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Olfactory Discrimination Ability for Aliphatic Esters in Squirrel Monkeys and Humans

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Abstract

Using a behavioral paradigm designed to simulate olfactory-guided foraging, the ability of five squirrel monkeys to distinguish iso-amyl acetate from *n*- and iso-forms of other acetic esters (ethyl acetate to decyl acetate) and from other esters carrying the iso-amyl group (iso-amyl propionate to iso-amyl capronate) was investigated. We found (i) that all five animals were clearly able to discriminate between all odor pairs tested; (ii) a significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of both the aliphatic alcohol group and the aliphatic acid group of the esters; and (iii) that iso- and *n*-amyl acetate were perceived as qualitatively similar despite different steric conformation. Using a triple-forced choice procedure, 20 human subjects were tested on the same tasks in parallel and showed a very similar pattern of discrimination performance compared with the squirrel monkeys. Thus, the results of this study provide evidence of well-developed olfactory discrimination ability in squirrel monkeys for aliphatic esters and support the assumption that human and non-human primates may share common principles of odor quality perception. **Chem. Senses 22: 457–465, 1997.**

Introduction

One of the fundamental questions in olfactory research concerns the relationship between the properties of a molecule and its perceived odor quality. Psychophysical studies using odor profiling (Dravnieks, 1985) or multidimensional scaling procedures (Schiffman, 1981; Lawless, 1986) have so far met with only limited success in the quest for structure–activity relationships allowing prediction of the odor quality of a molecule or of the perceived similarity between odor molecules (Ohloff *et al.*, 1991).

However, some studies suggest that within a group of structurally related odorants, molecular features like carbon chain length or steric conformation may not only be correlated with perceptibility in terms of detection thresholds (Punter, 1983; Christoph and Drawert, 1985; Laska, 1990; Cometto-Muniz and Cain, 1991, 1994), but may also be connected in a regular way with odor quality and thus with perceived similarity between members of a given class of chemicals (Engen, 1964; Polak *et al.*, 1978; Hatanaka *et al.*, 1991; Yoshii *et al.*, 1994).

One useful means of assessing possible correlations between odor quality and molecular properties which avoids the disadvantages of subjectivity and likely context

dependence of the aforementioned methods is to test the discrimination ability for structurally related odorants. Furthermore, this method is also applicable to non-human species and a comparative approach to this topic seems particularly reasonable, considering recent findings in the molecular biology of olfaction. A large multigene family coding for putative odor receptors has been identified and these genes can be grouped into subfamilies on the basis of nucleotide sequence similarity (Buck and Axel, 1991). Thus, members of a subfamily encode receptors that are highly related in amino acid sequence and therefore are postulated to recognize structurally related ligands (Ngai *et al.*, 1993). Further, *in situ* hybridization experiments using molecular probes for various odorant receptor subtypes suggest that closely related mammalian species might have a larger proportion of odor receptors in common compared with phylogenetically more distant species (Strotmann *et al.*, 1995).

Due to their close phylogenetic relationship to man, non-human primates may represent a particularly interesting taxon to investigate with regard to similarities and differences in odor quality perception between species. In previous studies we could show that squirrel monkeys (*Saimiri sciureus*) can be readily trained to attend to and discriminate between odor stimuli. Using a task based on the discrimination of simultaneously presented odorants (Hudson *et al.*, 1992), reliable measurements of this species' olfactory performance in response to both artificial (Laska and Hudson, 1993a; Laska *et al.*, 1995, 1996) and natural odors (Laska and Hudson, 1995) have been obtained, and striking similarities in discrimination ability between *Saimiri* and man for artificial odor mixtures have been found (Laska and Hudson, 1993b).

The purpose of the present study is to extend these findings in a first attempt systematically to compare the discrimination ability of human and non-human primates for structurally related odorants. Initially, we have chosen aliphatic esters, a group of odorants which is qualitatively and quantitatively predominant in a variety of edible fruits (Nursten, 1977) and thus is presumably of biological significance for both species. Further, as esters are composed of an alcohol and a carboxylic acid, both parts of the molecule can be systematically varied independently of each other, thus making it possible to assess the impact of each for determining the odor quality of the substance.

Thus, the aims of the study are threefold: (i) to provide first data on the olfactory discrimination ability of squirrel monkeys for aliphatic esters; (ii) to assess whether a correlation between discrimination ability and structural similarity of the odorants under investigation exists; and (iii) by testing a group of human subjects in parallel, to assess whether human and non-human primates may share common principles of odor quality perception.

Materials and methods

Animals

Testing was carried out using three adult female and two adult male squirrel monkeys *(Saimiri 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 and Hudson, 1993a,b, 1995; Laska *et al.*, 1995, 1996). 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 (Altromin®), fresh fruit, vegetables and water *ad libitum*.

Behavioral test

In a task designed to simulate olfactory-guided foraging, 1.5 ml Eppendorf® flip-top reagent cups were equipped with absorbent paper strips (35 × 7 mm; Sugi, Kettenbach, Germany) impregnated with 10 µl of an odorant signaling 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 (diameter 40 mm) fitted with seven cross-bars (diameter 20 mm) 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. Cups were used

only once and the odorized strips were prepared fresh at the start of each session.

All experimental conditions were tested for a total of four sessions (i.e. 20 × 1 min trials performed on 2 consecutive days). In order to prevent the more challenging conditions leading to extinction or to a decline in the animals' motivation, and in order to obtain a baseline value allowing the appraisal of the discrimination performance of the squirrel monkeys in the critical tasks, these were always followed by a return to an easy control task for two sessions. This consisted of the discrimination between iso-amyl acetate and (–)-carvone (substances 1 and 2, Table 1), a substance which does not share any functional group or other apparent similarities in its molecular structure with the esters.

Data analysis

In assessing performance, only cups inspected by the monkeys were scored. For each individual the percentage of correct choices from the best two sessions, that is from 10, 1 min trials comprising a total of at least 60 decisions, was calculated. Correct choices included animals both correctly rejecting negative cups by failing to open or remove them, and identifying positive cups by removing and opening them to obtain the food reward. Conversely, errors involved 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.

Comparisons across tasks were made using the Friedman two-way analysis of variance. When ANOVA detected differences between tasks, this was then followed by pairwise Wilcoxon signed-rank tests for related samples to evaluate which tasks were responsible.

Correlations between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length were evaluated using the Spearman rank correlation coefficient and tested for significance by computing t-values (Siegel and Castellan, 1988). All tests were two-tailed and the alpha level was set at 0.05. All data are reported as means ± SD.

Human subjects

Twenty healthy, unpaid volunteers (12 females and eight males), 23–36 years of age, participated in the study. All were non-smokers and none had any history of olfactory dysfunction. All of the subjects had previously served in olfactory tests and were familiar with the basic test procedure.

Table 1 Substances and concentrations used (g/l)

Substances		Abbreviations	Squirrel monkeys	Human subjects
1	Iso-amyl acetate[a]	iAA	8.7	8.7
2	(–)-Carvone[a]	Car	107	107
Experiment I				
3.	Ethyl acetate[a]	EA	100	3.0
4.	*n*-Propyl acetate[a]	nPA	99	4.5
5.	Iso-propyl acetate[a]	iPA	99	3.0
6	*n*-Butyl acetate[a]	nBA	98	4.4
7	Iso-butyl acetate[a]	iBA	98	4.4
8.	*n*-Amyl acetate[a]	nAA	8.7	8.7
9	*n*-Hexyl acetate[a]	nHA	8.7	8.7
10.	*n*-Octyl acetate[b]	nOA	45.8	45.8
11.	*n*-Decyl acetate[b]	nDA	45.8	45 8
12.	Cyclohexyl ethyl acetate[b]	CHEA	32.7	19.3
Experiment II				
13.	Iso-amyl propionate[c]	iAP	95	2.9
14.	Iso-amyl butyrate[c]	iAB	29 9	17.7
15.	Iso-amyl valerate[c]	iAV	29 6	29.6
16.	Iso-amyl caproate[c]	iAC	94 4	94.4
17.	Iso-amyl benzoate[a]	iABen	495	110
18	Iso-amyl alcohol[a]	iAAlc	90	8.2
19	*n*-Amyl alcohol[a]	nAAlc	90	8.2
20	Acetic acid[a]	AcAc	21.6	3.6

Obtained from [a]Merck, [b]Sigma, [c]Grau

Test procedure

A 40 ml aliquot of each odorant was presented in a 250 ml polyethylene squeeze bottle equipped with a flip-up spout which for testing was fitted with a hand-made Teflon nose-piece. Subjects were free in the manner of sampling and at the start of the first session were allowed time to familiarize themselves with the bottles and the sampling technique.

In a forced-choice triangular test procedure, subjects were asked to compare three bottles and identify the one containing the odd stimulus. Bottles could be sampled twice per trial. Pairs were presented pseudorandomly while taking care to avoid successive presentations of the same combinations and while systematically varying the order in which the stimuli were sampled. Approximately 30 s was allowed between trials and no feedback regarding the correctness of the subjects' choice was given.

Ten (or nine in experiment 2) different stimulus pairs were

presented twice per session so as to give a total of 20 (or 18 in experiment 2) judgements. Testing was repeated in four more sessions each 1–3 days apart, enabling 10 judgements per stimulus pair and panelist to be collected.

Data analysis

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. Comparisons of group performance across tasks were made using the Friedman two-way analysis of variance. When ANOVA detected differences between tasks, this was then followed by pairwise Wilcoxon signed-rank tests for related samples to evaluate which tasks were responsible. Correlations between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length were evaluated using the Spearman rank correlation coefficient and tested for significance by computing *t*-values (Siegel and Castellan, 1988). All tests were two-tailed and the alpha level was set at 0.05. All data are reported as means ± SD.

Odorants

A set of 20 odorants was used (Table 1). All substances had a nominal purity of at least 99%. They were diluted using diethyl phthalate (Merck) as the solvent. In an attempt to ensure that the odorants were of approximately equal strength when presented on the absorbent paper strips, intensity matching was performed by a panel using freshly prepared strips impregnated with 10 µl of a 8.7 g/l solution of iso-amyl acetate as the standard. This was chosen (i) because this odorant and concentration had been successfully used in a previous study (Laska *et al.*, 1996), and (ii) in order to provide odor concentrations which could be reliably detected by the animals but weak enough to prevent contamination of the test cage and to force the animals to sniff closely.

Likewise, in an attempt to ensure that the odorants were of approximately equal strength when presented in squeeze bottles, intensity matching was performed by a panel using a 8.7 g/l solution of iso-amyl acetate as the standard. As the mode of presentation of odorants differed between squirrel monkeys (absorbent paper strips, i.e. an open system allowing odorants to diffuse freely) and humans (squeeze bottles, i.e. a closed system allowing odorants to build an equilibrium in the headspace) the concentrations used for the two species differed for some of the odorants (cf. Table 1).

Experiment 1

In a first series of discrimination tasks, both species were tested for their ability to distinguish iso-amyl acetate from other esters carrying the acetate group (substances 3–12, Table 1). With the exception of cyclohexyl ethyl acetate (substance no. 12, Table 1), which carries a cyclic instead of an aliphatic alcohol group, all substances only differed from each other either in length or branching of the carbon chain of the alcohol group, with iso-amyl acetate taking an intermediate position among the substances presented.

Methods

For the squirrel monkeys, iso-amyl acetate (iAA) was assigned as the rewarded stimulus (S+) and all other acetates were used as S–. In order to prevent serial order or training effects from confounding the results, the tasks were not presented according to increasing carbon chain length (Table 1) but according to increasing structural similarity and thus presumed similarity in odor quality between S+ and S–. Thus, the order of task presentation was: iAA versus odor nos 3, 12, 4, 11, 5, 10, 6, 9, 7, 8.

For the human subjects, each of the ten stimulus pairs was presented twice per session taking care that the presentation of iso-amyl acetate as odd or even stimulus was balanced within and between sessions. The sequence of presenting the stimulus pairs was systematically varied between sessions.

Results

Figure 1 summarizes the mean performance of squirrel monkeys and human subjects in discriminating iso-amyl acetate from other esters carrying the acetate group.

Squirrel monkeys

All five animals performed significantly above chance level in all tasks, usually scoring ~90% correct choices, and thus were clearly able to discriminate between all odor pairs presented (binomial test, $P < 0.001$ for all tasks and individuals). Interindividual variability was remarkably low and generally smaller than 10% between the highest and lowest scoring animal (cf. SDs in Figure 1). In the majority of cases their scores were in the range of the easy-to-solve control task [iso-amyl acetate versus (–)-carvone]. However,

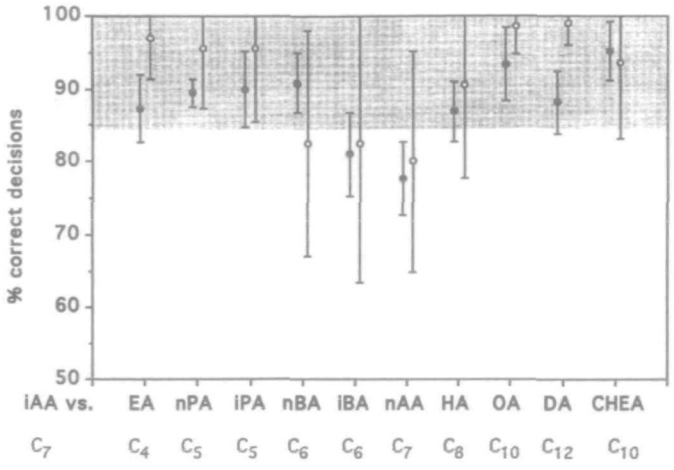

Figure 1 Performance (means ± SD) of five squirrel monkeys (filled circles) and 20 human subjects (open circles) in discriminating iso-amyl acetate from other esters carrying the acetate group. The hatched region indicates the range of performance shown by both species in a control task [iso-amyl acetate versus (–)-carvone]. The lower line of the abscissa indicates the number of carbon atoms of the respective substance. Abbreviations of substances are given in Table 1.

ANOVA detected significant differences in the animals' performance between tasks (Friedman, $P < 0.001$) and subsequent pairwise tests revealed that two of the substances (iso-butyl acetate and *n*-amyl acetate) were significantly more difficult to discriminate from iso-amyl acetate compared with the control and most of the other tasks (Wilcoxon, $P < 0.05$).

A significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of the aliphatic alcohol group of the esters was found (Spearman, $P < 0.05$).

Human subjects

As a group, the human subjects performed significantly above chance level in all tasks, usually scoring ~90% correct choices, and thus were clearly able to discriminate between all odor pairs presented (binomial test, $P < 0.001$ for all tasks) although marked interindividual differences in performance were apparent (cf. SDs in Figure 1). In the majority of cases mean scores were in the range of the easy-to-solve control task [iso-amyl acetate versus (–)-carvone]. However, ANOVA detected significant differences in the human subjects' performance between tasks (Friedman, $P < 0.001$) and subsequent pairwise tests revealed that three of the substances (*n*- and iso-butyl acetate, and *n*-amyl acetate) were significantly more difficult to discriminate from iso-amyl acetate compared with the control and all other tasks (Wilcoxon, $P < 0.05$). Accordingly, five (*n*-amyl acetate), four (iso-butyl acetate) and three (*n*-butyl acetate) out of 20 individuals respectively failed to significantly discriminate these substances from iso-amyl acetate (binomial test, $P > 0.05$).

A highly significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of the aliphatic alcohol group of the esters was found (Spearman, $P < 0.001$).

Experiment 2

In a second series of discrimination tasks, both species were tested for their ability to distinguish iso-amyl acetate from other esters carrying the iso-amyl group (substances 13–17, Table 1). With the exception of iso-amyl benzoate (substance no. 17, Table 1), which carries a cyclic instead of an aliphatic acid group, all substances only differed from each other in carbon chain length of the aliphatic acid group, with iso-amyl acetate having the shortest one among the substances presented.

Also included in this second series of experiments were tests of the squirrel monkeys' and the humans' ability to differentiate between iso-amyl acetate and its constituents, that is acetic acid and amyl alcohol in both its *n*- and iso-forms (substances 18–20, Table 1). Further, the human subjects had to distinguish between iso-amyl acetate and (–)-carvone, an odor pair which served as a control task for both species.

Methods

For the squirrel monkeys iso-amyl acetate (iAA) was assigned as the rewarded stimulus (S+) and all other substances including the iso-amyl esters were used as S–. In order to prevent serial order or training effects from confounding the results, the tasks using iso-amyl esters as S– were not presented according to increasing carbon chain length (Table 1) but in a pseudorandomized order (iAA versus odor nos 13, 16, 14, 15, 17) and followed by the remaining tasks.

For the human subjects, each of the nine stimulus pairs was presented twice per session taking care that the presentation of iso-amyl acetate as odd or even stimulus was balanced within and between sessions. The sequence of

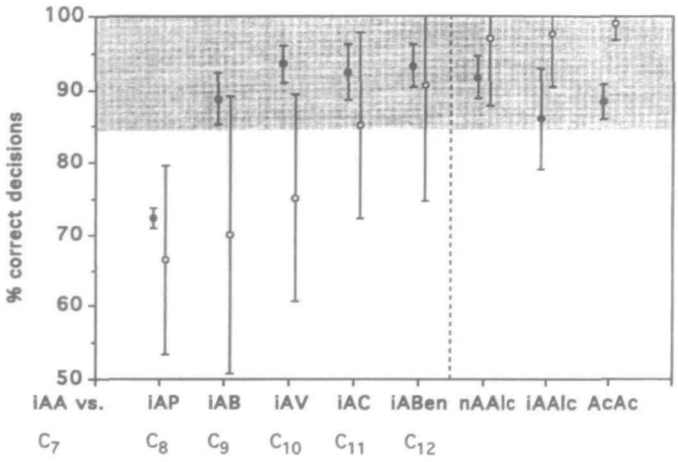

Figure 2 Performance (means ± SD) of five squirrel monkeys (filled circles) and 20 human subjects (open circles) in discriminating iso-amyl acetate from other esters carrying the iso-amyl group and from the constituents of iAA. The hatched region indicates the range of performance shown by both species in a control task [iso-amyl acetate versus (–)-carvone]. The dashed vertical line separates the two groups of substances tested in this experiment (iso-amyl esters and constituents of amyl acetate). The lower line of the abscissa indicates the number of carbon atoms of the respective substance. Abbreviations of substances are given in Table 1.

presenting the stimulus pairs was systematically varied between sessions.

Results

Figure 2 summarizes the mean performance of squirrel monkeys and human subjects in discriminating iso-amyl acetate from other esters carrying the iso-amyl group, and from its chemical constituents acetic acid and amyl alcohol.

Squirrel monkeys

All five animals performed significantly above chance level in all tasks, usually scoring ~90% correct choices, and thus were clearly able to discriminate between all odor pairs presented (binomial test, $P < 0.001$ for all tasks and individuals). Interindividual variability was remarkably low and generally smaller than 10% between the highest and lowest scoring animals (cf. SDs in Figure 2). In the majority of cases their scores were in the range of the easy-to-solve control task [iso-amyl acetate versus (–)-carvone]. However, ANOVA detected significant differences in the animals' performance between tasks (Friedman, $P < 0.001$) and subsequent pairwise tests revealed that iso-amyl propionate was significantly more difficult to discriminate from iso-amyl acetate compared with the control and all other tasks (Wilcoxon, $P < 0.05$).

A highly significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of the aliphatic acid group of the esters was found (Spearman, $P < 0.002$).

Human subjects

As a group, the human subjects performed significantly above chance level in all tasks, and thus were clearly able to discriminate between all odor pairs presented (binomial test, $P < 0.001$ for all tasks) although marked inter-individual differences in performance were apparent (cf. SDs in Figure 2). ANOVA detected significant differences in the human subjects' performance between tasks (Friedman, $P < 0.01$) and subsequent pairwise tests revealed that three of the substances (iso-amyl propionate, iso-amyl butyrate, and iso-amyl valerate) were significantly more difficult to discriminate from iso-amyl acetate compared with the control and all other tasks (Wilcoxon, $P < 0.05$). Accordingly, eight, six and four out of 20 individuals respectively failed significantly to discriminate these substances from iso-amyl acetate (binomial test, $P > 0.05$).

A highly significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of the aliphatic acid group of the esters was found (Spearman, $P < 0.001$).

Discussion

The results of this study demonstrate (i) that squirrel monkeys possess a well-developed olfactory discrimination ability for aliphatic esters; (ii) a significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of both the aliphatic alcohol group and the aliphatic acid group of the esters; (iii) that iso- and *n*-amyl acetate were perceived as qualitatively similar despite different steric conformation; and (iv) that human subjects tested on the same tasks in parallel showed a very similar pattern of discrimination performance compared with the squirrel monkeys.

Although only five animals were tested, the results appear robust, as interindividual variability of scores was remarkably low and the general pattern of performance across tasks was almost identical between individual monkeys (Spearman, $P < 0.01$). Further, two of the experimental

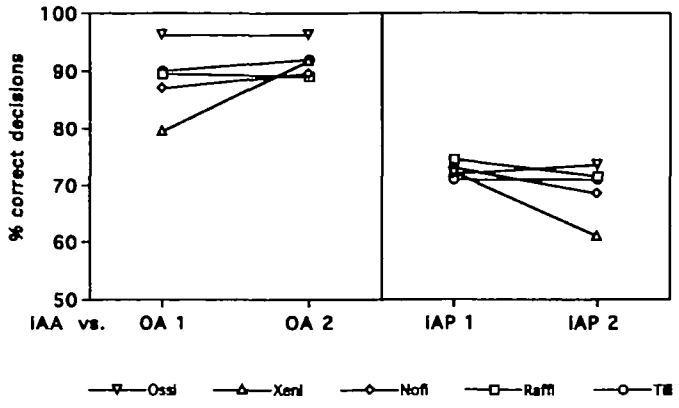

Figure 3 Comparison of the performance of the five squirrel monkeys in discriminating iso-amyl acetate (iAA) from octyl acetate (OA), and from iso-amyl propionate (iAP) during initial testing (1) and during retesting after 6 weeks (2) Each score represents the mean value of 10, 1 min trials per animal

conditions (iso-amyl acetate versus octyl acetate, and iso-amyl acetate versus iso-amyl propionate) were retested after 6 weeks and generally yielded very similar scores compared with their initial presentation (Figure 3), thus supporting the assumption that the results are not flawed by serial order or training effects but truly reflect differences in discrimination performance between tasks.

Given the presumed biological significance of aliphatic esters as indicators of the degree of ripeness (Maarse, 1991) and thus of the nutritional value of fruits (Nagy and Shaw, 1980), the finding of a well-developed olfactory discrimination ability of a frugivorous primate species for this group of substances may not be surprising. However, it should not be forgotten that in the real world odors are usually perceived in a given context, together with numerous non-olfactory cues which might help an animal to associate the odor with an odor source or a certain meaning. In our rather artificial experimental set-up, however, there were no such contextual cues, and therefore we think that the tasks employed were not at all trivial, an appraisal which is supported by the performance of the human subjects tested in parallel. Further, the good performance of *Saimiri sciureus* in the present study is in accordance with earlier reports of a highly developed discrimination ability in this species for artificial odor mixtures (Laska and Hudson, 1993a) and conspecific urine odors (Laska and Hudson, 1995), and thus gives additional support to the accumulating evidence that olfaction may play a significant role in the regulation of primate behavior (Epple *et al.*, 1993).

Correlations between molecular features like carbon chain length or steric conformation and perceptibility in terms of olfactory detection thresholds for various classes of substances including aliphatic esters have been established in humans (Punter, 1983; Christoph and Drawert, 1985; Cometto-Muniz and Cain, 1991, 1994) and in non-human species (Moulton, 1960; Laska, 1990). Surprisingly few studies, on the contrary, have systematically investigated correlations between carbon chain length and odor quality in structurally related substances. Pilgrim and Schutz (1957) and Engen (1964) have both reported perceptual similarity between members of a homologous series of aliphatic alcohols to be positively correlated with similarity in carbon chain length. Our finding of a significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length is in line with these reports and, to the best of our knowledge, is the first one using psychophysical methods in a non-human species. Polak *et al.* (1989) found amplitude reduction of the rat electro-olfactogram in response to *n*- and cycloalkanes after concanavalin A treatment to correlate with the size of the stimulus molecule, and concluded that the alkyl moiety may represent a primary quality-determining component in odor discrimination.

The fact that variation in carbon chain length of both constituent parts of an ester, the alcohol group and the acid group, were found to affect odor quality and thus perceptual similarity between odorants in the present study suggests that both parts of the molecule may be involved in stimulus–receptor interactions and thus supports the current concept of stimulus molecules having multiple epitopes which may interact independently of each other with complementary sites or ligand binding domains of the molecular receptor protein (Yoshii and Hirono, 1996).

Studies of correlations between steric conformation of a molecule and odor quality have so far concentrated on the discriminability of enantiomers, i.e. isomers with identical conformations except for chirality (e.g. Jones and Elliot, 1975; Chastrette *et al.*, 1992; Hummel *et al.*, 1992; Hormann and Cowart, 1993), whereas non-enantiomeric isomers of odorant molecules have only rarely been investigated with regard to structure–activity relationships (Polak *et al.*, 1978; Hatanaka *et al.*, 1991; Yoshii *et al.*, 1994). With both kinds of conformationally related substances, however, discrimination ability was usually found to be odor-pair specific, ranging from easily distinguishable odor pairs to

indiscriminable ones, and thus no generalizable correlation between odor quality and steric conformation has so far been at hand.

We found iso- and *n*-amyl acetate to be discriminable for both squirrel monkeys and humans but the comparatively poor performance of both species in this task suggests these two substances to be perceived as qualitatively similar, despite different steric conformation. It is interesting to note, however, that all five squirrel monkeys scored slightly better in the discrimination between iso-amyl acetate and *n*-amyl alcohol compared with the discrimination between iso-amyl acetate and iso-amyl alcohol (cf. Figure 2). Similarly, all five animals had more difficulties in discriminating between iso-amyl acetate and iso-butyl acetate than between iso-amyl acetate and *n*-butyl acetate (cf. Figure 1), suggesting that differences in steric conformation of functional groups may affect odor quality and thus discriminability of esters. This supposition is supported by the finding that replacement of the aliphatic forms of either the alcohol group or the carboxylic acid group of the esters by cyclic ones (cyclohexyl ethyl acetate and iso-amyl benzoate) seemed to affect odor quality in such a way that these substances were easily discriminated from iso-amyl acetate by both species.

Although the different methodologies employed with humans and squirrel monkeys do not allow valid comparisons of absolute discrimination scores between species, it seems admissible to compare the patterns of discrimination performance across tasks found with each species. In the present study, humans and squirrel monkeys showed apparent similarities in their relative discrimination performance, with both species scoring poorest in the tasks iso-amyl acetate versus *n*-amyl acetate, and iso-amyl acetate versus iso-butyl acetate in experiment 1, and iso-amyl acetate versus iso-amyl propionate in experiment 2 (cf. Figures 1 and 2). Further, both species showed a significant negative correlation between discrimination performance and structural similarity of odorants. These findings are in accordance with an earlier report which showed squirrel monkeys and humans to correspond in their patterns of discrimination ability for artificial odor mixtures which had been systematically varied in similarity in terms of the number of components the discriminanda shared (Laska and Hudson, 1993b).

Thus, the results of the present study further support the assumption that humans and squirrel monkeys may share common principles of odor quality perception. Given the recent advances in the understanding of the bimolecular process underlying the initial step of olfactory perception, it seems worthwhile to pursue our comparative approach to odor quality perception and discrimination using further groups of structurally related substances.

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REFERENCES

Buck, L. and Axel, R. (1991) A novel multigene family may encode odorant receptors. *Cell*, **65**, 175–187.

Chastrette, M., Rognon, C., Sauvegrain, P. and Amouroux, R. (1992) On the role of chirality in structure–odor relationships. *Chem. Senses*, **17**, 555–572.

Christoph, N. and Drawert, F. (1985) Olfactory thresholds of odour stimuli by gas chromatographic sniffing technique; structure–activity relationships. In Berger, R.G., Nitz, S. and Schreier, P. (eds), *Topics in Flavor Research*. Eichhorn, Marzling, pp. 59–77.

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. and Cain, W.S. (1994) Perception of odor and nasal pungency from homologous series of volatile organic compounds. *Indoor Air*, **4**, 140–145.

Dravnieks, A. (1985) *Atlas of Odor Character Profiles*. ASTM Data Series DS 61, American Society for Testing Materials, Philadelphia, PA.

Engen, T. (1964) Psychophysical scaling of odor intensity and quality. *Ann. NY Acad. Sci.*, **116**, 504–516.

Epple, G., Belcher, A.M., Küderling, I., Zeller, U., Scolnick, L.,

Greenfield, K.L. and Smith, A.B (1993) Making sense out of scents: species differences in scent glands, scent-marking behavior, and scent-mark composition in the Callitrichidae In Rylands, A.B (ed), *Marmosets and Tamarins: Systematics, Behavior, and Ecology.* Oxford University Press, Oxford, pp 123–151

Hatanaka, A., Kajiwara, T., Horino, H and Inokuchi, K. (1991) Odor-structure relationships in normal-hexenols and normal-hexenals *Z. Naturforsch C*, **47**, 183–189.

Hormann, C.A and Cowart, B.J. (1993) Olfactory discrimination of carvone enantiomers *Chem Senses*, **18**, 573.

Hudson, R., Laska, M and Ploog, D (1992) A new method for testing perceptual and learning capacities in unrestrained small primates *Folia Primatol* , **59**, 56–60.

Hummel, T., Hummel, C , Pauli, E. and Kobal, G. (1992) Olfactory discrimination of nicotine-enantiomers by smokers and non-smokers. *Chem Senses*, **17**, 13–21.

Jones, F.N. and Elliot, D. (1975) Individual and substance differences in the discriminability of optical isomers. *Chem Senses Flavor*, **1**, 317–321

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 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., Hübener, F. and Hudson, R. (1995) A study of odor learning capacity and odor memory in squirrel monkeys. *Chem Senses*, **20**, 79

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

Lawless, H.T. (1986) Multidimensional scaling. In Meiselman, H.L. and Rivlin, R.S. (eds), *Clinical Measurement of Taste and Smell.* MacMillan, New York, pp. 86–103

Maarse, H (1991) *Volatile Compounds in Foods and Beverages.* Marcel Dekker, New York.

Moulton, D.G. (1960) Studies in olfactory acuity. III. Relative detectability of *n*-aliphatic acetates by the rat. *Q. J. Exp Psychol.*, **13**, 203–213

Nagy, S. and Shaw, P.E. (1980) *Tropical and Subtropical Fruits. Composition, Nutritive Values, Properties, and Uses* Avi Publishing Co , Westport, CT.

Ngai, J., Dowling, M M., Buck, L , Axel, R. and Chess, A. (1993) The family of genes encoding odorant receptors in the channel catfish *Cell*, **72**, 657–666.

Nursten, H.E. (1977) The important volatile flavour components of foods. In Birch, G.G., Brennan, J G and Parker, K J (eds), *Sensory Properties of Foods.* Applied Science Publishers, London, pp 151–166.

Ohloff, G., Winter, B. and Fehr, C (1991) Chemical classification and structure–odour relationships In Müller, P.M. and Lamparsky, D. (eds), *Perfumes—Art, Science and Technology.* Elsevier, London, pp. 287–330.

Pilgrim, F.J. and Schutz, H G. (1957) Measurement of the qualitative and quantitative attributes of flavor. In *Chemistry of Natural Food Flavors.* Quartermaster Food Container Institute, Chicago, IL, pp 47–55

Polak, E., Trotier, D. and Baliguet, E (1978) Odor similarities in structurally related odorants *Chem Senses Flavor*, **3**, 369–380

Polak, E , Shirley, S G and Dodd, G H. (1989) Concanavalin A reveals olfactory receptors which discriminate between alkane odorants on the basis of size. *Biochem. J.*, **262**, 475–478.

Punter, P.H. (1983) Measurement of human olfactory thresholds for several groups of structurally related compounds. *Chem. Senses*, **7**, 215–237.

Schiffman, S S (1981) Characterization of odor quality utilizing multidimensional scaling techniques. In Moskowitz, H.R and Warren, C.B. (eds), *Odor Quality and Chemical Structure.* ACS Symp Series 148, Washington, pp. 1–21.

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

Strotmann, J , Beck, A , Kubick, S and Breer, H. (1995) Topographic patterns of odorant receptor expression in mammals: a comparative study *J. Comp. Physiol A*, **177**, 659–666

Yoshii, F. and Hirono, S (1996) Construction of a quantitative three-dimensional model for odor quality using comparative molecular field analysis (CoMFA) *Chem Senses*, **21**, 201–210.

Yoshii, F., Hirono, S. and Moriguchi, I (1994) Relation between the odor of (*R*)-ethyl citronellyl oxalate and its stable conformations. *Quant Struct –Act Relat.*, **13**, 144–147.

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