

Smell the mold: Olfactory sensitivity in spider monkeys (*Ateles geoffroyi*) for mold- associated odorants

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Division, Department

Department of Physics, Chemistry and Biology
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Datum
Date

Språk
Language

- Svenska/Swedish
 Engelska/English

Rapporttyp
Report category

- Licentiatavhandling
 Examensarbete
 C-uppsats
 D-uppsats
 Övrig rapport

ISBN

ISRN: LITH-IFM-A-EX--17/3358--SE

Serietitel och serienummer

Title of series, numbering

ISSN

URL för elektronisk version

Titel

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Författare

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Sammanfattning

Abstract

Primates are traditionally viewed as mainly visual animals with a poorly developed sense of smell. However, an increasing number of studies question the view that olfaction plays only a minor role in the daily life of non-human primates. Further, an increasing number of studies suggest that the behavioral relevance of odorants plays an important role for a species' olfactory sensitivity. Therefore, I assessed the olfactory sensitivity of spider monkeys for a set of eight mold-associated odorants using a food rewarded instrumental conditioning paradigm. I found that spider monkeys have a well-developed olfactory sensitivity to mold-associated odorants. With five of the eight odorants, all individuals reached olfactory detection thresholds lower than 1 ppm (parts per million), with single individuals performing even better. Positive relations between backbone carbon chain length and detectability, and between presence or absence of a branching of the carbon chain and detectability were found. However, no visible relation between olfactory sensitivity and the absence or presence of a double bond was found. The sensitivity for mold-associated odorants overlaps with that of other odorant classes studied previously in spider monkeys. There was no indication that olfactory sensitivity is correlated with neuroanatomical and genetic features. Behavioral significance of the odorants seems to better explain the between- and within-species differences in olfactory sensitivity.

Nyckelord

Keyword

Ateles geoffroyi, mold-associated odorants, olfactory sensitivity, spider monkeys

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1 Abstract

Primates are traditionally viewed as mainly visual animals with a poorly developed sense of smell. However, an increasing number of studies question the view that olfaction plays only a minor role in the daily life of non-human primates. Further, an increasing number of studies suggest that the behavioral relevance of odorants plays an important role for a species' olfactory sensitivity. Therefore, I assessed the olfactory sensitivity of spider monkeys for a set of eight mold-associated odorants using a food rewarded instrumental conditioning paradigm. I found that spider monkeys have a well-developed olfactory sensitivity to mold-associated odorants. With five of the eight odorants, all individuals reached olfactory detection thresholds lower than 1 ppm (parts per million), with single individuals performing even better. Positive relations between backbone carbon chain length and detectability, and between presence or absence of a branching of the carbon chain and detectability were found. However, no visible relation between olfactory sensitivity and the absence or presence of a double bond was found. The sensitivity for mold-associated odorants overlaps with that of other odorant classes studied previously in spider monkeys. There was no indication that olfactory sensitivity is correlated with neuroanatomical and genetic features. Behavioral significance of the odorants seems to better explain the between- and within-species differences in olfactory sensitivity.

Key words: *Ateles geoffroyi*, mold-associated odorants, olfactory sensitivity, spider monkeys

2 Introduction

Primates are traditionally viewed as mainly visual animals with a poorly developed sense of smell (King & Fobes 1974, Walker & Jennings 1991, Farbman 1992, Rouquier et al. 2000). This view is especially based on an interpretation of neuroanatomical features, such as the relative size of olfactory brain structures (Stephan et al. 1988, Brown 2001), or on genetic features, such as the number of functional olfactory receptor genes (Rouquier et al. 2000). However, a positive correlation between measures of neuroanatomical or genetic features and olfactory performance has not yet been found (De Winter & Oxnard 2000, Schoenemann 2001). In recent years an increasing number of studies question the widely held view that olfaction plays only a small role in the daily life of non-human primates. More and more evidence from non-human primate species indicates that the sense of smell is involved in food identification and selection (Ueno 1994, Bolen & Green 1997) and in social interactions like the

establishment and maintenance of rank (Kappeler 1998), territorial defense (Mertl-Millhollen 1986), identification of sexual partners (Heymann 1998), recognition of group members (Epple et al. 1993) and communication of reproductive status (Smith & Abbott 1998).

An increasing number of studies suggest that the behavioral relevance of odorants plays an important role for a species' olfactory sensitivity (Hernandez Salazar et al. 2003, Laska et al. 2005b, 2005d, Kjeldmand et al. 2011, Løtvedt et al. 2012, Eliasson et al. 2015, Laska & Hernandez Salazar 2015). Nevertheless, it is crucial to provide further data on olfactory detection thresholds in different species, across different sets of odorants in order to corroborate this notion. Furthermore, the set of odorants should share certain molecular structural properties but also differ in others to assess their impact on olfactory detectability.

Several studies demonstrated that spider monkeys (*Ateles geoffroyi*) possess a well-developed olfactory sensitivity for monomolecular solutions such as aliphatic esters (Hernandez Salazar et al. 2003), alcohols and aldehydes (Laska et al. 2006a), carboxylic acids (Laska et al. 2004), ketones, (Eliasson et al. 2015), monoterpenes (Joshi et al. 2006, Laska et al. 2006a), steroids (Laska et al. 2005a, Laska et al. 2006b), thiols and indols (Laska et al. 2007b) as well as alkylpyrazines (Laska et al. 2009), "green" odors (Løtvedt et al. 2012), and amino acids (Wallén et al. 2012). Further, these studies showed that spider monkeys have an excellent long-term memory for odors, is capable of rapid odor learning (Laska et al. 2003), and has an outstanding ability to distinguish between different degrees of ripeness in fruits based on their odors (Nevo et al. 2015).

Mold-associated odorants include several volatile metabolites produced by numerous strains of fungi species (Kaminski et al. 1974, Grove 1981). Substances like 3-methyl-1-butanol, 1-octen-3-one, 3-octanone, 1-octen-3-ol and trans-2-octen-1-ol are quantitatively prominent volatiles produced by fungi belonging to *Aspergillium*, *Penicillium* and Deuteromycota taxa (Kaminski et al. 1974, Grove 1981). However, other chemical compounds are also secreted by fungal species when exploiting a food item.

Mycotoxins are secondary metabolites produced by fungi and are known to pose health hazards to the organisms that ingest them (Börjesson et al. 1992). Such compounds are reported to be a defense mechanism of fungi against other organisms, as well as a protection mechanism to secure the food resource (Janzen 1977, Griffith et al. 2007). Besides, fungal species are also known to decrease nutritional content of the food material they develop in (Börjesson et al. 1992).

Thus, considering the potential dangers of spoiled food, frugivorous animals need to detect and avoid ingestion of spoiled food items. It is well-established that spider monkeys, a frugivorous New World primate, rely on their sense of smell in the context of food selection (Laska et al. 2007a, Pablo-Rodriguez et al. 2015). Further, spider monkeys have a higher sensitivity to putrefaction-associated odorants than to other studied odorants (Laska et al. 2007b), indicating an adaptation to the detection of degraded food material. Therefore, spider monkeys may have also adapted a high sensitivity to detect the odorous volatiles produced by fungal growths in food.

The aims of the present study were (1) to determine olfactory detection thresholds in spider monkeys for mold-associated odorants, (2) to assess the impact of molecular structural features on detectability of the tested odorants, and (3) to compare the threshold data obtained here to those of other species tested previously on the same set of odorants and to evaluate the impact of the number of functional olfactory receptor genes on olfactory sensitivity.

3 Materials and methods

3.1 Animals

Testing was carried out using one sub-adult male and two adult female spider monkeys, *A. geoffroyi* (Figure 1). The animals were born in captivity and were kept at the Field Station UMA Doña Hilda Ávila de O’Farrill, managed by the Universidad Veracruzana, near Catemaco, Veracruz, Mexico. The sub-adult male (Edgar) was the offspring of one of the females participating in the study (Kelly). Edgar and a female (Frida) were kept in separate outdoor enclosures measuring 6 x 4 x 4m, whereas Kelly was free-ranging. Therefore, the animals were exposed to natural environmental conditions regarding ambient temperature, relative humidity and sunlight. The two female subjects have participated in previous similar studies and thus were familiar with the experimental procedure. The male spider monkey, however, had to be trained on the method outlined below before the study.

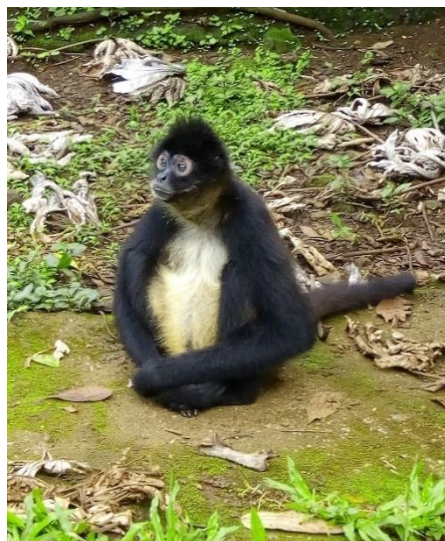


Figure 1 – A spider monkey (A. geoffroyi) at the Field Station UMA Doña Hilda Ávila de O’Farrill.

3.2 Odorants

A set of eight odorants was used: 1-octen-3-ol (CAS# 3391-86-4), 1-octen-3-one (CAS# 4312-99-6), 3-octanol (CAS# 589-98-0), 3-octanone (CAS# 106-68-3), trans-2-octen-1-ol (CAS# 18409-17-1), 2-methyl-1-propanol (CAS# 78-83-1), 2-methyl-1-butanol (CAS# 137-32-6), and 3-methyl-1-butanol (CAS# 123-51-3). All substances were obtained from Sigma-Aldrich (St. Louis, MO) and had a normal purity of at least 99%. They were diluted using the near-odorless solvent diethyl phthalate - DEP (CAS# 84-66-2). Gas phase concentrations for the headspace above the diluted odorants were calculated using published vapor pressure data (Dykyi et al. 2001) and corresponding formulae (Weast 1987). Figure 2 shows the molecular structure of the odorants. The odorants differed in the backbone carbon chain length, the type of functional group, the presence or absence of double bonds and type of structural isomerism.

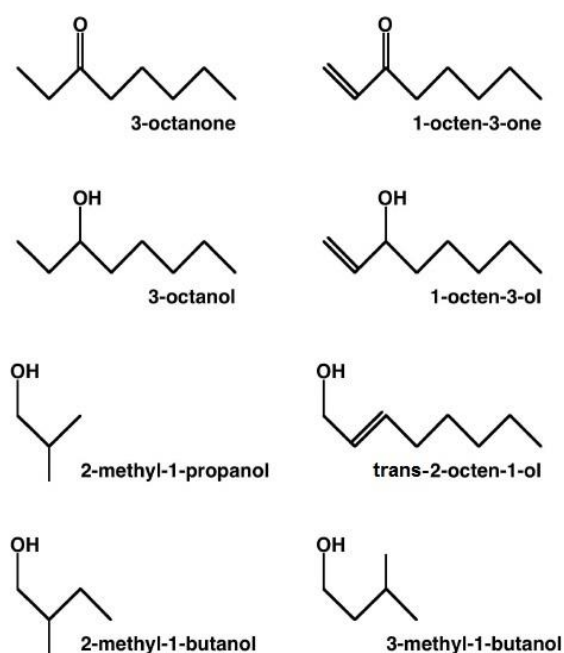


Figure 2 – Molecular structures of the eight odorants used in the study.

3.3 Behavioral test

The spider monkeys were tested using a food-rewarded instrumental conditioning paradigm (Laska et al. 2003). The test apparatus (Figure 3) consisted of a 50 cm long and 6 cm wide metal bar with two cube-shaped opaque PVC boxes with a side length of 5.5 cm attached to it at a distance of 22 cm from each other. Each container was equipped with a tightly closing hinged metallic lid, hanging 2 cm down the front of the container. From the center of the front part of the lid, a pin of 3 cm length extended toward the animal and served as a lever to open the lid. A metal clip was attached on top of each lid. This clip held a 70 mm x 10 mm absorbent paper strip (Schleicher & Schuell, Einbeck, Germany) which was impregnated at its distal end with 20 μ l of an odorant used as rewarded stimulus (S+) or with 20 μ l of the near-odorless solvent (DEP) used as unrewarded stimulus (S-). The paper strips extended approximately 3 cm into the cage when the apparatus was presented to the animals. The box with the odorized paper strip attached to the lid contained a food reward, a Kellogg's Froot Loop®, while the one with the odorless paper strip did not.



Figure 3 – The apparatus used in the study, as described by Laska et al. (2003).

When presented with the apparatus, the individual sniffed both paper strips for as long as it liked and then decided to open one of the boxes (Figure 4). The animal retrieved a food reward in case of a correct choice, or found the box empty in case of an incorrect choice. Also, only one of the boxes was allowed to be opened. Thus, in case of an incorrect choice, the animal was not allowed to correct its choice. After each decision, the apparatus was immediately removed, cleaned and prepared for the next presentation out of sight from the animals. These presentations were given in three blocks of 10 trials (i.e. three sessions) per day. Each one of the two boxes of the apparatus was baited with a food reward in five of the 10 trials that comprised a session. The order of the rewarded sides was randomized with the only condition being that the same box would not be baited more than three times in a row.

The animals were tested individually to avoid distraction from conspecifics. To this end, an animal voluntarily entered a small test cage (80 cm x 50 cm x 50 cm) adjacent to the enclosure. The animal sat on a bar mounted horizontally and parallel to the front side of the test cage. This front side of the test cage consisted of a stainless-steel mesh with a width of 1 cm and had two openings of 5 cm x 5 cm allowing the animal to reach through the mesh, open the lid of one of the boxes of the test apparatus and to retrieve the food reward. The test apparatus could be attached to the outside of the front side of the test cage in such a way that the lids of the boxes were at a height consistent with the reach-through openings. The free-ranging female – Kelly – was lured to a small hut in the field station in order to perform the behavior test.

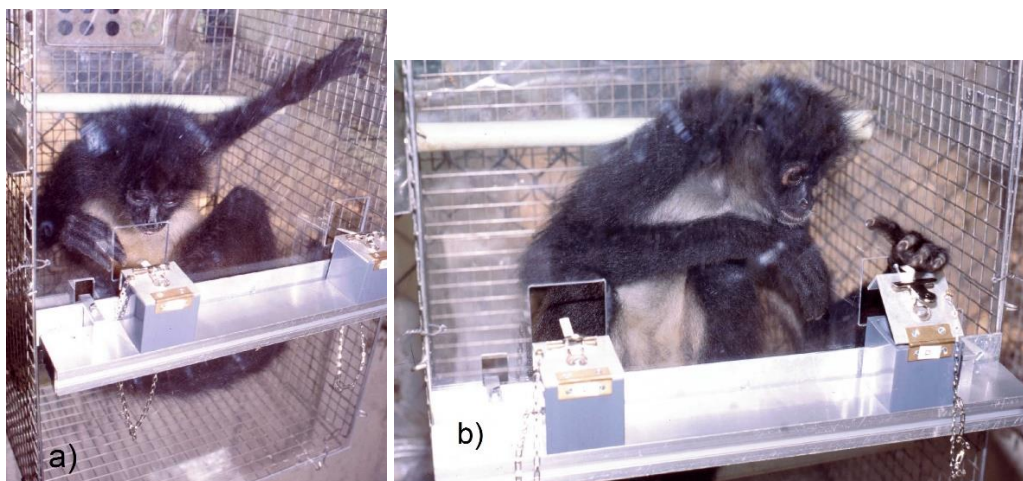


Figure 4 – Spider monkey performing the behavioral test. The animal first sniffs the impregnated paper strips (a) and then decides and opens one of the boxes (b). Photos taken by Matthias Laska.

Testing started at a 100-fold dilution of a given odorant. This dilution was presented on three subsequent days (i.e. for nine sessions comprising a total of 90 trials) to allow the animals to build a robust association between a given odorant and its reward value. To determine olfactory detection thresholds for the odorants, the monkeys were then presented with 10-fold increasing dilutions (i.e. lower concentrations) of the rewarded stimulus (S+) for three sessions (i.e. a total of 30 trials) per dilution step until they failed to discriminate it from the unrewarded stimulus (S-). Subsequently, they were presented with an intermediate dilution step (0.5 10-based logarithmic units between the lowest concentration that was detected and the first concentration that was not) for three sessions to determine the threshold value more exactly. Every time an individual failed to discriminate a dilution step for the first time, the dilution would be presented for a second time (i.e. three more sessions), so to double-check whether the failure was due to some reason (e.g. a lack of motivation) other than an incapacity to discriminate the odorant from the solvent. Data collection took place between June and November 2016. The spider monkeys were not kept on a food deprivation regime but were tested in the morning prior to the daily feeding time.

3.4 Data analysis

For each individual animal, the percentage of correct choices from 30 trials per dilution step was calculated. Correct choices consist of both animals identifying and opening the rewarded box (S+), and rejecting the non-rewarded box (S-). Conversely, errors consist of animals opening the non-rewarded box (S-) or failing to open the rewarded box (S+). Significance

levels were determined by calculating binomial z-scores corrected for continuity from the number of correct and false responses for each individual animal and condition. All tests were two-tailed and the alpha level was set at 0.05.

Even though no proper statistical comparisons can be drawn due to the small number of individuals used, I examined between-odorant differences (based on $n=3$ data points) by considering whether the ranges of threshold values overlap or not, in order to at least get a first impression of possible differences in sensitivity.

4 Results

4.1 Olfactory detection thresholds

Figure 5 shows the spider monkeys' ability in detecting different dilutions of the eight odorants under study. All three individuals were able to discriminate the odorant from the near-odorless solvent at dilutions as low as $1:10^4$ (trans-2-octen-1-ol, 2-methyl-1-propanol, 2-methyl-1-butanol, 3-methyl-1-butanol), as $1:10^5$ (1-octen-3-one, 3-octanol) and as $1:3 \times 10^5$ (3-octanone). Some individuals even detected an odorant at dilutions as low as $1:3 \times 10^4$ (2-methyl-1-propanol, 2-methyl-1-butanol, 3-methyl-1-butanol), as $1:10^6$ (3-octanol, trans-2-octen-1-ol), as $1:3 \times 10^6$ (1-octen-3-one) and as $1:10^7$ (3-octanone).

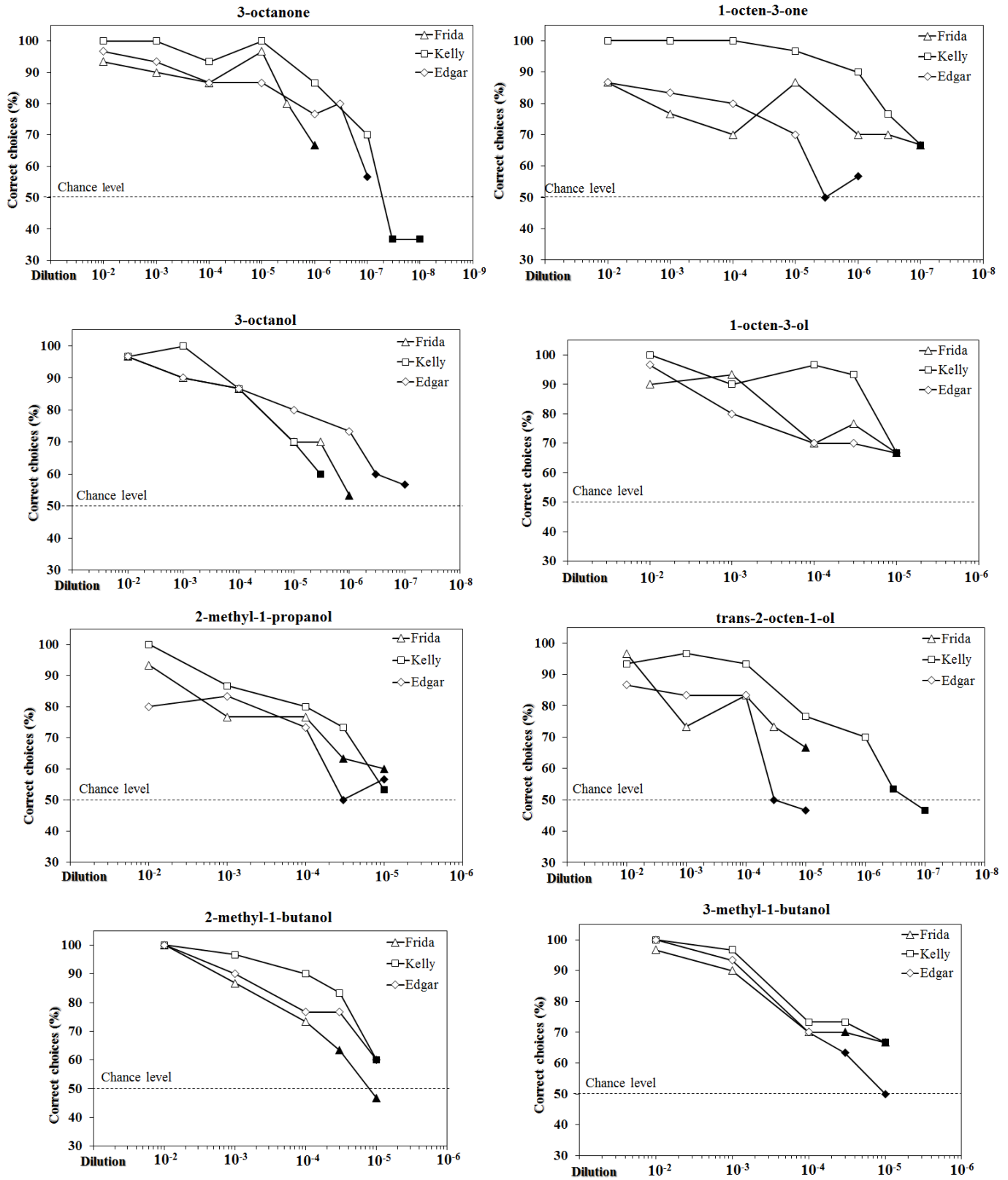


Figure 5 - Performance of three spider monkeys in detecting different dilutions of a mold-associated odorant. Each data point represents the percentage of correct choices from 30 decisions. Filled symbols indicate that the individual did not discriminate the odorant from the solvent significantly above chance level (binomial test, $p > 0.05$). Note that for the odorant 3-octanol one of the data points is not displayed.

4.2 Inter- and intra-individual variability

Olfactory performance varied among the individuals participating in the study, except for the odorant 1-octen-3-ol, in which the detection thresholds of all three individuals were identical ($1:3 \times 10^4$). The individuals' detection thresholds varied, at the most, by a dilution factor of 100, for trans-2-octen-1-ol. Kelly reached the lowest detection thresholds with six of the odorants, followed by Frida, with whom she shared two odorants with the lowest detection threshold. Finally, Edgar had the highest detection thresholds with four of the odorants.

Table 1 displays the different olfactory detection threshold values expressed as gas phase concentration measures for each odorant. The majority of the detection thresholds correspond to gas phase concentrations lower than 1 ppm (parts per million). Furthermore, one of the animals reached a concentration lower than 1 ppb (parts per billion) with 3-octanone.

Table 1 – Olfactory detection thresholds for the eight mold-associated odorants expressed in different gas phase concentration measures. N indicates the number of individuals that reached a given threshold value.

Odorant	N	Liquid dilutions	Gas phase concentration				
			Molec./cm ³	ppm	log (ppm)	mol/L	log (mol/L)
1-octen-3-one	1	1:10 ⁵	1.1×10 ¹²	0.041	-1.39	1.83×10 ⁻⁹	-8.74
	2	1:3×10 ⁶	3.67×10 ¹⁰	0.0014	-2.87	6.09×10 ⁻¹¹	-10.22
1-octen-3-ol	3	1:3×10 ⁴	2.83×10 ¹²	0.011	-0.98	4.7×10 ⁻⁹	-8.33
3-octanone	1	1: 3×10 ⁵	3.67×10 ¹¹	0.0136	-1.87	6.09×10 ⁻¹⁰	-9.22
	1	1:3×10 ⁶	3.67×10 ¹⁰	0.0014	-2.87	6.09×10 ⁻¹¹	-10.22
3-octanol	1	1:10 ⁷	1.1×10 ¹⁰	0.00041	-3.39	1.83×10 ⁻¹¹	-10.74
	1	1:10 ⁵	8.5×10 ¹¹	0.032	-1.5	1.41×10 ⁻⁹	-8.85
	1	1:3×10 ⁵	2.83×10 ¹¹	0.011	-1.98	4.7×10 ⁻¹⁰	-9.33
trans-2-octen-1-ol	1	1:10 ⁶	8.5×10 ¹⁰	0.0032	-2.5	1.41×10 ⁻¹⁰	-9.85
	1	1:10 ⁴	4.1×10 ¹²	0.152	-0.82	6.81×10 ⁻⁹	-8.17
	1	1:3×10 ⁴	1.37×10 ¹²	0.051	-1.3	2.27×10 ⁻⁹	-8.64
2-methyl-1-propanol	1	1:10 ⁶	4.1×10 ¹⁰	0.0015	-2.82	6.81×10 ⁻¹¹	-10.17
	2	1:10 ⁴	10 ¹⁴	3.70	0.57	1.66×10 ⁻⁷	-6.78
2-methyl-1-butanol	1	1:3×10 ⁴	3.33×10 ¹³	1.23	0.09	5.53×10 ⁻⁸	-7.26
	2	1:10 ⁴	4.5×10 ¹³	1.67	0.22	7.47×10 ⁻⁸	-7.13
3-methyl-1-butanol	1	1:3×10 ⁴	1.5×10 ¹³	0.56	-0.25	2.49×10 ⁻⁸	-7.60
	2	1:10 ⁴	3.9×10 ¹³	1.44	0.16	6.48×10 ⁻⁸	-7.19
3-methyl-1-butanol	1	1:3×10 ⁴	1.3×10 ¹³	0.48	-0.32	2.16×10 ⁻⁸	-7.67

5 Discussion

The results of this study show that spider monkeys have a well-developed olfactory sensitivity for mold-associated odorants. Other studies using the same experimental procedures have shown a well-developed olfactory sensitivity for other odorant classes in this primate species, too (Hernandez Salazar et al. 2003, Laska et al. 2004, Laska et al. 2009, Løtvedt et al. 2012, Eliasson et al. 2015). The findings of the present study do not support the long-held belief that primates have a poorly developed sense of smell (King & Fobes 1974, Walker & Jennings 1991, Farbman 1992, Rouquier et al. 2000).

Interindividual variability was generally low, varying at the most by a dilution factor of 100 for trans-2-octen-1-ol, which in turn is smaller than the range of interindividual variability reported in studies on human olfactory sensitivity (Johnson et al. 2007). For 1-octen-3-ol all three individuals even reached the same detection threshold value. This confers some robustness and reliability on the data obtained. It is also important to mention that a new individual, Edgar, was trained and submitted to this behavioral test for the first time and the detection thresholds reported for him were not disparate from those found in the other, more experienced, individuals. This shows that spider monkeys are capable of learning an operant conditioning paradigm in a relatively short period of time and perform generally as good as highly-experienced animals.

After several studies similar to the one reported here in which only female animals were used, the present study included a male individual. This impediment was mainly due to female spider monkeys being more willing to cooperate and less easily distracted than males (Eliasson et al. 2015). No evident differences between sexes were observed in this study, a finding in line with others in both animals and human studies where no systematic sex-related difference in olfactory sensitivity was found (Hernandez Salazar et al. 2003, Laska et al. 2004). In only one study, Laska and co-workers (2006b) reported a possible sex-related difference in olfactory sensitivity in spider monkeys. However careful conclusions should be drawn as only two odorous steroids were used in the study and these were relevant in terms of sexual behavior.

Some considerations may be withdrawn from the comparison of the ranges of threshold values of structurally-related odorants, which will be discussed in the following paragraphs. However, due to the small number of individuals used in this study, only tentative conclusions are possible.

5.1 Comparison among the mold-associated odorants

The lowest detection thresholds found here were generally below 1 ppm and correspond to the odorants 1-octen-3-one, 1-octen-3-ol, 3-octanone, 3-octanol and trans-2-octen-1-ol, all of them being aliphatic compounds with an unbranched backbone of eight carbons. On the other hand, the odorants with a branched backbone of only four or five carbons used in this study were found to have detection thresholds higher than 1 ppm for all individuals, except Edgar and Kelly for 2-methyl-1-butanol and Kelly for 3-methyl-1-butanol. Furthermore, the detection thresholds for 2-methyl-1-propanol ranged from 1.23 ppm to 3.7 ppm, whereas the ones for 2-methyl-1-butanol range from 0.56 ppm to 1.67 ppm, indicating that spider monkeys are slightly more sensitive to the latter. Besides differing in their threshold values, these two substances also differ in the backbone carbon chain length: 2-methyl-1-propanol having three carbon atoms and 2-methyl-1-butanol having four carbon atoms. These findings lend further support to an existing correlation between backbone carbon chain length and detectability in spider monkeys, as found in earlier studies on aliphatic esters (Hernandez Salazar et al. 2003), aliphatic alcohols and aldehydes (Laska et al. 2006a) and putrefaction-associated odorants (Laska et al. 2007b).

The odorant-pairs 3-octanone/3-octanol and 1-octen-3-one/1-octen-3-ol differed only in the type of functional group. There is an overlap of the detection threshold values in the first odorant pair, but not in the second pair (Figure 6).

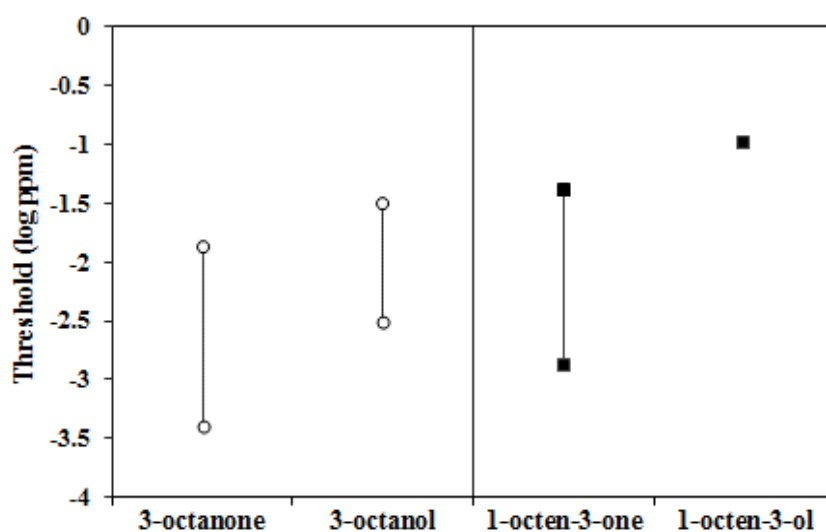


Figure 6 – Comparison of the detection threshold values for the odorant pairs 3-octanone/3-octanol (white circles) and 1-octen-3-one/1-octen-3-ol (black squares).

The observed trend in both these odorant pairs is a higher olfactory sensitivity to the ketones than to the alcohols. These results do not support the ones reported by Eliasson and co-workers (2015), who found spider monkeys being less sensitive to aliphatic ketones than to other aliphatic compounds, including alcohols. However, in the study conducted by Eliasson and co-workers (2015), the position of the functional group of the odorants was different from the ones used in the present study. Furthermore, the researchers did not compare ketones and alcohols with a double bond in their carbon backbone chains. These factors may explain the difference in the findings of both studies and future research needs to re-visit this issue.

The ranges of detection thresholds for the odorants 2-methyl-1-butanol and 3-methyl-1-butanol overlapped each other. As these odorants only differ in terms of the position of the methyl group in the carbon backbone chain, it seems that this may not affect the olfactory sensitivity in this species.

Finally, some conclusions may be drawn from the odorant pairs 1-octen-3-one/3-octanone and 1-octen-3-ol/3-octanol (Figure 7), which both differ with regard to the presence or absence of a double bond in the molecule.

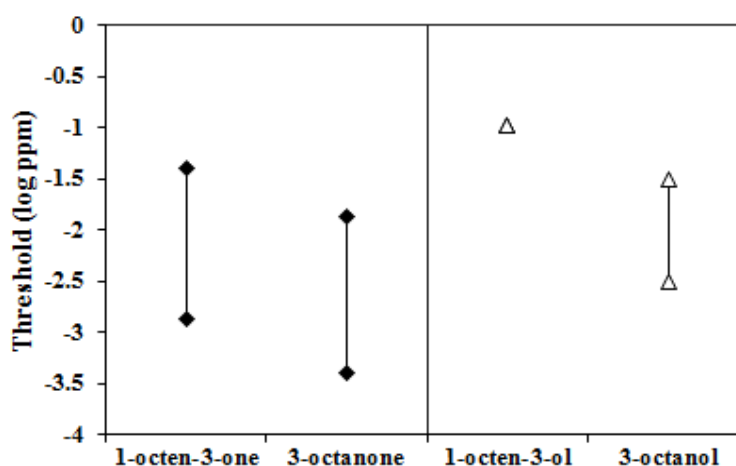


Figure 7 – Comparison of the detection threshold values for the odorant pairs 1-octen-3-one/3-octanone (black diamonds) and 1-octen-3-ol/3-octanol (white triangles).

In the first pair, the detection threshold ranges of both odorants overlapped, suggesting that spider monkeys are not more sensitive to one of the substances. This corroborates with the findings of Løtvedt and co-workers (2012) that the presence or absence of a double bond does not systematically affect olfactory sensitivity. However, in the second one, spider monkeys had lower detection thresholds for 3-octanol than for 1-octen-3-ol, indicating a higher sensitivity to the substance lacking a double bond. Due to the inconclusive nature of the findings in the present study, more research should be conducted to unveil whether the presence of a double bond affects olfactory sensitivity in a systematic manner or whether some odorant classes may be an exception to the rule in spider monkeys.

5.2 Comparison with structurally related odorants tested previously in *Ateles*

Comparisons between the detection threshold values for the odorants tested in the present study and other studies can also provide further insight into structure-activity relationships among odorants in spider monkeys. The detection thresholds for the odorant 3-octanol (tested here) ranged between 3.2 ppb and 32 ppb, whereas the olfactory detection threshold determined for 1-octanol (Laska et al. 2006a) was 4.8 ppb. These molecules differ from each other in the position of the functional alcohol group. No difference in olfactory sensitivity can be concluded from these findings, agreeing with what was reported by Eliasson and colleagues (2015) that the position of the functional alcohol group does not affect olfactory sensitivity.

Furthermore, the olfactory detection thresholds for 3-octanone (tested here) ranged from 0.41 ppb to 4.1 ppb, while the range of the threshold values for 2-octanone (Eliasson et al. 2015) reached as low as 0.034 ppm to as high as 0.34 ppm. Here, though, there is a remarkable difference in terms of the olfactory sensitivity of substances that differ in their position of the functional group, i.e., spider monkeys are more sensitive to 3-octanone than to 2-octanone. This difference is rather interesting, posing an exception to previous findings on the effect of the position of the functional group on detectability. Some conclusions can be drawn from this discrepancy. The results obtained in the present study are reliable and comparable with previous ones, as the same method was used, as well as a low inter-individual variability was reported. The most straightforward explanation is that the position of the functional group may have an effect on detectability only in some odorant classes and may not be a general rule. Thus, future research should focus on this issue.

The odorants *trans*-2-octen-1-ol (tested here; detection range: 1.5 – 152 ppb) and 1-octanol (Laska et al. 2006a; detection threshold value: 4.8 ppb) differ in the presence or absence of a double bond in the carbon backbone chain. Here, too, no difference in detectability is apparent, further suggesting that the presence or absence of a double bond may not affect olfactory sensitivity in spider monkeys.

Finally, further conclusions can be drawn by comparing the olfactory detection thresholds of structural isomers, i.e., molecules with the same atomic composition but having a different structural arrangement. The threshold values of the odorant 2-methyl-1-propanol (tested here) ranged between 0.56 ppm and 1.57 ppm, whilst the range of threshold values for the odorant 1-butanol (Laska et al. 2006a) was 0.26 – 0.86 ppm. There is a small overlap between these value ranges but the detection thresholds outside of the overlapping area indicate that spider monkeys are more sensitive to the unbranched odorant, 1-butanol, than to the branched one, 2-methyl-1-propanol. Also, the odorants 2-methyl-1-butanol (detection threshold range: 0.56 – 1.57 ppm) and 3-methyl-1-butanol (detection threshold range: 0.48 – 1.44 ppm), both tested in the present study, are branched structural isomers of the odorant 1-pentanol (Laska et al. 2006a; detection threshold range: 0.4 ppb – 0.04 ppm). Spider monkeys are clearly more sensitive, again, to the unbranched odorant 1-pentanol than to its branched isomers. These findings have not been reported in earlier studies, and indicate that another odor structure-activity relationship may be at play. Thus, future studies should systematically investigate the characteristics of this relationship.

5.3 Comparison with odorants belonging to other chemical classes tested previously with *Ateles*

The olfactory detection threshold values determined in the present study ranged from 0.41 ppb for 3-octanone to 3.70 ppm for 2-methyl-1-propanol. Figure 8 depicts a comparison of the detection threshold ranges for spider monkeys across the odorant groups available on the literature, including the ones used in the present study.

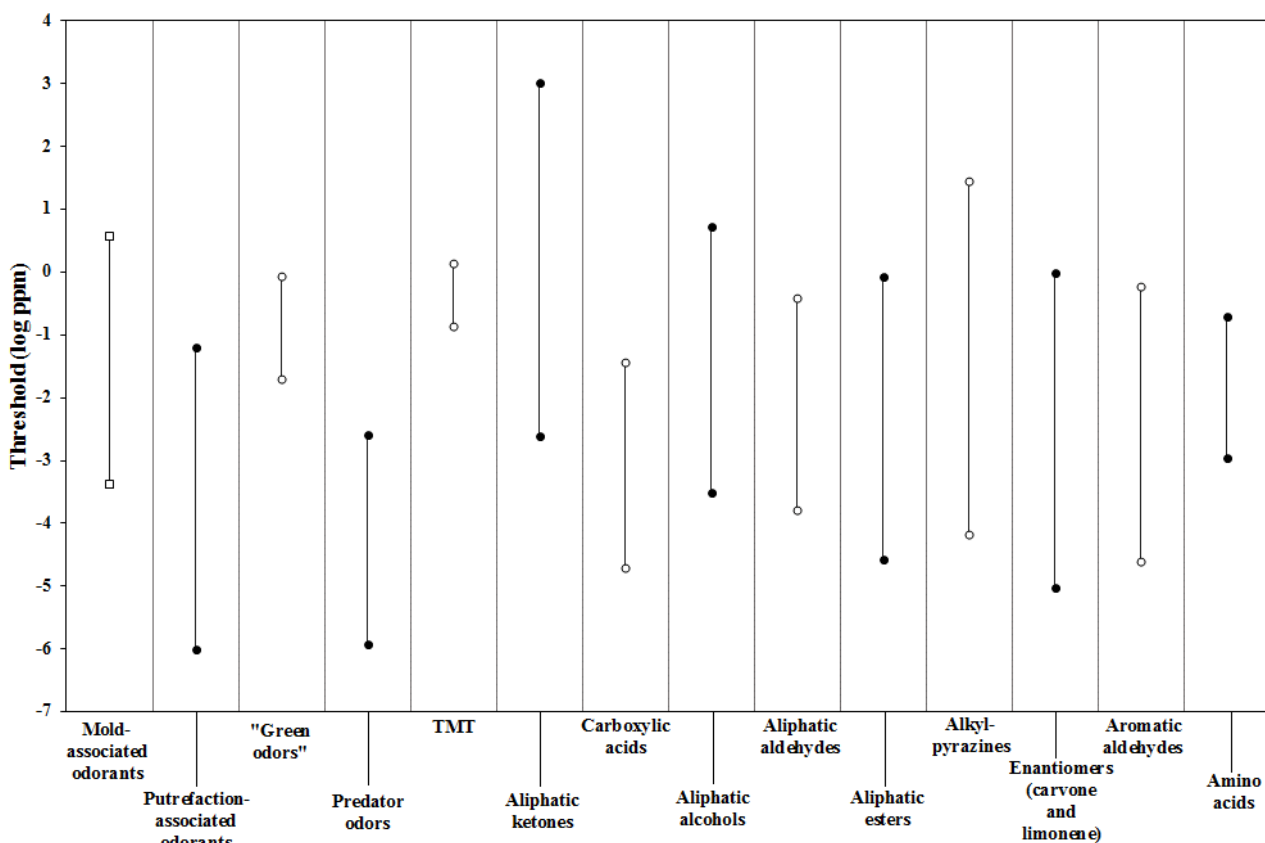


Figure 8 – Comparison of the olfactory detection threshold ranges in spider monkeys between mold-associated odorants used in the present study and other odorant groups cited in the literature: putrefaction-associated odorants (Laska et al. 2007a), “green odors” (Løtvedt et al. 2012), predator odors (Sarrafchi et al. 2013), 2,4,5-trimethylthiazoline (Laska et al. 2005c), aliphatic ketones (Eliasson et al. 2015), carboxylic acids (Laska et al. 2004), aliphatic alcohols and aldehydes (Laska et al. 2006a), aliphatic esters (Hernandez Salazar et al. 2003), alkylpyrazines (Laska et al. 2009), a set of enantiomers (Joshi et al. 2006), aromatic aldehydes (Kjeldmand et al. 2011) and amino acids (Wallén et al. 2012).

Considering the numerous studies conducted on the sensitivity of spider monkeys to different odorant classes, one may conclude that sensitivity for mold-associated odorants overlaps with the sensitivity for most of the other chemical classes tested so far in spider monkeys.

5.4 Comparison with other species

Across the available literature, olfactory detection thresholds for the odorants used in the present study have only been reported for humans.

Figure 9 shows the ranges of olfactory detection threshold values for both humans and spider monkeys for mold-associated odorants. Humans are

clearly more sensitive to five of the eight mold-associated odorants tested in the present study than spider monkeys, whereas for three of the eight odorants, the human threshold range encompasses that of spider monkeys.

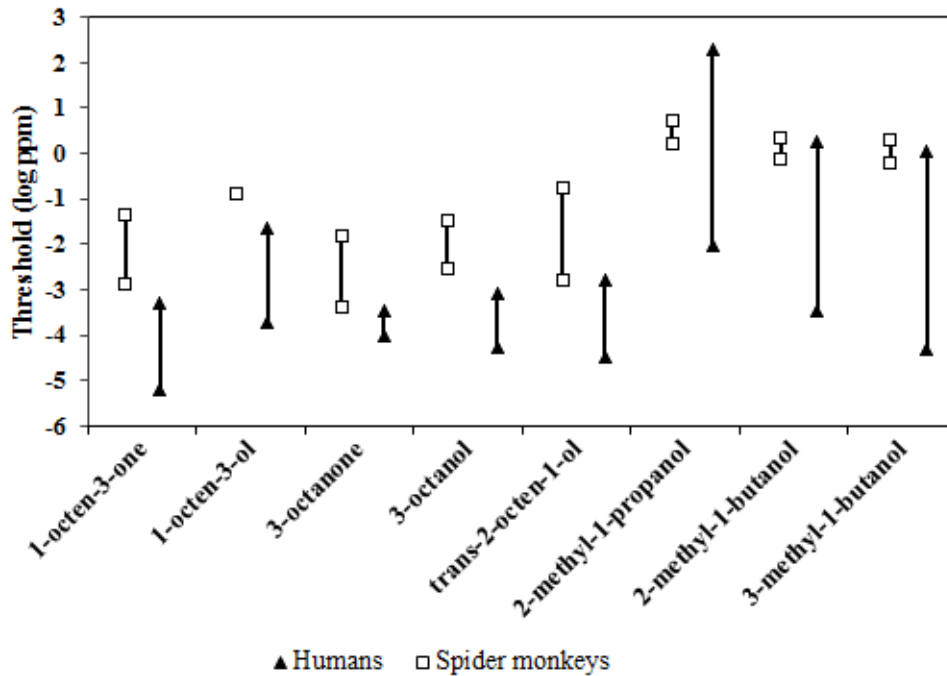


Figure 9 – Ranges of the olfactory detection thresholds for humans (black triangles) and spider monkeys (white squares) for the mold-associated odorants used in the present study. The range for humans was determined using the highest and the lowest detection values found in an odorant threshold compilation (van Gemert 2011).

Several explanations for a difference in olfactory performance among different species have been proposed. Some authors suggested that the olfactory capabilities are correlated with the absolute or relative sizes of the olfactory bulbs (Fobes & King 1982, Stephan et al. 1988). Humans have a higher absolute size of the main olfactory bulb (114 mm³) compared to spider monkeys (90.4 mm³). The same is not observed in terms of relative main olfactory bulb size, where spider monkeys surpass humans (0.9% vs. 0.09%, respectively) (Stephan et al. 1988). These findings indicate that olfactory bulb size does not explain a between-species difference in olfactory sensitivity, along with other findings found throughout the literature (Hernandez Salazar et al. 2003, Laska et al. 2005d, Kjeldmand et al. 2011, Løtvedt et al. 2012, Eliasson et al. 2015).

Other authors proposed that the number of functional olfactory receptor genes or the proportion of olfactory receptor pseudogenes are indicators of the olfactory sensitivity of a certain species (Rouquier et al. 2000, Gilad et al. 2004). Spider monkeys have a higher number of functional olfactory receptor genes (≈ 900) than humans (≈ 396) (Nei et al. 2008, Niimura 2012). If a clear correlation would exist, spider monkeys should be expected to be more sensitive to mold-associated odorants than humans, which is not the case. Once again, the lack of a correlation between genetic factors and olfactory sensitivity has also been reported in other studies (Hernandez Salazar et al. 2003, Laska et al. 2005d, Laska & Hernandez Salazar 2015), lending further support to the notion that genetic factors are not good predictors of olfactory performance.

Finally, the behavioral relevance of the odorants has been suggested to explain between-species differences in olfactory detection thresholds and increasing evidence supports this hypothesis (Hernandez Salazar et al. 2003, Laska et al. 2005d, Kjeldmand et al. 2011, Løtvedt et al. 2012, Eliasson et al. 2015, Laska & Hernandez Salazar 2015). A species should be expected to be particularly sensitive to a certain odorant not only if it is present in its chemical environment, but also if it is relevant for its behavioral repertoire. For example, rats are markedly more sensitive to the odorant 2,4,5-trimethylthiazoline (TMT), found in the anal gland secretions of the red fox, than spider monkeys or pigtail macaques (Laska et al. 2005c). As red foxes are known to predate rats, but not spider monkeys and pigtail macaques, it is, therefore, intuitive that rats are more adapted to detect this odorant at lower concentrations than the primate species.

5.5 Behavioral significance

As mentioned above, olfactory sensitivity seems to be better explained by the behavioral relevance of the odorants than by anatomical and genetic features, not only in a between-species comparison but also in a within-species comparison. Mold-associated odorants comprise a group of volatile substances produced by numerous strains of fungi (Kaminski et al. 1974, Grove 1981). Fungal species are known to decrease nutritional content of the food material they develop in as well as to pose health hazards by means of mycotoxins and spores (Börjesson et al. 1992). Moreover, some substances (e.g. 1-octen-3-ol) are reported to be harmful at the tissue level in humans (Kreja & Seidel 2002), rendering food-spoiling fungi potentially more hazardous than food-spoiling bacteria (Janzen 1977). Therefore,

mold-associated odorants may work as cues of fruit edibility for the animals that depend on them, such as spider monkeys.

Spider monkeys have a well-developed olfactory sensitivity for mold-associated odorants, though not as high as for predator- and putrefaction-associated odorants. Two explanations can be brought up regarding this difference. Although the consumption of fungi-infested food may pose a risk of intoxication, such risk may not be as high as the risk of being caught by a predator. Thus, the ability to detect the presence of a predator may bring higher fitness benefits to the individual compared to the consumption of fungi-infested food, as encounters with a predator can injure an individual or even kill it.

Putrefaction-associated odorants are composed of a set of indols and thiols, substances that indicate microbial degradation of food but are also found in primate body odors (Laska et al. 2007a). Two hypotheses can be formulated in this context: (a) microbial food degradation may pose a bigger risk to spider monkeys than fungal degradation, because it may be more abundant or because more harmful substances are produced, though the latter may not be so likely as food-spoiling fungi are reported to be potentially more hazardous than food-spoiling bacteria (Janzen 1977); and (b) the social information conveyed in body odors may be of higher relevance, as many species of primates, being social animals, provide a considerable amount of information (e.g. health status, age, gender, genetic relatedness) by means of body-borne odors (Epple et al. 1989, Kappeler 1998, Laska et al. 2004).

For many years it was implied that vision would be the predominant sense involved in the food selection process, as primates are traditionally viewed as “visual” animals (Fobes & King 1982). However, several studies documented that primates rely on other sensory information as well in the food selection context. For example, it has been reported that primates often smell, manipulate and lick food items in their natural habitat before consuming them (Kappeler 1984, van Roosmalen 1985, Kinzey & Norconk 1990, Laska 2001). Even in captivity, studies with spider monkeys indicate that they rely on their senses of smell and touch to assess the quality of novel food and in the following inspections individuals tend to use their vision for familiar food items (Laska et al. 2007b), though familiar food items may be still inspected by means of olfaction to check the quality of the fruit if other external cues, like color, do not clearly indicate so (Dominy et al. 2001). This interplay of the senses in foraging and food

selection indicates that there is valuable olfactory information that can be gathered from food prior to its consumption.

The olfactory sensitivity of the spider monkeys to mold-associated odorants may be high enough to detect fungi-spoiled food when it is already contaminated with mycotoxins or even slightly before this stage, as there is a reported positive correlation between mycotoxin and volatile metabolites production (Pasanen et al. 1996). Furthermore, research indicates that the knowledge about the edibility of potential food needs to be learned (Hughes 1990) and thus relying on various sensory information throughout that learning process is adaptive.

Future research should put extra effort in assessing the sensitivity to other mold-associated odorants referred in the literature, such as geosmin, a substance reported to have a mushy, earthy odor (Mattheis & Roberts 1992). Furthermore, other species of non-human primates and other non-primate mammals should be tested to shed light on the impact that the chemical environment has on the species' olfactory capabilities.

5.6 Societal and ethical considerations

The experiments reported here comply with the *Guides and Guide for the Care and Use of Laboratory Animals* (The National Academies Press, Washington DC, 2011) as well as with current Swedish and Mexican laws. They were performed according to a protocol approved by the ethical board of the Federal Government of Mexico's Secretariat of Environment and Natural Resources (SEMARNAT; Official permits number 09/GS-2132/05/10). The participating animals were in no way forced or coerced, but participated voluntarily in the experiments, and no food-deprivation in order to enforce cooperation in the experiments was imposed. Furthermore, there was no indication that the experiments posed any stress or discomfort to the animals.

This study is part of a more extensive research on the olfactory capacity of non-human primates, using different odorant classes. Studies of this nature provide an increase in the knowledge regarding the use of the sense of smell in both spider monkeys and other mammals, on the relationship between olfactory sensitivity and environmental factors and even on the phylogeny of the primate order.

Information on this topic also brings benefits for animal conservation. Spider monkeys are listed in the IUCN Red List as “Endangered” (Cuarón et al. 2008) and therefore knowing more about the way this species makes use of the sensory information available may help in improving the

conservation actions done. This knowledge can also be brought to the public by means of the social media and the facilities dedicated to the conservation of species (e.g. zoos, wildlife sanctuaries) and the welfare of these species held in said facilities can be improved, for example, by the use of odors as environmental enrichment, as already used in other species.

5.7 Conclusions

The results of the present study show that spider monkeys have a well-developed olfactory sensitivity towards mold-associated odorants. Further support to the notion of a positive correlation between backbone carbon chain length and detectability was found. There is indication of a possible correlation between olfactory sensitivity and branching of the carbon chain. However, no further support was found for a correlation between olfactory sensitivity and structural features such as the absence or presence of a double bond. There were disparate findings on the effect of the type and position of the functional group on olfactory sensitivity of spider monkeys. The sensitivity towards mold-associated odorants overlaps with that of other odorant classes studied previously in spider monkeys. Finally, spider monkeys have a lower olfactory sensitivity to mold-associated odorants compared to humans with five out of eight odorants tested. Nevertheless, further research with a higher number of individuals is needed to corroborate the findings in this study. There is no indication that olfactory sensitivity is correlated with neuroanatomical and genetic features. Behavioral significance of the odorants seems to explain better the between- and within-species difference in sensitivity.

6 Acknowledgements

I would like to thank Matthias Laska for the opportunity given to me and the helpful guidance through the study and Laura Hernandez Salazar for all the help while conducting the tests at Papiapan. My special thanks to Gil, Marco and Jorge, Papiapan's caretakers and friends, for guiding me in this adventure through the Mexican jungle filled with memorable, funny but also stressful moments. Also, my deepest thanks to my friend Cecilia, for supporting me and for cheering all my days.

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