macaques

Fig. 4 shows the performance of the pigtail macaques in discriminating between various dilutions of a given aliphatic alcohol with a terminal functional group and the odourless solvent. All four animals significantly distinguished dilutions as low as 1:300 ethanol, 1:1000 1-propanol, 1:3000 1-butanol, 1:1000 1-pentanol, 1:30 000 1-hexanol, 1:30 000 1-heptanol and 1:30 000 1-octanol from the solvent (binomial test, P<0.05), with some individuals scoring even better.

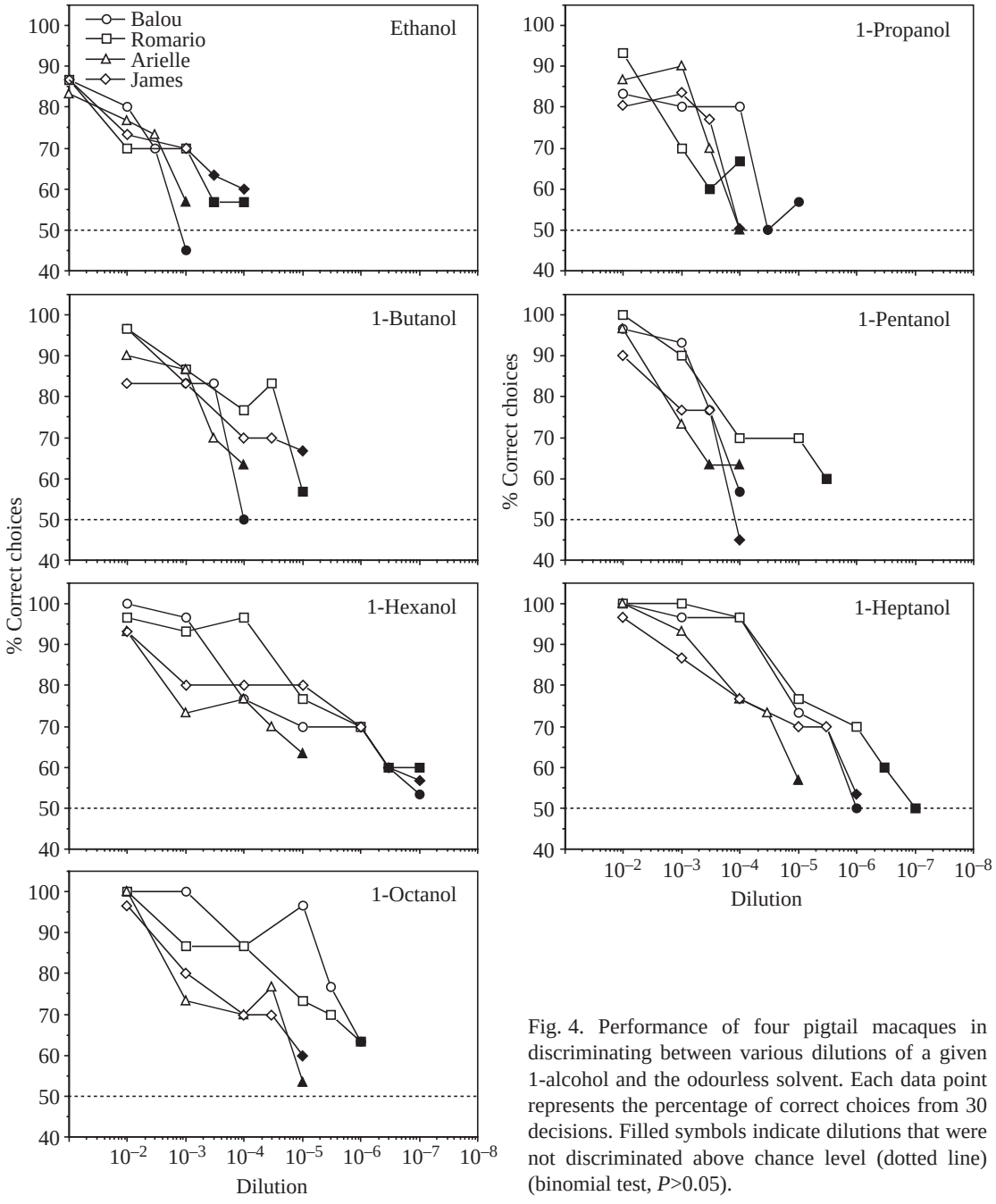

Fig. 4. Performance of four pigtail macaques in discriminating between various dilutions of a given 1-alcohol and the odourless solvent. Each data point represents the percentage of correct choices from 30 decisions. Filled symbols indicate dilutions that were not discriminated above chance level (dotted line) (binomial test, $P>0.05$).

Fig. 5 shows the performance of the pigtail macaques in discriminating between various dilutions of a given aliphatic alcohol with a non-terminal functional group and the odourless solvent. All four animals significantly distinguished dilutions as low as 1:1000 2-propanol, 1:1000 2-butanol, 1:3000 2-pentanol and 1:3000 3-pentanol from the solvent (binomial test, $P<0.05$), with some individuals scoring even better.

The individual pigtail macaques demonstrated very similar threshold values and usually differed only by a dilution factor of three or ten between the highest- and the lowest-scoring animal. In the case of 2-propanol, they even showed identical threshold values. The largest difference in sensitivity for a given odorant between individuals comprised a dilution factor of 100 and was found with 1-pentanol.

Similar to the findings with the squirrel monkeys, a significant negative correlation between perceptibility in terms of olfactory detection thresholds and carbon chain length of the 1-alcohols was found (Spearman, $r_s=-0.90$, $P<0.01$; Fig. 6). Also in line with the squirrel monkeys, a corresponding significant correlation was found for the three 2-alcohols tested (Spearman, $r_s=-0.97$, $P=0.01$; Fig. 6).

Table 2 summarizes the threshold dilutions for both the best- and the poorest-performing pigtail macaques and shows various measures of corresponding vapour phase

Table 2. *Olfactory detection threshold values in four* Macaca nemestrina *expressed in various measures of vapour phase concentrations*

		Vapour phase concentration				
Stimulus	Dilution	(molecules cm^{-3})	(p.p.m.)	log (p.p.m.)	(mol l^{-1})	log (mol l^{-1})
Ethanol	1:300	1.0×10^{16}	368.55	2.57	1.7×10^{-5}	–4.78
	1:1000	3.0×10^{15}	110.56	2.04	5.0×10^{-6}	–5.30
1-Propanol	1:1,000	1.4×10^{15}	53.56	1.73	2.4×10^{-6}	–5.62
	1:10 000	1.4×10^{14}	5.36	0.73	2.4×10^{-7}	–6.62
1-Butanol	1:3000	2.3×10^{14}	8.65	0.94	3.9×10^{-7}	–6.41
	1:30 000	2.3×10^{13}	0.86	–0.06	3.9×10^{-8}	–7.41
1-Pentanol	1:1,000	3.4×10^{14}	12.57	1.10	5.6×10^{-7}	–6.25
	1:100 000	3.4×10^{12}	0.13	–0.90	5.6×10^{-9}	–8.25
1-Hexanol	1:30,000	5.4×10^{12}	0.20	–0.70	8.9×10^{-9}	–8.05
	$1:1\times10^{6}$	1.6×10^{11}	0.006	–2.22	2.7×10^{-10}	–9.57
1-Heptanol	1:30,000	2.8×10^{12}	0.11	–0.98	4.7×10^{-9}	–8.33
	$1:1\times10^{6}$	8.5×10^{10}	0.0032	–2.50	1.4×10^{-10}	–9.85
1-Octanol	1:30 000	1.3×10^{12}	0.048	–1.32	2.1×10^{-9}	–8.67
	1:300 000	1.3×10^{11}	0.0048	–2.32	2.1×10^{-10}	–9.67
2-Propanol	1:1,000	2.6×10^{15}	95.64	1.98	4.3×10^{-6}	–5.37
	1:1,000	2.6×10^{15}	95.64	1.98	4.3×10^{-6}	–5.37
2-Butanol	1:1,000	1.3×10^{15}	49.82	1.70	2.2×10^{-6}	–5.65
	1:10 000	1.3×10^{14}	4.98	0.70	2.2×10^{-7}	–6.65
2-Pentanol	1:3,000	2.6×10^{13}	0.98	–0.0086	4.4×10^{-8}	–7.36
	1:10 000	7.9×10^{12}	0.29	–0.53	1.3×10^{-8}	–7.88
3-Pentanol	1:3,000	2.5×10^{14}	9.30	0.97	4.2×10^{-7}	–6.38
	1:30 000	2.5×10^{13}	0.93	–0.03	4.2×10^{-8}	–7.38

For each stimulus, the upper value gives the lowest concentration that all four animals were able to detect and the lower value gives the lowest concentration that the best-performing animal was able to detect.

p.p.m., parts per million.

concentrations (Weast, 1987). In the majority of cases, threshold dilutions correspond to vapour phase concentrations below 1 part per million, and with 1-heptanol the best-scoring animal was even able to detect a concentration of 4 parts per billion.

Discussion

The results of this study demonstrate, for the first time, that squirrel monkeys and pigtail macaques have a well-developed olfactory sensitivity for monomolecular odorants belonging to the class of aliphatic alcohols. These findings are in line with earlier studies using the same methods and animals that reported both species to have a well-developed olfactory sensitivity for carboxylic acids (Hübener and Laska, 2001; Laska et al., 2000) and an outstanding olfactory sensitivity for acetic esters (Laska and Seibt, 2001) and squirrel monkeys to have excellent olfactory discrimination capabilities (Laska and Freyer, 1997; Laska and Hudson, 1993ab, 1995; Laska and Teubner, 1998; Laska et al., 1999a,b). Thus, the present results lend further support to the idea that olfaction may play a significant and hitherto underestimated role in the regulation of behaviour in these primate species.

Although only three or four animals were tested per species, the results appear robust because interindividual variability was remarkably low and generally smaller than the range reported in studies on human olfactory sensitivity, i.e. within three orders of magnitude (Stevens et al., 1988). In fact, for the majority of substances tested, there was only a factor of three or ten between the threshold values of the highest- and the lowest-scoring animal of a species. Further, for all substances tested, the animals' performance at the lowest concentration 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 odour perception and not on other cues.

Fig. 7 compares the olfactory detection threshold values obtained with squirrel monkeys and pigtail macaques for the substances tested with those from other mammalian species. Although such across-species comparisons should be considered with caution because different methods may lead to widely differing results – as can be seen with the threshold values depicted for 1-hexanol in the rat – it seems admissible to state that *Saimiri sciureus* and *Macaca nemestrina* are far from being 'microsmats', i.e. species with a poorly developed sense of smell. With the majority of the aliphatic 1-alcohols

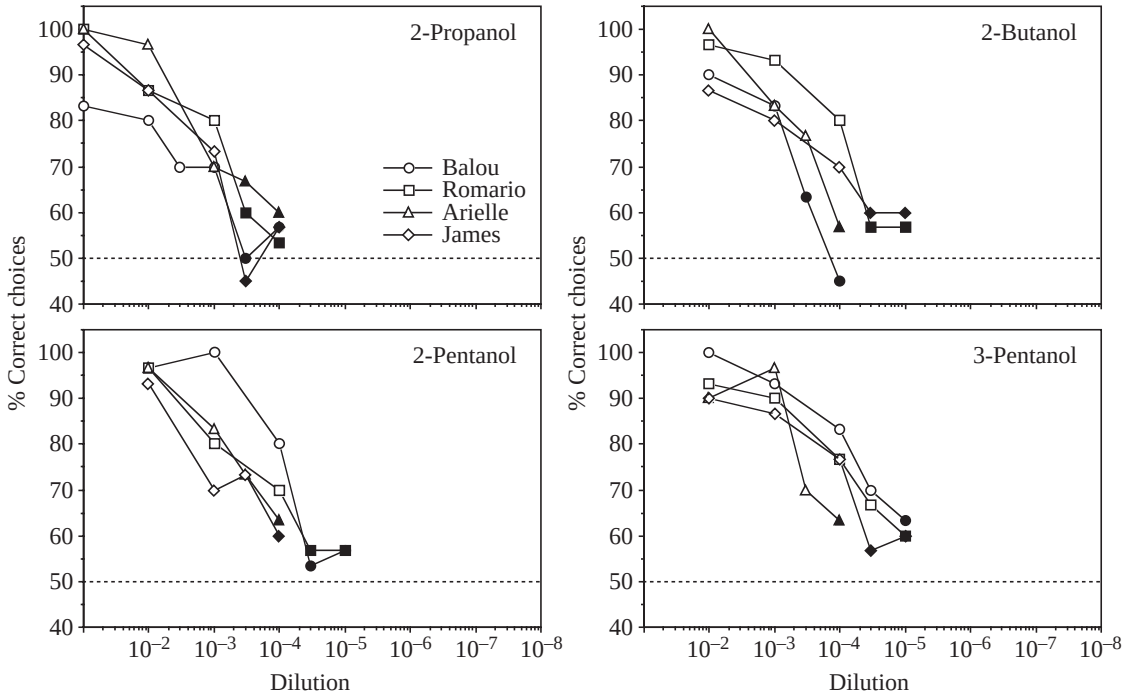

Fig. 5. Performance of four pigtail macaques in discriminating between various dilutions of a given isomeric alcohol and the odourless solvent. Each data point represents the percentage of correct choices from 30 decisions. Filled symbols indicate dilutions that were not discriminated above chance level (dotted line) (binomial test, $P>0.05$).

tested, for example, both species demonstrated olfactory threshold values lower than those of the rat, which is traditionally regarded as a 'macrosmatic' animal, i.e. a species with a highly developed sense of smell. Interestingly, human subjects showed an olfactory sensitivity for the alcohols employed here quite similar to that of the two non-human primate species and thus better than the traditional view suggests (see Fig. 7). It should be mentioned that the threshold values of the human subjects for the 1-alcohols as depicted in Fig. 7 are taken from the study by Cometto-Muniz and Cain (1990). Although some other studies reported slightly lower values for some of the substances (e.g. for 1-propanol, Corbit and Engen, 1971; for 1-butanol, Laing, 1982; for 1-hexanol, Hellman and Small, 1974), all these other studies had tested only one or a few members of the homologous series of alcohols and none of them had used signal detection methods and a comparably sophisticated mode of stimulus presentation to that of Cometto-Muniz and Cain (1990).

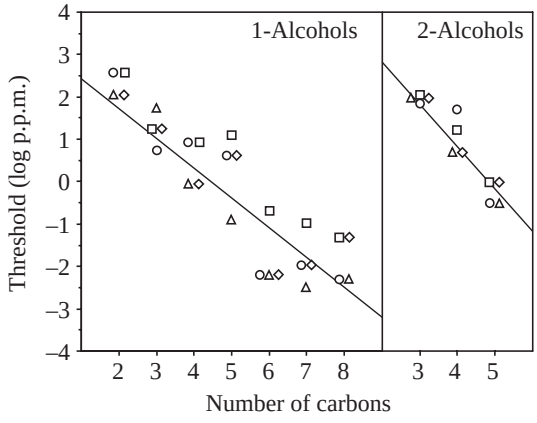

Fig. 6. Olfactory detection threshold values (expressed as vapour phase concentrations) of the four pigtail macaques as a function of carbon chain length of the aliphatic alcohols tested.

Across-species comparisons of olfactory performance raise the question as to possible reasons for the observed similarities and, sometimes marked, differences in olfactory sensitivity for a given substance. Similarly, within-species comparisons of olfactory performance should be discussed with regard to possible explanations for differences in sensitivity among substances.

It seems appropriate to assume that the efficiency of a sensory system reflects an evolutionary adaptation of a species to its ecological niche. Although this idea is widely recognised and well supported by numerous examples in the visual and auditory modalities (Dusenbery, 1992), surprisingly few authors 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 that are interpreted as indicating either a pivotal or a negligible role of the sense of smell in a given species and only rarely on experimental assessments of olfactory performance. Our finding of a well-developed olfactory sensitivity for aliphatic alcohols in squirrel monkeys and pigtail macaques 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 or of the pigtail macaque (Stephan et al., 1988). Our data, however, clearly show that such comparisons of neuroanatomical structures do not allow us to draw generalizable conclusions about the 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 have usually been 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 odour 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.

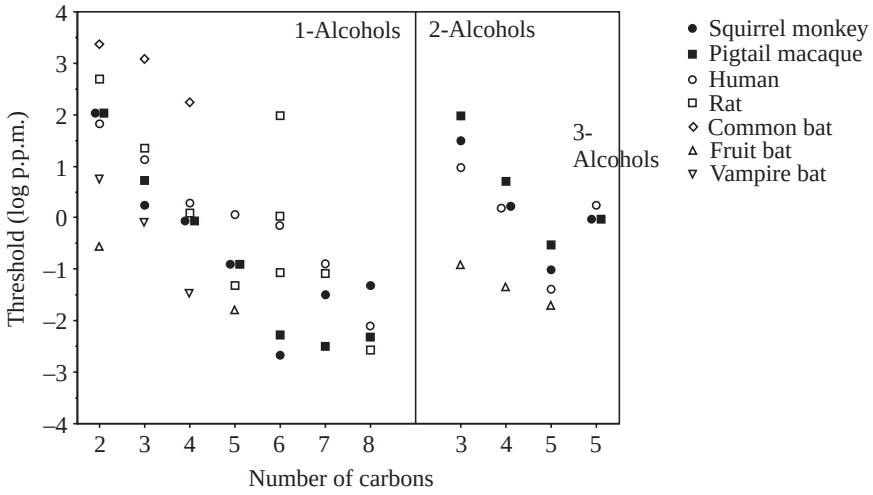

Fig. 7. Comparison of the olfactory detection threshold values (expressed as vapour phase concentrations) of the squirrel monkeys and the pigtail macaques for aliphatic alcohols with those of other mammalian species. Human data are from Cometto-Muniz and Cain (1990) and Devos et al. (1990); animal data are from Laska (1990) and Passe and Walker (1985). Threshold is measured in parts per million.

To explain similarities or differences in olfactory performance among or within species, it might be more appropriate to consider whether given odorants or classes of odorant differ in their degree of behavioural relevance for a species.

Squirrel monkeys and pigtail macaques have been reported to include a considerable proportion of fruit into their diets (Clutton-Brock and Harvey, 1977; Ross, 1992). Our finding that both species are generally at least as sensitive as rats to aliphatic alcohols and clearly outperform common bats (see Fig. 7) appears to make sense in terms of an evolutionary adaptation to optimal foraging because these substances are known to be products of microbial fermentation processes in fruits and are thus indicative of their degree of ripeness. Therefore, it seems plausible to assume that aliphatic alcohols may be more relevant for species feeding on fruit than for a granivorous species such as the rat or an insectivorous species such as the common bat. In line with this idea, short-tailed fruit bats have also been shown to be more sensitive than rats to aliphatic alcohols (Laska, 1990; see Fig. 7).

Carnivorous, insectivorous or sanguivorous species such as the dog, the hedgehog and the vampire bat, respectively, have been found to be more sensitive than the squirrel monkey or the pigtail macaque to short-chained carboxylic acids (Hübener and Laska, 2001; Laska et al., 2000). This class of odorants makes up the main component of body-borne prey odour (Flood, 1985) and is thus believed to be highly relevant for species feeding on animal prey, but presumably less important for mainly frugivorous primates.

A comparison of the olfactory performance of squirrel monkeys and pigtail macaques in detecting aliphatic esters (Laska and Seibt, 2001) and aliphatic alcohols reveals that both species are considerably more sensitive to the former group of substances than to the latter group. This finding concurs with the idea that not only the behavioural relevance but also the frequency of occurrence of a substance or substance class in a species' chemical world may determine its chemosensory capabilities because aliphatic alcohols, probably because of their high degree of chemical reactivity, are found in a much lower number of naturally occurring complex odours and usually at lower concentrations than aliphatic esters, which are known to comprise the qualitatively and quantitatively predominant aliphatic components in a wide variety of plant odours (Maarse, 1991; Knudsen et al., 1993).

Despite the obvious role played by the sense of smell 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 that 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.

A final aspect of the present study is our finding of a significant negative correlation between detection thresholds obtained in both squirrel monkeys and pigtail macaques and carbon chain length of the aliphatic 1- and 2-alcohols tested (see Figs 3, 6). The same regular association between olfactory sensitivity and this molecular property of the odorants has been found in human subjects (Cometto-Muniz and Cain, 1990; see Fig. 7) and in rats (Moulton, 1960; see Fig. 7). Corresponding correlations have also been found for homologous series of aliphatic carboxylic acids (Laska et al., 2000) and acetic esters (Laska and Seibt, 2001) in squirrel monkeys and pigtail macaques as well as in humans (Cometto-

Muniz and Cain, 1991; Cometto-Muniz et al., 1998), suggesting that this type of correlation might not be restricted to the class of odorants tested here but may represent a more general phenomenon.

In contrast, we found no correlation between olfactory detection thresholds and the second molecular feature studied here, i.e. the position of the functional alcohol group. Both squirrel monkeys and pigtail macaques showed very similar threshold values for 1-, 2- and 3-pentanol (see Fig. 7) and for 1- and 2-propanol and for 1- and 2-butanol, respectively, suggesting that, at least for the class of aliphatic alcohols, the position of the oxygen moiety has little effect on detectability. This finding, too, is in agreement with reports in human subjects (see Fig. 7).

In conclusion, the results of the present study provide further evidence of a well-developed olfactory sensitivity in two non-human primate species, the squirrel monkey and the pigtail macaque. These findings support the idea that olfaction may play an important role in the regulation of behaviour in these species. Further, they suggest that across-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 that attempts to correlate sensory performance with the behavioural relevance of odour stimuli might offer a promising approach in appraising the significance of the sense of smell for a particular species.

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