Department of Physics, Chemistry and Biology

Master Thesis

Olfactory sensitivity of spider monkeys (*Ateles geoffroyi*) for six structurally related aromatic aldehydes

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Contents

1 Abstract
For many years, primates have been considered to be animals with a poorly developed sense of smell. However, in recent years several studies have shown that at least some primate species have a high olfactory sensitivity for a variety of odorants. The present study used a two-choice instrumental conditioning paradigm to test the olfactory sensitivity for six aromatic aldehydes in four spider monkeys (*Ateles geoffroyi*). With helional, cyclamal, canthoxal and lilial all animals discriminated concentrations below 1 ppm from the odorless solvent, with single individuals even scoring better. With 3-phenyl-propionic aldehyde all animals detected concentrations below 2 ppb, and with bourgeonal even below 0.3 ppb. The detection thresholds of the odorants changed systematically with molecular structure. Addition of a dioxo or methoxy group to the benzene ring led to an increase in threshold values, while the absence of a methyl group close to the aldehyde moiety was linked to a low threshold value for the odorant. The study shows that spider monkeys have a well developed olfactory sensitivity for aromatic aldehydes.

Keywords
Aromatic aldehydes, olfactory detection thresholds, spider monkeys

2 Introduction

Primates are traditionally viewed as animals with a poorly developed sense of smell compared to animals like the mouse, rat and dog. This opinion is mainly based on an interpretation of anatomical features (Insausti et al, 2002) as only a comparatively small proportion of the primate brain is dedicated to this sense and on a comparison of the number of functional olfactory receptor genes which is thought to be reduced in primates. Instead, most primates are often considered visual animals (Fobes and King, 1982), especially diurnal species such as, for example, the spider monkey (Baron et al, 1983). However, in recent years several studies have shown that primates have a well developed sensitivity for several classes of odorants (Laska et al, 2004; Laska et al, 2005; Joshi et al, 2006; Laska et al, 2006; Persson, 2008).

Olfactory receptors can be found not only in the nasal epithelium but in several tissues of the body, such as the heart, liver, muscles, testes (Zhang et al, 2006; Feldmesser et al, 2006; Gaillard et al. 2004) and mature sperm cells of several species (Vanderhaeghen et al, 1993). The presence of olfactory receptors in mature sperm cells raises the question of their purpose, and it has been demonstrated that they cause chemotaxis upon binding to an odorant (Spehr et al, 2004). It has been suggested that this is used as a means to navigate towards the egg for fertilization. This idea is supported by the discovery that different species express their own repertoire of olfactory receptors (Vanderhaeghen et al, 1997). Lately, a few studies have investigated the identity of the receptors expressed by the sperm and their specific ligands (Spehr et al, 2003; Fukuda et al, 2004; Jacquier et al, 2006). In humans, a receptor which may be involved in the sperm’s chemotaxis has been identified. It is coded by the gene named hOR17-4, and binds to molecules consisting of an aldehyde group attached to an aromatic ring by a short carbon chain (Jacquier et al 2006). This is the description of bourgeonal and other aromatic aldehydes with similar structures, such as helional, canthoxal and lilial (Bartram and Boland, 2003; Spehr et al, 2003).

In the present study, bourgeonal and five other aromatic aldehydes were used to test spider monkeys’ sensitivity to change in molecular structures. The odorants are structurally related, with an aldehyde group, an aromatic ring and short carbon chain connecting the two (Jacquier et al, 2006). Most of the odorants also contain additional functional groups, either on the

carbon chain or attached to the aromatic ring. Such small changes in structure can cause marked changes in detectability.
The aim of this study was therefore to determine olfactory detection threshold values of spider monkeys for six aromatic aldehydes, and to assess the impact of small changes in the molecular structure of the odorant on detectability.

3 Materials and Methods

3.1 Animals

Four adult female black-handed spider monkeys (*Ateles geoffroyi*) were used in this study (Figure 1). The study was conducted at the research station Pipiapan run by the Universidad Veracruzana outside of Catemaco, Veracruz in Mexico. Three of the monkeys were kept in an enclosure together while the fourth monkey was kept in another enclosure together with one adult male and one juvenile male, and a baby which was still carried by the female. The enclosures were situated next to each other providing the possibility of visual and auditory contact between the two groups. Adjacent to the enclosures were simple houses with small test cages attached to the side of the enclosure. The houses provided the animals and students with shelter from the elements during testing. The test cages could be closed by sliding doors allowing temporary separation of animals for individual testing. The animals were already trained to enter the test cages voluntarily when their names were called and they were free to leave when they were not being tested. All animals had participated in similar olfactory tests before and were familiar with the experimental procedure. All monkeys were fed ripe fruit and vegetables once every day.

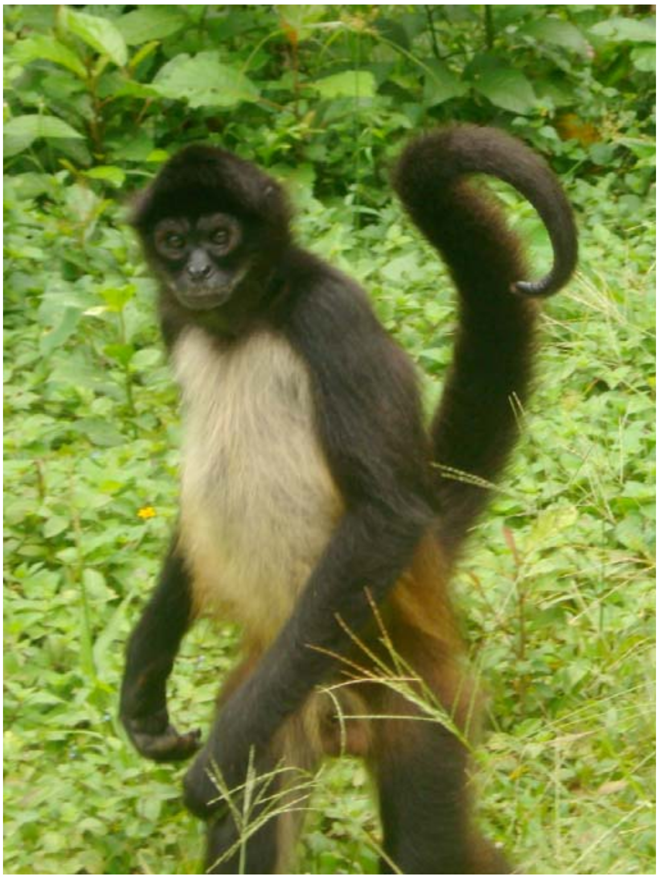

Figure 1 Ateles geoffroyi

3.2 Experimental set-up

Testing was carried out using a two-choice instrumental conditioning paradigm (Laska et al., 2003). The test apparatus consisted of a 50 cm long and 6 cm wide metal bar with two cube-shaped PVC boxes attached to it at a distance of 22 cm from each other. Each box had a lid on the upper side that also hung 2 cm down in front of the box. In the centre of the front part of the lid a 3 cm pin was extended. The pin served as a lever that the monkeys used to open the box. On top of each lid there was a metal clip attached. This clip held a 70 × 10 mm absorbent paper strip which was impregnated with 20µl of the odorant or the control substance. The paper strips extended approximately 3cm in to the cage when the apparatus was presented to the animals (Figure 2).

Figure 2. The apparatus used in the present study.

The box with the odorized paper strip attached to the lid contained a food reward (a Kellogg's Fruit Loop or Honey Loop) while the one with the odorless paper strip did not. When presented with the test apparatus the monkeys sniffed both paper strips (as much as they liked) and then decided to open one of the boxes. After the decision the apparatus was removed and prepared for the next presentation out of sight from the monkeys. If a monkey tried to open a box without sniffing, the apparatus was immediately removed from the test cage and reintroduced after a short time-out until the monkey sniffed both options. Presentations of the rewarded stimulus on the left or on the right side followed a pseudo randomized order. Every day three sessions of ten trials each were conducted with each monkey.

To determine detection thresholds for the odorants, the monkeys were presented with 10-fold increasing dilutions of the rewarded stimulus (S+) until they failed to discriminate it from the unrewarded stimulus (S-).

For each concentration three sessions of ten trials were conducted, corresponding to a total of 30 trials. Testing started at a dilution of 1:10 or 1:100 depending on the intensity of the pure odorant. If an animal failed to discriminate between a given concentration and the blank stimulus above chance level, that is: at least 21 out of 30 trials, it was given a second chance. The monkey was again presented with the dilution that it first failed to distinguish above chance level for another three sessions of ten trials. When an animal failed for the second time it was presented with an intermediate dilution that lay halfway between the lowest concentration that was detected and the first concentration that was not, to determine a more exact threshold value. If the monkey, for example, mastered the 1:100,000 dilution but failed the 1:1 million dilution it was presented with a dilution of 1:300,000.Whenever an animal failed to discriminate above chance level it was presented with an easily detectable dilution for three sessions of ten trials to increase its motivation before the second chance was initiated.

3.3 Odorants

A set of 6 structurally related floral odorants belonging to the chemical class of aromatic aldehydes was used: bourgeonal, helional, 3-phenyl-propionic aldehyde (3-PPA), canthoxal, cyclamal and lilial (Figure 3). The odorants share molecular structural features such as a saturated benzene ring and a functional aldehyde group, but differ in the presence or absence of additional methyl or oxygen-containing functional groups.
In recent years, bourgeonal has been identified as a ligand for the human olfactory receptor, hOR17-4, which is expressed in human sperm, causing chemotaxis of sperm cells towards the bourgeonal source. The same receptor is also present in the human olfactory epithelium (Rouquier and Giorgi, 2007), and it would therefore be interesting to investigate how sensitive a primate species is to this odorant, and other similar aromatic aldehydes.

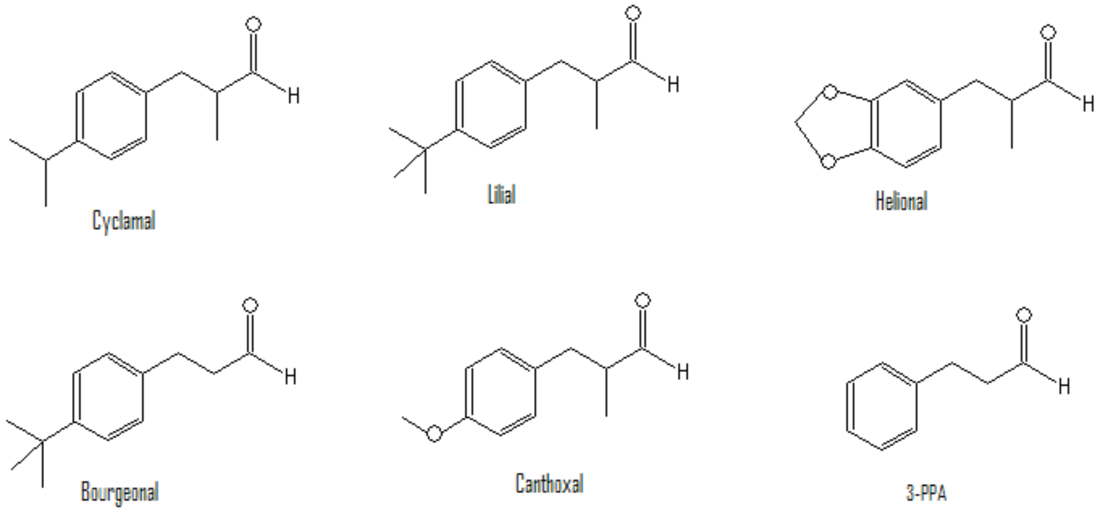

Figure 3 Molecular structure of the six stimuli used in this study.

The substances were diluted using odorless diethyl phthalate, which was also used as the unrewarded stimulus (S-).

3.4 Statistical analysis

For every dilution step the percentage of correct choices was calculated for each monkey. Significance levels were then determined by calculating binomial z-scores corrected for continuity (Siegel & Castellan 1988). The p-value was set at 0.05 and all tests were two-tailed.

4 Results

4.1 Discrimination performance

Figure 4 shows the animals' ability to detect bourgeonal at different dilutions. Two of the animals (Soky and Kelly) reached threshold values of 1:100,000 and one animal (Piolina) a value of 1:300,000. The lowest dilution of bourgeonal was detected by Nanny who reached a threshold of 1:1 million.

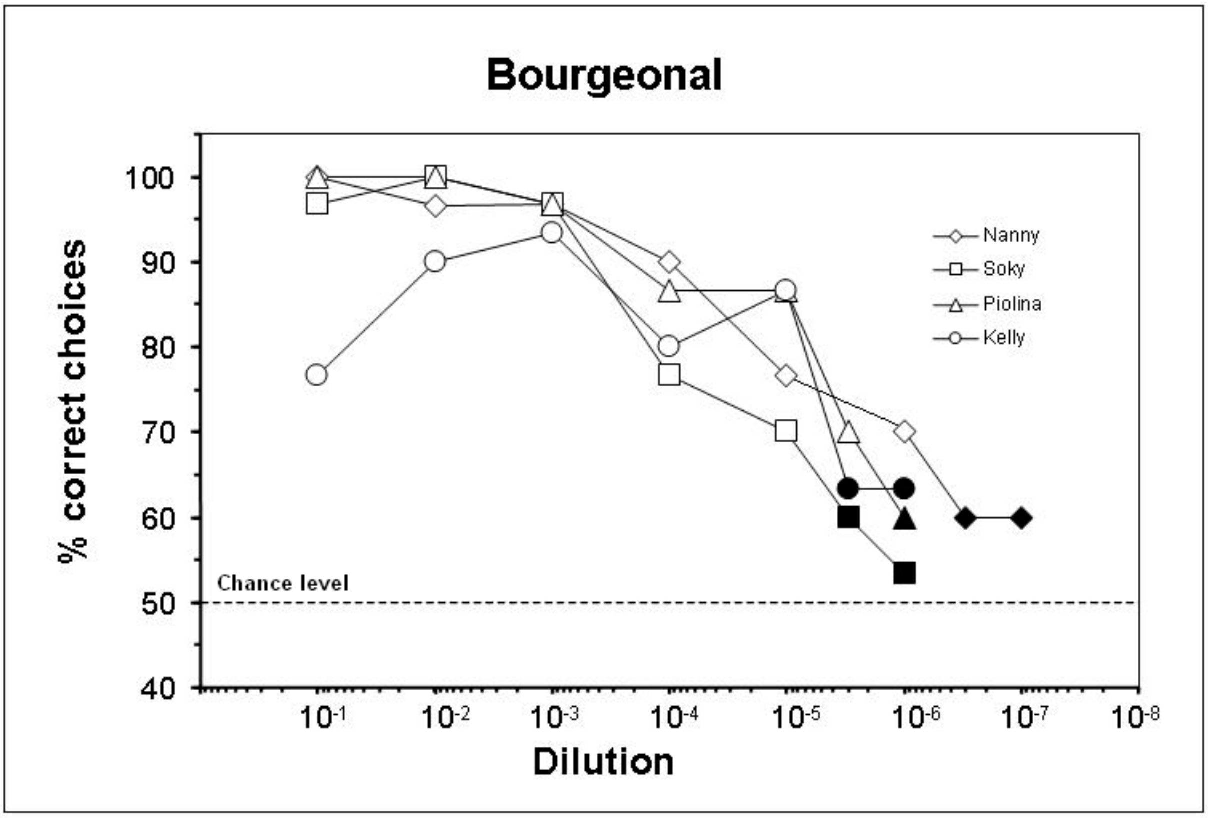

Figure 4. Performance of the spider monkeys in detecting various dilutions of bourgeonal. Each data point represents the percentage of correct choices out of 30 trials. Filled symbols indicate dilutions that the spider monkeys did not discriminate significantly above chance level (binomial test, $p > 0.05$).

Figure 5 shows the animal's ability to detect helional at different dilutions. One animal (Piolina) reached a threshold of 1:100, while two of the animals (Nanny and Soky) reached 1:300. One animal (Kelly) reached a much lower threshold at a dilution of 1:10,000

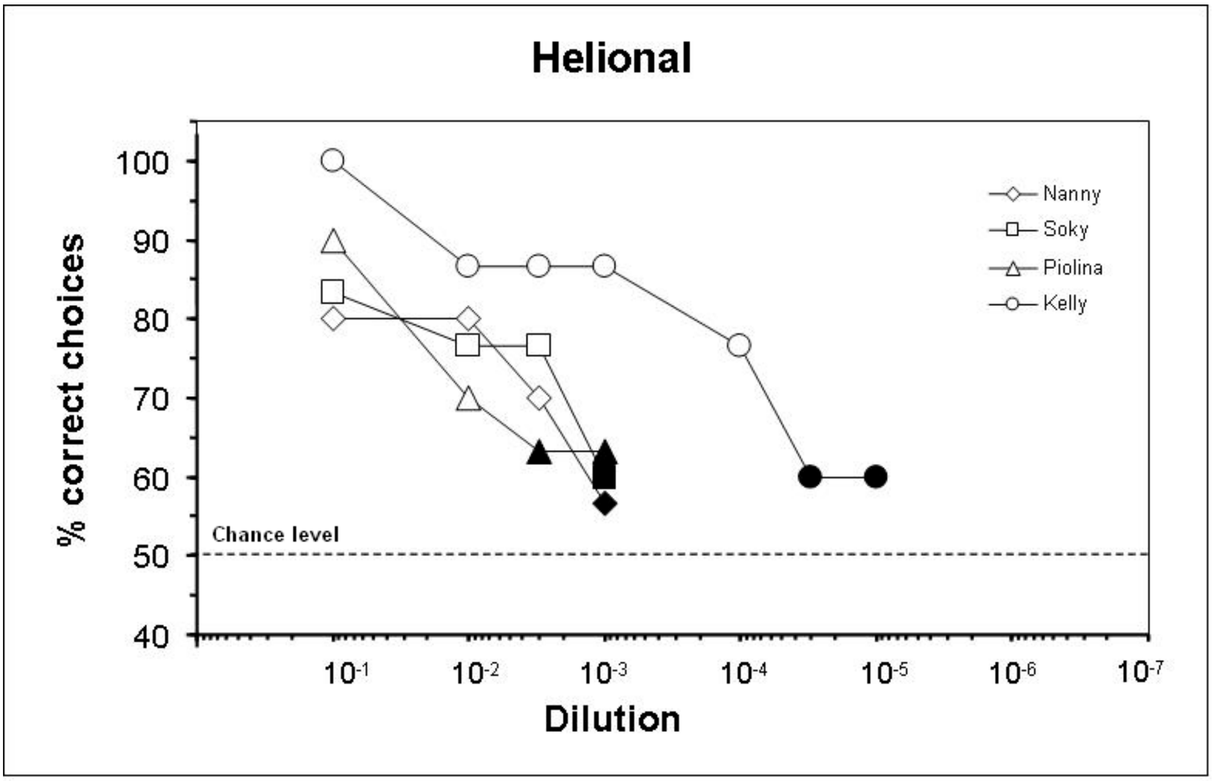

Figure 5. Performance of the spider monkeys in detecting various dilutions of helional. Each data point represents the percentage of correct choices out of 30 trials. Filled symbols indicate dilutions that the animals did not discriminate significantly above chance level (binomial test, $p > 0.05$).

Figure 6 shows the animals' ability to detect 3-PPA at different dilutions. Three of the animals (Soky, Piolina and Kelly) reached a threshold of 1:300,000, while one animal (Nanny) reached 1:1,000,000.

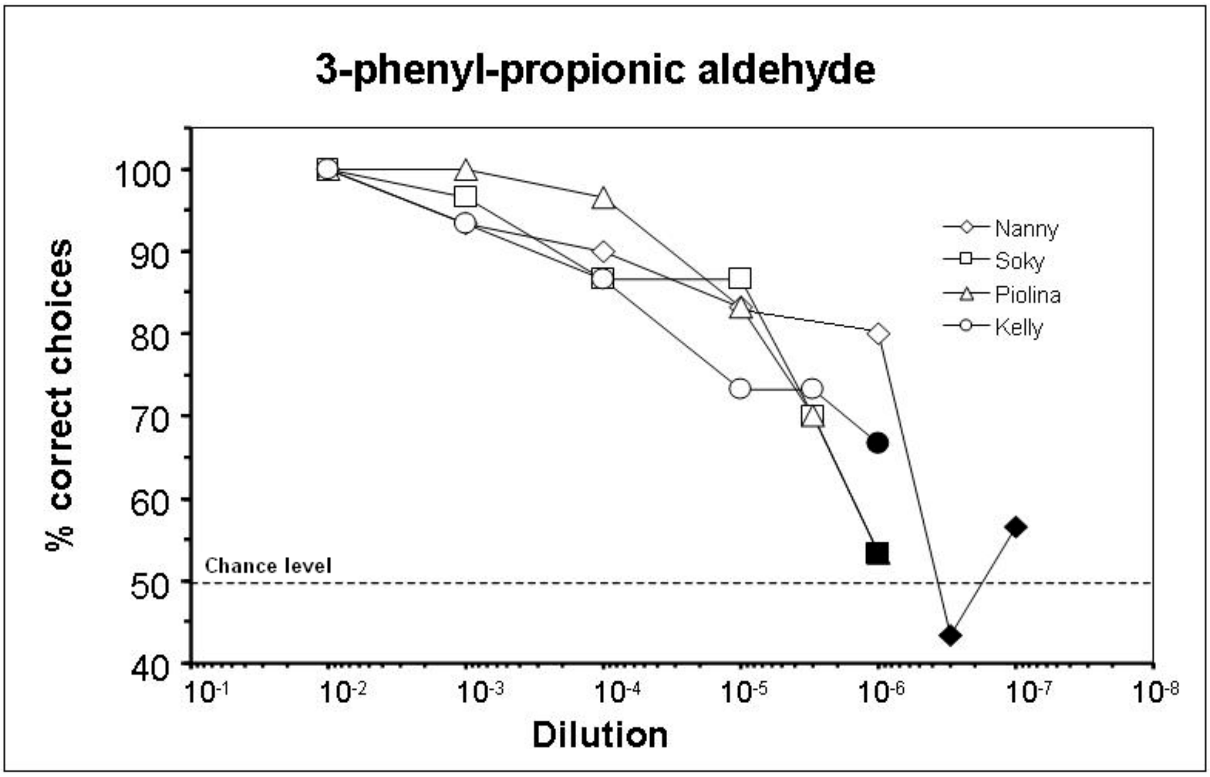

Figure 6. Performance of the four spider monkeys in detecting various dilutions of 3-phenyl-propionic aldehyde. Each data point represents the percentage of correct choices out of 30 trials. Filled symbols indicate dilutions that the spider monkeys did not discriminate significantly above chance level (binomial test, $p > 0.05$).

Figure 7 shows the animals' ability to detect cyclamal at different dilutions. Three of the animals (Nanny, Soky and Kelly) reached thresholds of 1:1,000 while one of the animals (Piolina) reached 1:3,000 before failing.

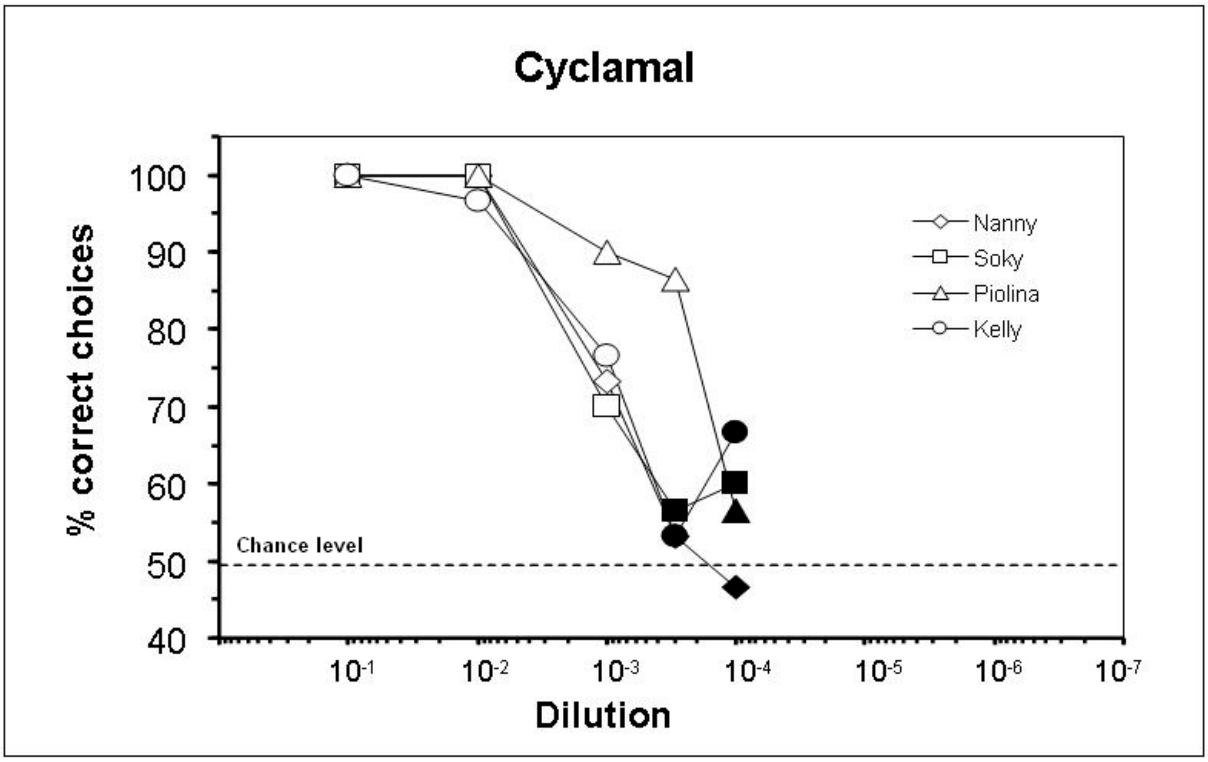

Figure 7. Performance of the four spider monkeys in detecting various dilutions of cyclamal. Each data point represents the percentage of correct choices out of 30 trials. Filled symbols indicate dilutions that the animals dud not discriminate significantly above chance level (binomial test, p > 0.05).

Figure 8 shows the animals' ability to detect canthoxal at different dilutions. Two of the animals (Nanny and Piolina) reached threshold values of 1:300, while the two remaining animals (Soky and Kelly) reached 1:1,000 before failing.

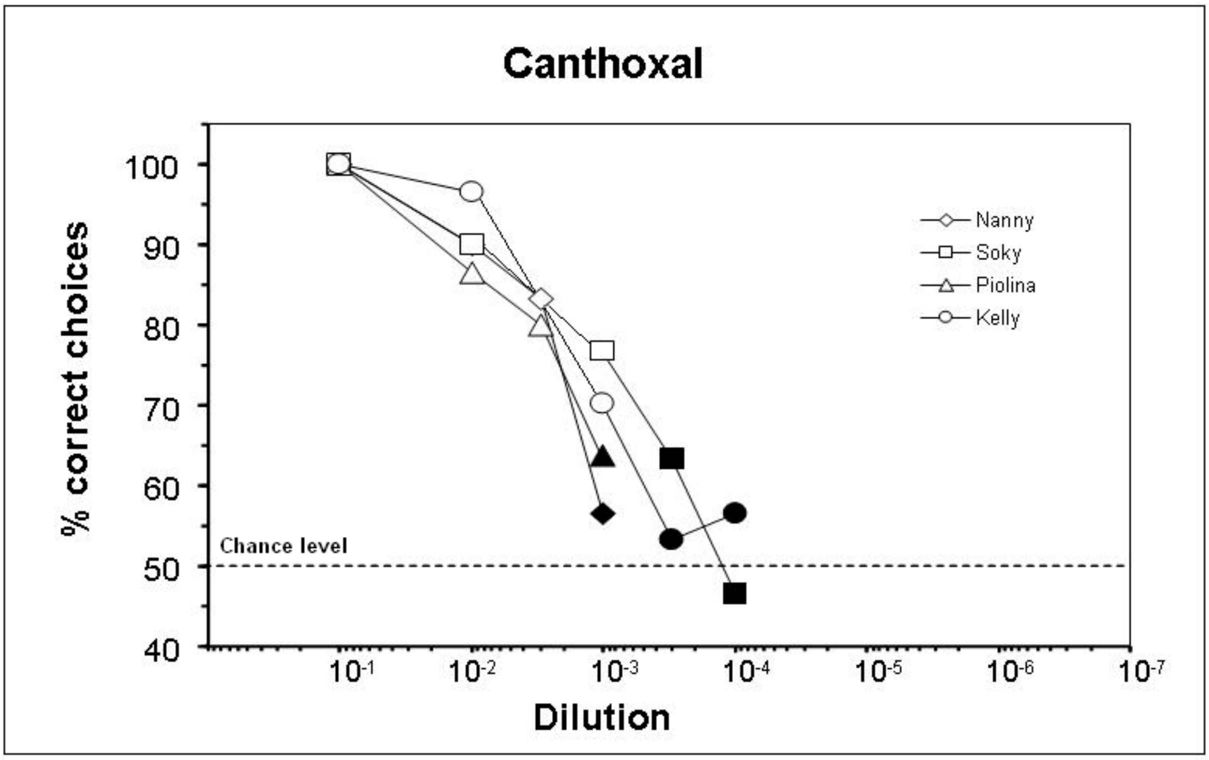

Figure 8. Performance of the spider monkeys in detecting various dilutions of canthoxal. Each data point represents the percentage of correct choices out of 30 trials. Filled symbols indicate dilutions that were not discriminated significantly above chance level (binomial test, $p > 0.05$).

Figure 9 shows the animals' ability to detect lilial at different dilutions. One animal (Nanny) reached 1:1,000 while one (Piolina) reached 1:3,000. The two remaining animals (Soky and Kelly) reached a threshold of 1:10,000.

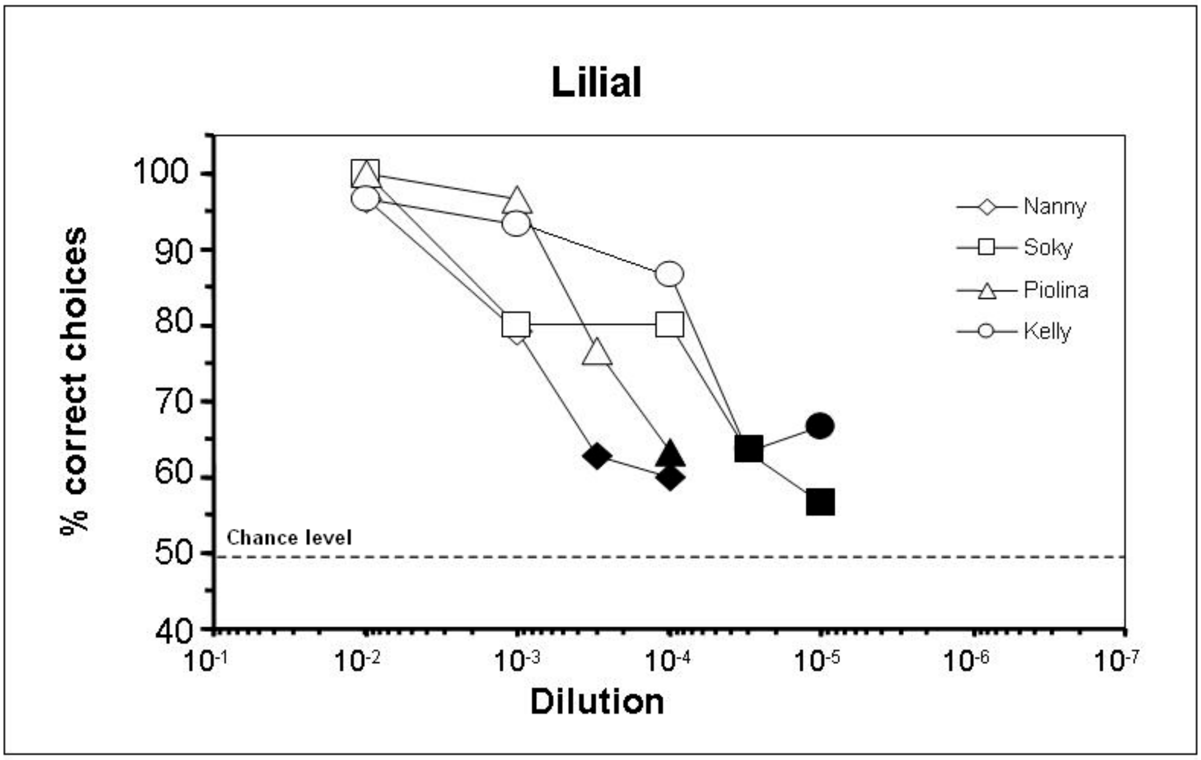

Figure 9. Performance of the spider monkeys in detecting various dilutions of lilial. Each data point represents the percentage of correct choices out of 30 trials. Filled symbols indicate dilutions that the four spider monkeys dud not discriminate significantly above chance level (binomial test, $p > 0.05$).

4.2 Inter- and intraindividual variability

With three of the six odorants tested, cyclamal, 3-PPA and canthoxal, the range between the best and the worst performing animal was only a factor of 3. With bourgeonal and lilial, the difference was larger with a factor of 10, and for helional, the odorant with the largest difference in thresholds, the animals differed by a factor of 100.

A comparison among the animals showed that Kelly was among the best with three of the six substances tested, helional, canthoxal and lilial. Soky shared the lowest thresholds with Kelly on canthoxal and lilial. Nanny had the best results with two of the six stimuli, bourgeonal and 3-PPA. Piolina only outperformed the other animals with one of the six odorants, cyclamal.

Table 1 summarizes the results of the animals for the six substances tested in this study in a range of measures. Conversion from liquid to vapor phase concentrations is necessary to make proper comparisons between substances since they differ in vapor pressures. Bourgeonal yielded the lowest thresholds among the aromatic aldehydes, with 3-PPA as a close second. Helional and canthoxal yielded the highest thresholds, several orders of magnitude above bourgeonal.

Table 1 Olfactory detection thresholds of the four spider monkeys for the six aromatic aldehydes, expressed in different gas phase concentrations.

		Liquid	Gas phase concentration				
substance	N	dilution	molec/cm^3 air	M	logM	ppm	log ppm
Bourgeonal	2	1:100,000	6.6×10^{9}	1.0×10^{-11}	-10.960	0.00024	-3.61
	1	1:300,000	2.2×10^{9}	3.7×10^{-12}	-11.437	0.000081	-4.09
	1	1:1,000,000	6.6×10^{8}	1.1×10^{-12}	-11.960	0.000024	-4.61
Helional	1	100	1.6×10^{13}	2.7×10^{-8}	-7.576	0.593	-0.23
	2	300	5.5×10^{12}	9.1×10^{-9}	-8.039	0.204	-0.69
	1	1:10,000	1.6×10^{11}	2.6×10^{-10}	-9.576	0.006	-2.23
3-PPA	3	1:300,000	4.7×10^{10}	7.6×10^{-11}	-10.117	0.002	-2.77
	1	1:1,000,000	1.4×10^{10}	2.3×10^{-11}	-10.634	0.001	-3.28
Cyclamal	3	1:1000	2.6×10^{12}	4.3×10^{-9}	-8.365	0.096	-1.02
	1	1:3000	8.7×10^{11}	1.5×10^{-9}	-8.835	0.033	-1.49
Canthoxal	2	1:300	1.2×10^{13}	2.0×10^{-8}	-7.701	0.444	-0.35
	2	1:1000	3.6×10^{12}	6.0×10^{-9}	-8.224	0.133	-0.88
Lilial	1	1:1000	2.0×10^{12}	3.3×10^{-9}	-8.479	0.074	-1.13
	1	1:3000	6.7×10^{11}	1.1×10^{-9}	-8.960	0.024	-1.61
	2	1:10,000	2.0×10^{11}	3.3×10^{-10}	-9.479	0.007	-2.13

N indicates the number of individuals who reached a given threshold

5 Discussion

5.1 Comparison among odorants

The present study shows that the ability of spider monkeys (*Ateles geoffroyi*)
to detect aromatic aldehydes varies considerably between stimuli. This illustrates that even small changes in the molecular structure of members of this chemical class may lead to marked changes in detectability. The two odorants helional and canthoxal yielded the highest threshold values among the six tested. Bourgeonal and 3-PPA yielded the lowest threshold values, with lilial and cyclamal falling in between (see table 1). The only explanation for this is the small differences in molecular structure of the different stimuli (Figure 3).
Helional and canthoxal were the two odorants for which the animals performed clearly poorer compared to the other stimuli. Here the molecules/cm^3 needed for detection was between 1.6×10^{13} and 1.6×10^{11} for helional and 1.2×10^{13} to 3.6×10^{12} for canthoxal. This may be due to a specific molecular feature of these two aromatic aldehydes, as they are the only molecules, among the ones tested, with additional oxygen atoms in their structure. Helional has a dioxo group, and canthoxal has a methoxy group attached to the benzene ring (Figure 10).

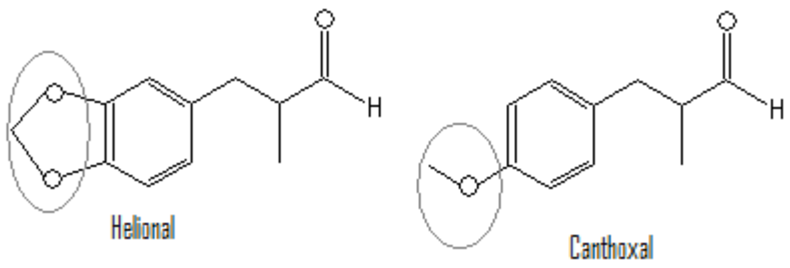

Figure 10 Molecular structure of helional and canthoxal, showing the oxygen atoms attached to the benzene ring, which is the likely cause of the high threshold values.

The two stimuli for which the animals had the lowest threshold values were bourgeonal and 3-PPA. They differ in their molecular structures from the other four odorants tested here in the absence of an extra methyl group next to the aldehyde group (Figure 11). This could possibly explain the threshold values between 10^8 and10^{10} molecules/cm^3 which are low values for spider monkeys (see next section). In addition to the absence of a methyl group, bourgeonal has a tertiary butyl group attached to the ring, a feature that it shares with lilial. Lilial, however, has the methyl group that bourgeonal lacks, and threshold values between 2.0×10^{12} and 2.0×10^{11} molecules/cm^3, which are considerably higher than those for bourgeonal, which suggests that the presence of a tertiary butyl group alone is not predictive of a low detection threshold. The structures of lilial and cyclamal are very similar and differ only from each other in the presence of a tertiary butyl group and an isopropyl group, respectively (Figure 12). The two stimuli were found to have almost identical threshold values. The threshold for cyclamal was 8.7×10^{11} to 2.6×10^{12} molecules/cm^3, compared to lilal's 2.0×10^{11} to 2.0×10^{12} molecules/cm^3. The values are higher than those for bourgeonal and 3-PPA, but lower than the thresholds for helional and canthoxal.

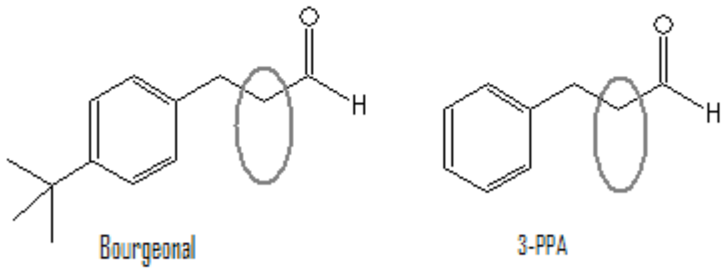

Figure 11 Molecular structures of bourgeonal and 3-PPA, the two stimuli with the lowest threshold values. Grey circles show were the other odorants have an extra methyl group next to the aldehyde group.

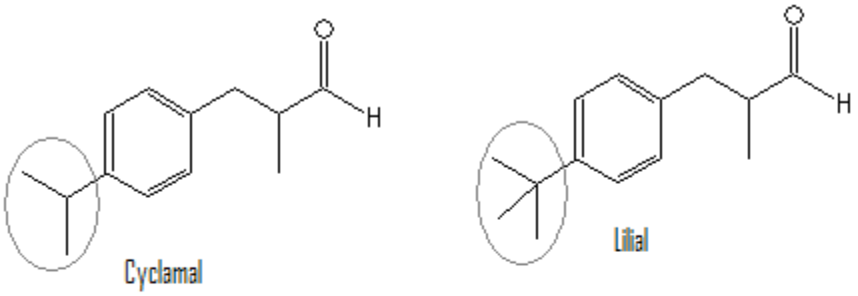

Figure 12 Molecular structure of cyclamal with an isopropyl group and lilial with the tertiary butyl group.

3-PPA is the only odorant of the six tested without a functional group attached to the ring opposite the aldehyde group, or a methyl group attached to the carbon chain. And as previously mentioned, 3-PPA was found to have a relatively low threshold value among the aromatic aldehydes at between 1.7×10^{10} and 4.7×10^{10} molecules/cm^3. This indicates that among the aromatic aldehydes additional functional groups are not required for the spider monkeys to be able to detect them.

Among the aromatic aldehydes the presence of an oxygen-containing methoxy or dioxo group in the structure appears to lead to an increase in threshold compared to the other odorants lacking such a functional group. The absence of a methyl group attached to the carbon chain next to the aldehyde group appears to be linked to a low threshold value. When comparing threshold levels of the odorants with tertiary butyl groups or isopropyl groups it appears that these structural features have a lesser impact on detection threshold for the spider monkeys.

The presence of a methyl group in the structure of an odorant has been found to have an effect on threshold values in previous studies performed in other non human primate species. When comparing the thresholds for indol and 3-methyl indol both squirrel monkeys (*Saimiri sciureus*) and pigtail macaques (*Macaca nemestrina*) had considerably lower threshold values for indol compared to 3-methyl indol which contains a methyl group, the same pattern as found in the present study. The squirrel monkeys' thresholds were 8.2×10^5 molecules/cm^3 and 3.0×10^8 molecules/cm^3 for indol and 3-methyl indol, respectively. The same pattern was found in pigtail macaques whose threshold values were $8.2\ \times10^5$ molecules/cm^3 for indol and 1.0×10^9 molecules/cm^3 for 3-methyl indol (Laska et al, 2007). For pyrazines, the threshold value for spider monkeys decreased systematically with added methyl groups. Pyrazine, lacking any methyl groups, has a threshold value of 7.5×10^{14} molecules/cm^3, while 2-methylpyrazine, a pyrazine ring with one single added methyl group had a threshold value up to a 100 fold lower than that of pyrazine. 2,5-dimethylpyrazine, a pyrazine ring with two added methyl groups, had a threshold of 1.8×10^9 molecules/cm^3. With a slight shift in position of the methyl groups, 2,6-dimethylpyrazine had a slightly higher threshold value than the former odorant at 5.9×10^{10} molecules /cm^3. However, the threshold did not decrease by adding even more methyl groups as 2,3,5,6-tetramethylpyrazine has a threshold value at about the same level as 2,6-dimethylpyrazine (Persson, 2008).

5.2 Comparison with other odorants tested with spider monkeys

Spider monkeys do not seem to be particularly sensitive to aromatic aldehydes compared to other chemical classes, although bourgeonal and 3-PPA are among the lower threshold values found (Figure 13). In a study performed by Laska et al (2006), threshold values for aliphatic alcohols and aliphatic aldehydes were determined in spider monkeys. The five animals tested had threshold values between 1.4×10^{13} and 1.4×10^{14} molecules/cm^3 for 1-propanol while they reached much lower threshold values for 1-heptanol at between 8.5×10^{10} and 8.5×10^{9} molecules/cm^3. With the aliphatic aldehydes they reached similar threshold values spanning between 4.0×10^{10} and 1.1×10^{13} molecules/cm^3. Compared to the threshold values obtained for aliphatic alcohols and aliphatic aldehydes, the threshold values for aromatic aldehydes are in the same general range.

In a similar study in which the olfactory sensitivity for structurally related pyrazines in spider monkeys was investigated, threshold values once again varied considerably between the different stimuli (Persson, 2008). Pyrazine had a comparatively high threshold value at 7.5×10^{14} molecules/cm^3 while 2,5-dimethylpyrazine had a threshold value of 1.8×10^{9}, which is as low as the lower threshold values reached among the aromatic aldehydes. The lowest thresholds among the aromatic aldehydes are the ones for bourgeonal ranging between 6.6×10^{9} and 6.6×10^{8}, and for 3-PPA at between 4.7×10^{10} and 1.4×10^{10} molecules /cm^3.

Studies have also been carried out using aliphatic esters, a chemical class that comprises important components in fruit odors. The olfactory detection thresholds of the spider monkeys for these stimuli, just as for the other odorants discussed here, varied considerably. With five of the ten stimuli the spider monkeys reached threshold values between 9.8×10^{9} and 7.3×10^{8} molecules/cm^3 which among other odorants tested are quite low values. However, with n-propyl acetate and iso-butyl acetate the animals had thresholds as high as 1.2×10^{13} and 2.3×10^{13}, respectively (Hernandez Salazar et al, 2003).

The Spider monkeys' sensitivity to carboxylic acids was examined by Laska et al (2004). They found that the animals had a well developed sensitivity to the odorants, with all animals reaching 9.7×10^{11} molecules/cm^3 for *n*-propionic acid, the substance with the highest threshold. For *n*-hexanoic acid all animals discriminated as low as 9.0×10^{9} molecules/cm^3 from the solvent, and for *n*-heptanoic acid, the odorant with the lowest threshold, individuals reached as low as 5.0×10^{8} molecules/cm^3. Among the carboxylic acids, the threshold values reached by the individual animals differed little from each other and compared to other odorant groups tested the threshold values were rather low.

Spider monkeys are not especially sensitive to aromatic aldehydes compared to other classes of odorants tested nor are they insensitive to them. They lie within the common range found in other studies performed until this day. Figure 13 shows the olfactory detection threshold values of spider monkeys for six different odorant groups, aromatic aldehydes, pyrazines, aliphatic alcohols, aliphatic aldehydes and acetic esters and carboxylic acids. One can see that the range of the spider monkeys' olfactory sensitivity with aromatic aldehydes is similar to that of the other classes of odorants tested.

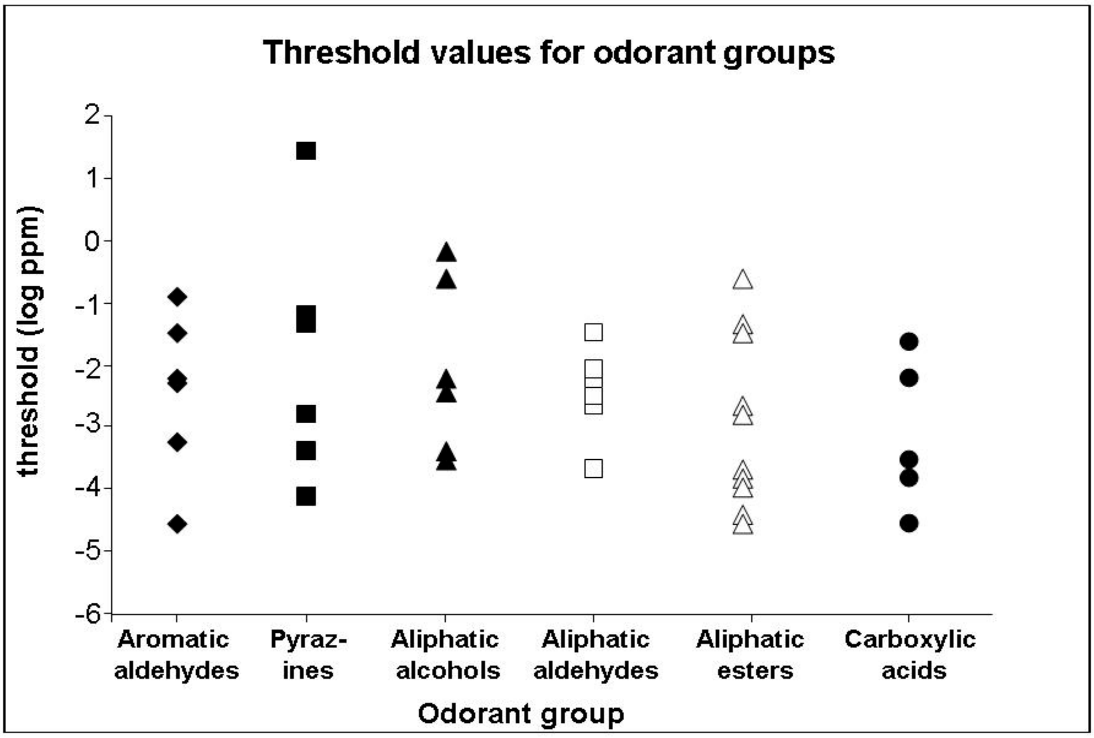

Figure 13 A comparison of olfactory detection threshold values (expressed as vapor phase concentrations) of spider monkeys for several classes of odorants, aromatic aldehydes, pyrazines, aliphatic alcohols (C3 to C8), aliphatic aldehydes (C4 to C9), aliphatic esters (C4 to C10) and carboxylic acids (C3 to C7), expressed in log ppm. Each symbol shows the lowest threshold value for each odorant in every group.

5.3 Comparison with other species

To the best of my knowledge, no studies so far determined olfactory detection threshold values for the aromatic aldehydes tested here in other animal species. However, a recent study determined olfactory detection thresholds for bourgeonal and helional in humans. In the study, 500 men and women were tested and the threshold values obtained were clearly higher than those found in the spider monkeys. For bourgeonal, men had a slightly lower threshold than women at 3.4×10^{11} molecules/cm^3 compared to 5.9×10^{11}, while the spider monkeys' threshold ranges between 6.6×10^{9} and 6.6×10^{8}. For helional, the men and women had threshold values of 1.4×10^{13} and 1.3×10^{13} molecules/cm^3, respectively. These threshold values are slightly lower than that of one of the four spider monkeys who had a threshold value of between 1.6×10^{13}. However, the three remaining spider monkeys scored lower threshold values than the humans, between 5.5×10^{12} molecules/cm^3 and1.6×10^{11} molecules/cm^3 (Olsson, 2009).

In a separate study, 20 human subjects were tested for their olfactory sensitivity to three additional aromatic aldehydes, canthoxal, cyclamal and 3-PPA. The pattern of detection thresholds was the same for humans as the one found for spider monkeys, with higher thresholds for canthoxal and cyclamal, and a lower threshold for 3-PPA. The human detection threshold for canthoxal was found to be 1.4×10^{13} molecules/cm^3, which is almost the same as the spider monkeys' threshold value. For cyclamal, humans discriminated the odorant from the blank stimulus at 1.0×10^{13} molecules/cm^3, which is slightly higher than spider monkeys. 3-PPA had the lowest threshold of the three at 4.5×10^{11} molecules/cm^3, about ten times higher than the threshold value of the spider monkeys for the same odorant (Laska, unpublished data).

There may be several reasons why the spider monkeys have a keener sense of smell than humans when detecting bourgeonal. One reason may be that, compared to humans, New World monkeys like spider monkeys have a higher number of functional olfactory receptor genes, about 900, than humans do with their ~390 genes. A high number of functional olfactory receptor genes leads to a larger receptor repertoire which, in turn, may lead to a higher sensitivity in detecting odorants (Rouquier and Giorgi, 2007). The difference in sensitivity for odorants could also be due to the relative size of the olfactory bulb, one part of the brain which processes olfactory information. In New World monkeys, the olfactory bulb varies greatly in relative size. In the spider monkey it makes up approximately 0.9% of the total brain volume (Baron et al, 1982), while it only comprises ~0.01% of the human brain (Fobes and King, 1982). The relative olfactory brain size is considered indicative of olfactory sensitivity by some authors (Fobes and King, 1982). However, humans do not always perform poorer than other mammals when detecting odors, despite the difference in relative brain structure size (Laska et al, 2005). There is also evidence that if a group of odorants has a behavioral importance to a species, the species will develop a higher sensitivity to this odorant, compared to odorants not present in their immediate surroundings, or important for their survival. This could be a group of odorants common in ripe fruit or odorants indicating toxins. It would then make sense that the species is highly sensitive to the odorants, increasing the chances of survival for the animal (Brown, 2001; Clutton-Brock and Harvey, 1980; Laska, 2006).

It is difficult to determine the cause of the difference in detection thresholds for helional and bourgeonal between species without investigating the subject further. Most likely it is a combination of all or several of the reasons listed above.

5.4 Odor structure-activity relationships

1-5% of the entire genome, ~1% in humans (Consortium, 2001), codes for one single gene family, olfactory receptors (Gaillard et al., 2004). This gene family was first described by Buck and Axel in 1991 (Buck and Axel, 1991), a discovery for which they were awarded the Nobel Prize in Physiology or Medicine 2004. Since then, the number of genes coding for olfactory receptors has been determined in different species. Animals often used in olfactory experiments such as dogs and mice have roughly 1300 genes and 1500 genes, respectively, of which approximately 20% are pseudogenes, leaving 1040 and 1200 functional genes, respectively (Ache and Young, 2008). Among primates, the number of genes is smaller and the number of pseudogenes higher. Old World monkeys have approximately 740 to 500 functional genes coding for olfactory receptors and among humans the number is only 350-390 (Rouquier and Giorgi, 2007; Ache and Young, 2008) .

Each olfactory receptor gene codes for one type of receptor but each receptor can bind to several different volatile molecules and a molecule may be bound by several different receptors, resulting in a spatiotemporal pattern of coding of odors. This is what enables animals such as humans and other Old World primates with only a few hundred functional olfactory receptors to distinguish between thousands upon thousands of odors (Buck, 2004).

Many studies have found that even small changes in molecular structure can significantly change the perception of both odor quality and intensity (Buck and Axel, 1991; Araneda et al, 2000; Dryer, 2000; Johnson and Leon, 2000; Joshi et al, 2006). In these studies, threshold values for or the neural representation of odorants or groups of odorants with similar molecular structures have been investigated. Structural features such as carbon chain length have been found to be an important factor in the interaction between an odorant and an olfactory receptor, affecting how strongly the odorant is bound by the receptor and how well the odor is perceived. Laska et al. (2006) determined olfactory detection threshold values for aliphatic alcohols and aliphatic aldehydes in spider monkeys. The study showed a significant negative correlation between carbon chain length and threshold values for aliphatic aldehydes, in which 1-propanol, with three carbons in its backbone, had a threshold value far higher than that of 1-heptanol with its seven carbon atoms. However, this negative correlation was not found among the aliphatic aldehydes, which shows that there is a difference between different odorant groups and how their structure affects detection. A similar study using three squirrel monkeys (*Saimiri sciureus*), and three pigtail macaques (*Macaca nemestrina*) found the same negative correlation between carbon chain length and detection threshold for aliphatic ketones (Laska et al, (2005). Additional structural features of molecules may also affect detection threshold. For example, addition of functional groups may lower or increase the threshold value at which a odorant can be detected by the animal. One example is pyrazines, for which added methyl groups have been found to lower the detection threshold in spider monkeys (Persson, 2008).

Olfactory receptors require a specific molecular feature and functional groups (Buck, 2004) such as an aldehyde group to bind a ligand. If the functional group is replaced, the molecule may fail to activate the receptor, even if the concentration is increased by a factor of 10 (Araneda et al, 2000).

5.6 Conclusion

The results of this study show that spider monkeys have a well developed sense of smell for aromatic aldehydes. The results also show that subtle changes in molecular structure affect the threshold values of the odorants. Few other studies have been performed to determine detection threshold for aromatic aldehydes in other species, for example mouse and dog, so this would be an appropriate future project.

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