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Olfactory Responsiveness to Two Odorous Steroids in Three Species of Nonhuman Primates

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Abstract

Social communication by means of odor signals is widespread among mammals. In pigs, for example, the C19-steroids 5-α-androst-16-en-3-one and 5-α-androst-16-en-3-ol are secreted by the boar and induce the mating stance in the sow. In humans, the same substances have been shown to be compounds of body odor and are presumed to affect human behavior. Using an instrumental conditioning paradigm, we here show that squirrel monkeys, spider monkeys and pigtail macaques are able to detect androstenone at concentrations in the micromolar range and thus at concentrations at least as low as those reported in pigs and humans. All three species of nonhuman primates were considerably less sensitive to androstenol, which was detected at concentrations in the millimolar range. Additional tests, using a habituation–dishabituation paradigm, showed that none of the 10 animals tested per species was anosmic to the two odorous steroids. These results suggest that androstenone and androstenol may be involved in olfactory communication in the primate species tested and that the specific anosmia to these odorants found in ~30% of human subjects may be due to their reduced number of functional olfactory receptor genes compared with nonhuman primates.

Key words: androstenol, androstenone, nonhuman primates, olfactory detection thresholds, specific anosmia

Introduction

Primates are typically regarded as visual animals with a poorly developed sense of smell. Recent studies, however, suggest that the olfactory capabilities of members of this order of mammals may be much better than previously thought (Shepherd, 2004), and that both human and nonhuman primates may use olfactory cues for social communication (Epple, 1986; Wyatt, 2003). In fact, there is accumulating evidence to support the presence of primer, signaler, modulator and, perhaps, also releaser pheromones in humans (McClintock, 2002; Wysocki and Preti, 2004) as well as in monkeys (Chiarelli, 2001). Although the chemical nature of possible human pheromones has not been identified yet, gas chromatographic analyses of human body odor suggest that, in addition to a complex mixture of aliphatic carboxylic acids, volatile steroids are prime candidates to serve pheromonal functions. The C-19 steroids 5-α-androst-16-en-3-one (androstenone) and 5-α-androst-16-en-3-ol (androstenol) have been found in human axillary secretions as well as in urine, peripheral blood plasma and saliva from men and women (Gower and Ruparelia, 1993). In each case, marked sex differences in androstenone and androstenol levels were noted, and several studies reported the odor of these steroids to affect human behavior in a sex-dependent manner (Grammer, 1993; Cornwell *et al.*, 2004; Pause, 2004). Given the high degree of similarity in hormone physiology and steroid metabolism between human and nonhuman primates, it seems reasonable to assume that androstenone and androstenol may also be compounds of primate body odor and that these odorants may also play a role in chemical communication of nonhuman primates. Therefore, we assessed the olfactory sensitivity for androstenone and androstenol in pigtail macaques, squirrel monkeys and spider monkeys. As a considerable proportion of the human population has been shown to be anosmic to these odorous steroids (Gower and Ruparelia, 1993), that is, unable to detect them at a concentration more than two standard deviations higher than the mean value of a population (Amoore, 1971), we also assessed the ability to detect above-threshold concentrations of the odors of androstenone and androstenol in a larger number of indidividuals of the three nonhuman primate species.

The possibility to assess olfactory capabilities in both New World primates and Old World primates, and to compare

them with those of human subjects and nonprimate mammals, allowed us to additionally address the question whether differences in the relative size of olfactory brain structures or in the number of functional olfactory receptor genes correlate with differences in olfactory sensitivity for and/or general detectability of odorous steroids.

Materials and methods

Animals

Detection threshold testing was carried out using three adult male and one adult female squirrel monkeys (*Saimiri sciureus*), three adult male and one adult female pigtail macaques (*Macaca nemestrina*), and one adult male and three adult female spider monekys (*Ateles geoffroyi*). General detectability testing was carried out using five adult males and five adult females (including the animals used for detection threshold testing) per species. All animals had served as subjects in previous olfactory experiments and were completely familiar with the basic test procedures. Conditions of the animals' maintenance have been described in detail elsewhere (Laska and Seibt, 2002a; Hernandez Salazar *et al.*, 2003). The experiments reported here comply with the *Guide for the Care and Use of Laboratory Animals* (National Institutes of Health Publication no. 86-23, revised 1985), and also with current German and Mexican laws.

Odorants

5-α-Androst-16-en-3-one (androstenone) and 5-α-androst-16-en-3-ol (androstenol) were obtained from Steraloids (Newport, RI). Both substances were diluted using odorless diethyl phthalate from Merck (Darmstadt, Germany) as the solvent.

Behavioral tests

The experimental procedures for assessing olfactory sensitivity have been described in detail elsewhere (Laska and Hudson, 1993; Hübener and Laska, 2001; Laska *et al.*, 2003a,b).

Briefly, the animals were tested using a food-rewarded instrumental conditioning paradigm. Olfactory detection threshold values were determined by testing the animals' ability to discriminate between increasing dilutions of an odorant and the odorless solvent diethyl phthalate. In each test trial, each monkey sniffed at both options and then decided for one of the alternatives by performing an operant response which, in the case of a correct decision, was food-rewarded. Ten such trials were conducted per animal and session, and at least three sessions per experimental condition were performed. Starting with a dilution of 2 g/l androstenone and 5 g/l androstenol, respectively, an odorant was successively presented in 10-fold dilution steps until an animal failed to significantly discriminate it from the solvent. Subsequently, this descending staircase procedure was repeated. Finally, intermediate dilutions were tested in order to determine the threshold value more exactly. For each individual animal, the percentage from the best three sessions per stimulus pair, comprising a total of at least 30 decisions, was calculated. Significance levels were determined by calculating binomial z-scores corrected for continuity from the number of correct and false responses for each individual and condition.

The experimental procedures for assessing general detectability of androstenone and androstenol employed a habituation–dishabituation paradigm. Odor stimuli were presented by pipetting 10 μl of either odorless diethyl phthalate or androstenone at a concentration of 2 g/l or androstenol at a concentration of 5 g/l onto a cotton wad. This was put into a fine-meshed aluminum tube (1 cm diam.) which was attached horizontally to the inner side of the mesh of the cage so that the individually tested animals were able to smell the odorant but unable to make physical contact with the odor source. Each test session was composed of three consecutive presentations of the odorless solvent followed by three presentations of an odorant. Each stimulus was presented for 1 min, with 1 min intervals between each successive stimulus presentation. The number of seconds during each presentation that a subject placed its nose against the tube bearing the stimulus was recorded. Non-parametric Wilcoxon tests were used to compare the time subjects spent investigating the third solvent versus the first odorant stimulus.

Results

Figure 1 shows the performance of the three primate species in discriminating between various dilutions of androstenone and the odorless solvent. The pigtail macaques were able to detect androstenone at concentrations as low as 25 μM (three animals) and 73 μM (one animal). The squirrel monkeys significantly distinguished dilutions as low as 25 μM (one animal), 73 μM (one animal) and 250 μM (two animals) androstenone from the solvent, and the spider monkeys displayed detection thresholds of 7.3 μM (one animal) and 25 μM (three animals) androstenone.

The individual animals of a given species demonstrated very similar threshold values and differed only by a dilution factor of three (pigtail macaques and spider monkeys) or 10 (squirrel monkeys) between the highest- and the lowest-scoring animals.

Figure 2 shows the performance of the three primate species in discriminating between various dilutions of androstenol and the odorless solvent. The four pigtail macaques, the four spider monkeys and three of the four squirrel monkeys were able to detect androstenol at concentrations as low as 6.2 mM. The remaining squirrel monkey significantly distinguished dilutions as low as 0.62 mM androstenol from the solvent.

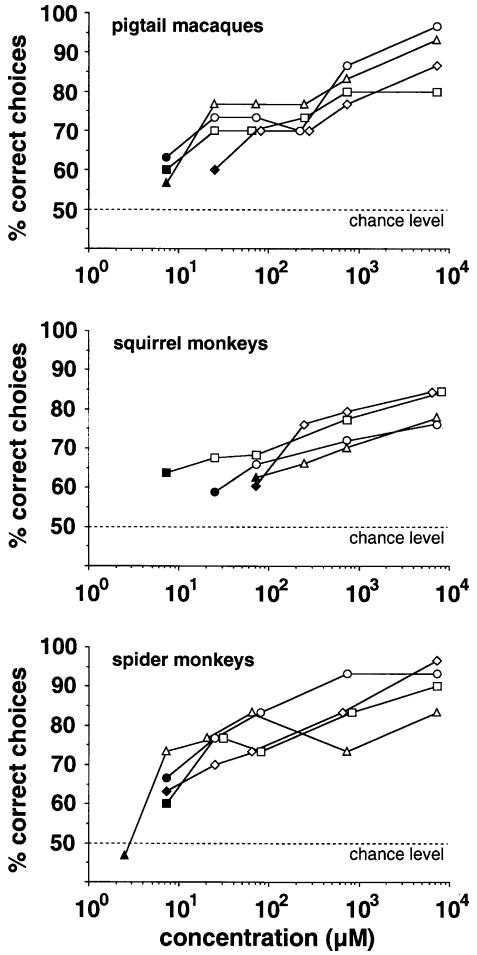

Figure 1 Performance of four pigtail macaques, four squirrel monkeys and four spider monkeys in discriminating between various dilutions of androstenone and the odorless solvent diethyl phthalate. Each data point represents the percentage of correct choices from a total of at least 30 decisions per individual animal. Filled symbols indicate dilutions that were not discriminated significantly above chance level (binomial test, $P > 0.05$).

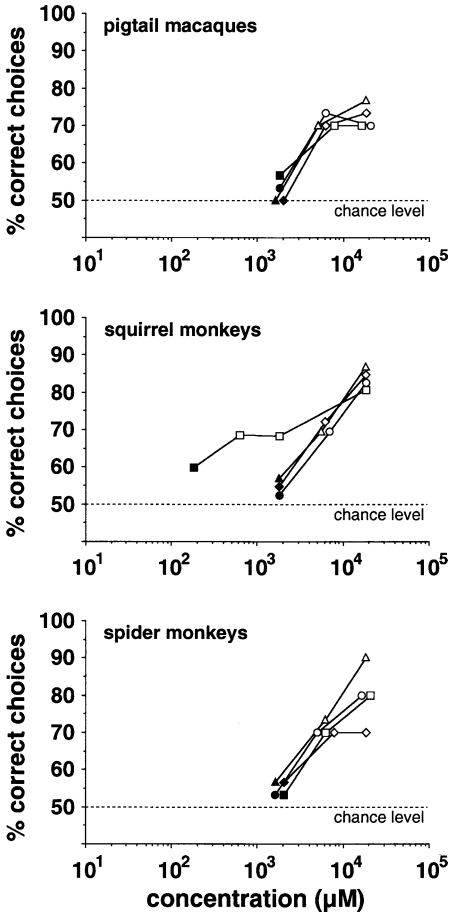

Figure 2 Performance of four pigtail macaques, four squirrel monkeys and four spider monkeys in discriminating between various dilutions of androstenol and the odorless solvent diethyl phthalate. Each data point represents the percentage of correct choices from a total of at least 30 decisions per individual animal. Filled symbols indicate dilutions that were not discriminated significantly above chance level (binomial test, $P > 0.05$).

Thus, the individual squirrel monkeys demonstrated very similar threshold values and differed only by a dilution factor of 10 between the highest- and the lowest-scoring animals. The individual pigtail macaques and the spider monkeys even showed identical threshold values with androstenol.

Figure 3 shows the performance of the three primate species in the habituation–dishabituation paradigm with androstenone as stimulus. All 10 animals tested per species showed a marked and at least three-fold increase in the time spent sniffing at the first androstenone stimulus compared with the third solvent stimulus indicating that they were clearly able to perceive the odor of this steroid at a concentration of 2 g/l. At the group level, this increase was statistically significant (Wilcoxon, $P < 0.001$). Males and females of a given species did not differ significantly from each other in their responses to any of the three solvent and the three androstenone presentations (Mann–Whitney U-test, $P > 0.05$).

Figure 4 shows the performance of the three primate species in the habituation–dishabituation paradigm with androstenol as stimulus. All 10 animals tested per species showed a marked and at least threefold increase in the time spent sniffing at the first androstenol stimulus compared with the third solvent stimulus, indicating that they were clearly able to perceive the odor of this steroid at a concentration of 5 g/l. At the group level, this increase was statistically significant (Wilcoxon, $P < 0.001$). Males and females of a given species did not differ significantly from each other in their responses to any of the three solvent and the three androstenol presentations (Mann–Whitney U-test, $P > 0.05$).

Discussion

The results of this study demonstrate, for the first time, that pigtail macaques, squirrel monkeys and spider monkeys have a well-developed olfactory sensitivity for androstenone and androstenol, two odorous steroids presumed to affect

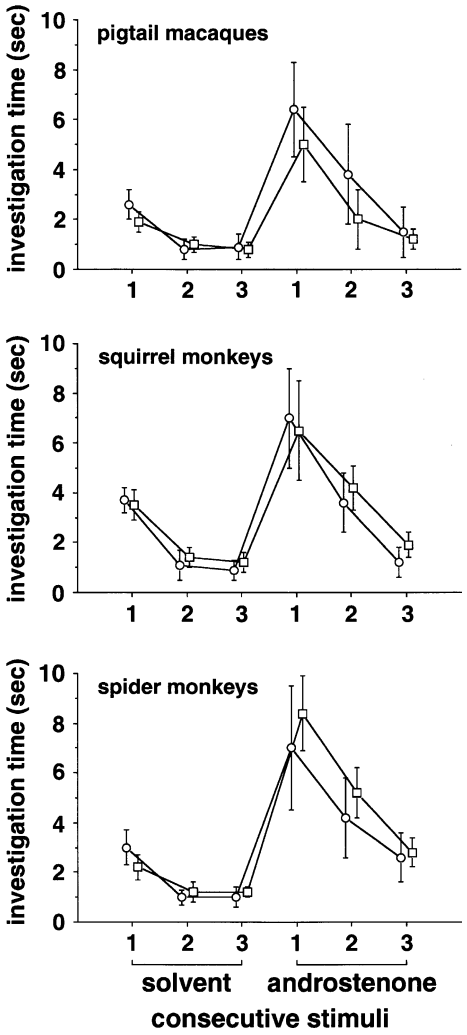

Figure 3 Investigation time during three consecutive presentations of odorless diethyl phthalate followed by three consecutive presentations of a 2 g/l solution of androstenone in diethyl phthalate. Each data point represents the mean (± SE) value of five female (circles) and five male (squares) pigtail macaques, squirrel monkeys and spider monkeys, respectively.

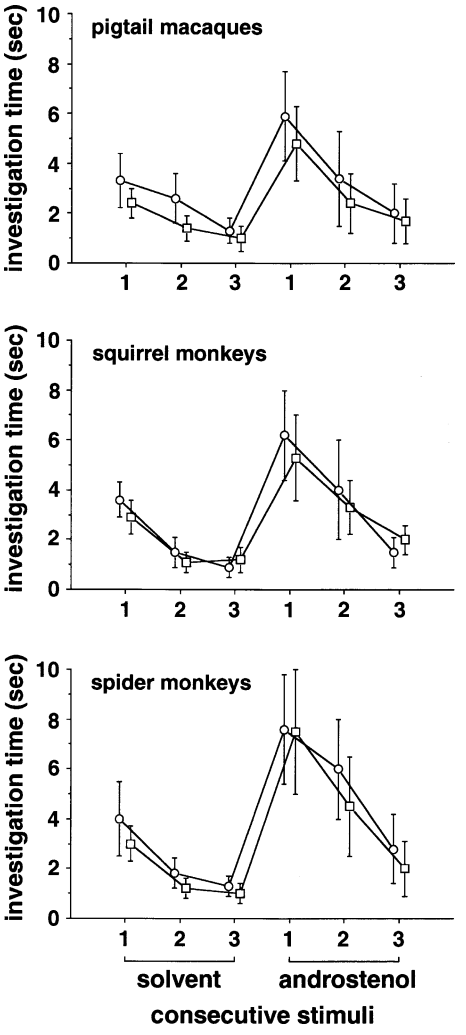

Figure 4 Investigation time during three consecutive presentations of odorless diethyl phthalate followed by three consecutive presentations of a 5 g/l solution of androstenol in diethyl phthalate. Each data point represents the mean (± SE) value of five female (circles) and five male (squares) pigtail macaques, squirrel monkeys and spider monkeys, respectively.

human behavior. These findings are in line with earlier studies using the same methods and animals that reported all three species to have a well-developed olfactory sensitivity for carboxylic acids (Laska *et al.*, 2000, 2004), acetic esters (Laska and Seibt, 2002a; Hernandez Salazar *et al.*, 2003), aliphatic alcohols (Laska and Seibt, 2002b; Laska *et al.*, 2005c) and aliphatic aldehydes (Laska *et al.*, 2003b, 2005c). Thus, the present results lend further support to the idea that olfaction may play a significant role in the regulation of behavior in these primate species.

Although only four animals per species were tested for their sensitivity, the results appear robust as interindividual variability was remarkably low and generally smaller than the range reported in studies on human olfactory sensitivity, that is, within three orders of magnitude (Stevens *et al.*, 1988). In fact, with both substances tested there was even only a factor of 10 between the threshold values of the highest- and the lowest-scoring animal of a species. Further, for both substances, the animals' performance with the lowest concentrations presented dropped to chance level, suggesting that the statistically significant discrimination between higher concentrations of an odorant and the odorless diluent was indeed based on chemosensory perception and not on other cues.

Figure 5 compares the olfactory detection threshold values obtained with the three nonhuman primate species for androstenone to those from human subjects and other mammals. Although such across-species comparisons should be considered with caution as different methods may lead to widely differing results (Hastings, 2003), it seems admissible to state that, compared with human subjects (tested using sophisticated signal detection methods) and pigs (tested

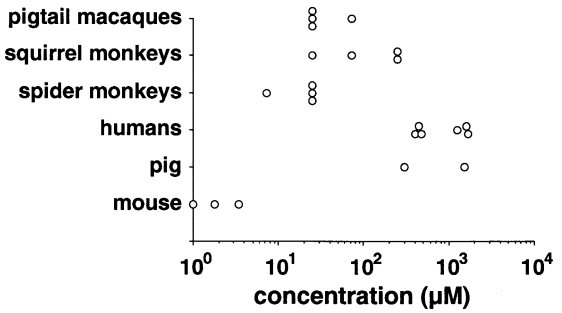

Figure 5 Comparison of the olfactory detection threshold values of the pigtail macaques, squirrel monkeys and spider monkeys for androstenone and those of other mammalian species. Data points of the three nonhuman primate species represent threshold values of individual animals. Data points of human subjects and mice represent mean values from different studies (human data: Wysocki and Beauchamp, 1984; Dorries *et al.*, 1989; Gross-Isseroff *et al.*, 1992; Annor-Frempong *et al.*, 1997; Sirota *et al.*, 1999; Knecht *et al.*, 2002; mouse data: Voznessenskaya *et al.*, 1999; Yee and Wysocki, 2001). Data points of the pigs represent mean values for female and male animals, respectively.

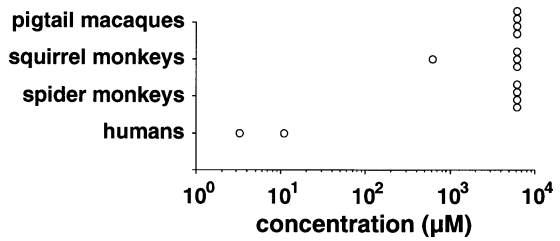

Figure 6 Comparison of the olfactory detection threshold values of the pigtail macaques, squirrel monkeys and spider monkeys for androstenol and those of human subjects. Data points of the three nonhuman primate species represent threshold values of individual animals. Data points of human subjects represent mean values from two different studies (Brooks and Pearson, 1989; Morofushi *et al.*, 2000).

using an instrumental conditioning paradigm), the primates tested in the present study are at least as sensitive to androstenone, if not more so. They are less sensitive, however, than the mouse.

Interestingly, whereas the pig's sensitivity to androstenone has been reported to show a sexual dimorphism, with females being more sensitive than males (Dorries *et al.*, 1995), no such difference was found in any of the nonhuman primates tested here and also not in human subjects (Wysocki and Beauchamp, 1984; Dorries *et al.*, 1989; Gross-Isseroff *et al.*, 1992; Annor-Frempong *et al.*, 1997; Sirota *et al.*, 1999; Knecht *et al.*, 2002). However, it is important to note that pigtail macaques as well as squirrel monkeys and spider monkeys were able to detect androstenone at concentrations that have been shown to induce immediate behavioral (Dorries *et al.*, 1997) and sustained endocrinological (Mattioli *et al.*, 1986) responses in the pig.

Figure 6 compares the olfactory detection threshold values obtained with the three nonhuman primate species for androstenol to those from human subjects. For this odorous steroid, human subjects were considerably more sensitive than the pigtail macaques, the squirrel monkeys and the spider monkeys—despite the fact that the relative size of the human olfactory brain structures devoted to processing olfactory information is markedly smaller than that of the nonhuman primates (Stephan *et al.*, 1988), and despite the fact that the number of functional olfactory receptor genes in *Homo sapiens* (~350) is considerably smaller than that of *Macaca nemestrina* (~700), and of *Saimiri sciureus* and *Ateles geoffroyi* (~1000) (Rouquier *et al.*, 2000; Glusman *et al.*, 2001; Gilad *et al.*, 2004).

It should be mentioned that the threshold values of the human subjects for androstenone and androstenol as depicted in Figures 5 and 6 represent mean values from different studies whereas the data points of the nonhuman primates represent individual threshold values. Nevertheless, the human subjects demonstrated lower threshold values with androstenol than all three species of monkeys.

Similarly, the pigtail macaques did not perform any more poorly than the squirrel monkeys and the spider monkeys with both odorous steroids—again despite the fact that the relative size of the olfactory bulbs and the number of functional olfactory receptor genes in Old World primates are smaller than in New World primates (Stephan *et al.*, 1988; Rouquier *et al.*, 2000). These findings are in line with earlier studies showing that human subjects do not generally perform more poorly than nonhuman primates in detecting aliphatic alcohols (Laska and Seibt, 2002b) and carboxylic acids (Laska *et al.*, 2000, 2004), and that Old World primates do not generally have a poorer sensitivity for aliphatic alcohols (Laska and Seibt, 2002b) and aldehydes (Laska *et al.*, 2003b, 2005c) than New World primates.

Thus, the present findings lend additional support to the notion that—at least within the order of primates—allometric comparisons of olfactory brain structures or differences in the number of functional olfactory receptor genes do not allow us to draw generalizable conclusions about the olfactory sensitivity of any two species.

A within-species comparison of the sensitivity of pigtail macaques, squirrel monkeys and spider monkeys for the two steroids tested here shows that all three species are considerably more sensitive to androstenone, a ketone, than to androstenol, an alcohol, despite the high degree of structural similarity of these odorants (see Figures 5 and 6). This is remarkable considering that both *Saimiri sciureus* and *Macaca nemestrina* have been shown to be consistently more sensitive to aliphatic alcohols compared with aliphatic ketones sharing the same number of carbons (Laska and Seibt, 2002b; Laska *et al.*, 2005a,b). An increasing number of studies, however, suggest that the behavioral relevance of odorants is an important determinant of sensitivity (Laska *et al.*, 2005a,b). Thus, the marked difference in detection thresholds for androstenone and androstenol found in the present study

might reflect a more important role for androstenone in the social behavior of the primate species tested. This hypothesis, however, warrants further investigation.

Several studies have shown that ~30% of the human population are anosmic to androstenone (Gower and Ruparelia, 1993), and that the ability to perceive this odorant is likely to be genetically determined (Wysocki and Beauchamp, 1984). This raises the possibility that the gene(s) coding for olfactory receptor(s) responsive to androstenone may belong to that fraction of the olfactory genome that became inactivated in the course of human (or Old World primate) evolution. In order to address this question, we assessed the occurrence of specific anosmia to androstenone and androstenol in pigtail macaques, squirrel monkeys and spider monkeys, employing a larger number of animals than used for the detection threshold test.

The presumed absence of a functional vomeronasal organ (VNO) in human subjects as opposed to its presumed presence in many nonhuman primates might represent an explanation for the observed lack of specific anosmia to androstenone and androstenol in the three nonhuman primate species tested here. Although this explanation cannot be ruled out completely, it appears unlikely for the following reasons: first, pigtail macaques have been shown to lack a functional VNO (Smith *et al.*, 2001). Secondly, a recent study has demonstrated that the ability of human subjects to detect androstenone is independent of vomeronasal function (Knecht *et al.*, 2002). Thirdly, and perhaps most importantly, the detection of odors implicated in mammalian social communication does not always involve the vomeronasal system. The female pig's behavioral response to androstenone and androstenol, for example, is mediated by the main olfactory system and not by its fully functional VNO (Dorries *et al.*, 1997). Similarly, the rabbit pup's nipple search response to its mother's mammary pheromone does not depend on the vomeronasal system, again despite the fact that it is fully functional in this species (Hudson and Distel, 1986).

A more likely explanation for our finding that all individual animals of the two New World primate species and the Old World primate species tested here displayed the general ability to detect androstenone and androstenol is that the specific anosmia for these odorous steroids found in a considerable proportion of human subjects may be due to their markedly reduced number of functional olfactory receptor genes. Given the recent advances in the characterization of the olfactory genome in human and nonhuman primates (Enard and Pääbo, 2004), a logical next step would be to screen for genetic polymorphisms of olfactory receptor genes that are consistent with the ability or inability to perceive androstenone or androstenol in human subjects and, if they exist, to search for homologs in the nonhuman primates tested here.

Such an approach should allow us, for the first time, to link the ability to detect a certain odorant to the functionality of a single human olfactory receptor gene. A comparison with the olfactory genome of nonhuman primates should allow us to gain further insight into the evolutionary processes underlying the marked loss of functional olfactory receptor genes in humans.

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References

Amoore, J.E. (1971) *Olfactory genetics and anosmia.* In Beidler, L.M. (ed.), Handbook of Sensory Physiology. Springer, New York, Vol. 4, pp. 245–256.

Annor-Frempong, I.E., Nute, G.R., Whittington, F.W. and **Wood, J.D.** (1997) *The problem of taint in pork. I. Detection thresholds and odour profiles of androstenone and skatole in a model system*. Meat Sci., 46, 45–55.

Brooks, R.I. and **Pearson, A.M.** (1989) *Odor thresholds of the C19-delta-16-steroids responsible for boar odor in pork*. Meat Sci., 24, 11–19.

Chiarelli, B. (2001) *Pheromonal communication and socialization.* In Falk, D. and Gibson, K.R. (eds), Evolutionary Anatomy of the Primate Cerebral Cortex. Cambridge University Press, Cambridge, pp. 165–176.

Cornwell, R.E., Boothroyd, L., Burt, D.M., Feinberg, D.R., Jones, B.C., Little, A.C., Pitman, R., Whiten, S. and **Perrett, D.I.** (2004) *Concordant preferences for opposite-sex signals? Human pheromones and facial characteristics*. Proc. R. Soc. Lond. B Biol. Sci., 271, 635–640.

Dorries, K.M., Schmidt, H.J., Beauchamp, G.K. and **Wysocki, C.J.** (1989) *Changes in sensitivity to the odor of androstenone during adolescence*. Dev. Psychobiol., 22, 423–435.

Dorries, K.M., Adkins-Regan, E. and **Halpern, B.P.** (1995) *Olfactory sensitivity to the pheromone androstenone is sexually dimorphic in the pig*. Physiol. Behav., 57, 255–259.

Dorries, K.M., Adkins-Regan, E. and **Halpern, B.P.** (1997) *Sensitivity and behavioral responses to the pheromone androstenone are not mediated by the vomeronasal organ in domestic pigs*. Brain Behav. Evol., 49, 53–62.

Enard, W. and **Pääbo, S.** (2004) *Comparative primate genomics*. Annu. Rev. Genom. Hum. Genet., 5, 351–378.

Epple, G. (1986) *Communication by chemical signals.* In Mitchell, G. and Erwin, J. (eds), Comparative Primate Biology. Alan R. Liss, New York, Vol. 2A, pp. 531–580.

Gilad, Y., Wiebe, V., Przeworski, M., Lancet, D. and **Pääbo, S.** (2004) *Loss of olfactory receptor genes coincides with the acquisition of full trichromatic vision in primates*. PLoS Biol., 2, 120–125.

Glusman, G., Yanai, I., Rubin, I. and **Lancet, D.** (2001) *The complete human olfactory subgenome*. Genome Res., 11, 685–702.

Gower, D.B. and **Ruparelia, B.A.** (1993) *Olfaction in humans with special reference to odorous 16-androstenes: their occurrence, perception and possible social, psychological and sexual impact*. J. Endocrinol., 137, 167–187.

Grammer, K. (1993) *5-α-Androst-16-en-3-alpha-one: a male pheromone? A brief report*. Ethol. Sociobiol., 14, 210–208.

Gross-Isseroff, R., Ophir, D., Bartana, A., Voet, H. and **Lancet, D.** (1992) *Evidence for genetic determination in human twins of olfactory thresholds for a standard odorant*. Neurosci. Lett., 141, 115–118.

Hastings, L. (2003) *Psychophysical evaluation of olfaction in mammals*. In Doty, R.L. (ed.), Handbook of Olfaction and Gustation, 2nd edn. Marcel Dekker, New York, pp. 385–401.

Hernandez Salazar, L.T., Laska, M. and **Rodriguez Luna, E.** (2003) *Olfactory sensitivity for aliphatic esters in spider monkeys,* Ateles geoffroyi. Behav. Neurosci., 117, 1142–1149.

Hudson, R. and **Distel, H.** (1986) *Pheromonal release of suckling in rabbits does not depend on the vomeronasal organ*. Physiol. Behav., 37, 123–128.

Hübener, F. and **Laska, M.** (2001) *A two-choice discrimination method to assess olfactory performance in pigtail macaques,* Macaca nemestrina. Physiol. Behav., 72, 511–519.

Knecht, M., Witt, M., Hüttenbrink, K.B. and **Hummel, T.** (2002) *Assessment of olfactory function and androstenone odor thresholds in man with or without covering the vomeronasal duct.* Chem. Senses, 27, A111.

Laska, M. and **Hudson, R.** (1993) *Assessing olfactory performance in a New World primate,* Saimiri sciureus. Physiol. Behav., 53, 89–96.

Laska, M. and **Seibt, A.** (2002a) *Olfactory sensitivity for aliphatic esters in squirrel monkeys and pigtail macaques*. Behav. Brain Res., 134, 165–174.

Laska, M. and **Seibt, A.** (2002b) *Olfactory sensitivity for aliphatic alcohols in squirrel monkeys and pigtail macaques*. J. Exp. Biol., 205, 1633–1643.

Laska, M., Seibt, A. and **Weber, A.** (2000) *'Microsmatic' primates revisited—olfactory sensitivity in the squirrel monkey.* Chem. Senses, 25, 47–53.

Laska, M., Hernandez Salazar, L.T. and **Rodriguez Luna, E.** (2003a) *Successful acquisition of an olfactory discrimination paradigm by spider monkeys* (Ateles geoffroyi). Physiol. Behav., 78, 321–329.

Laska, M., Hofmann, M. and **Simon, Y.** (2003b) *Olfactory sensitivity for aliphatic aldehydes in squirrel monkeys and pigtail macaques*. J. Comp. Physiol. A, 189, 263–271.

Laska, M., Wieser, A., Rivas Bautista, R.M. and **Hernandez Salazar, L.T.** (2004) *Olfactory sensitivity for carboxylic acids in spider monkeys and pigtail macaques*. Chem. Senses, 29, 101–109.

Laska, M., Fendt, M., Wieser, A., Endres, T., Hernandez Salazar, L.T. and **Apfelbach, R.** (2005a) *Detecting danger—or just another odorant? Olfactory sensitivity for the fox odor component 2,4,5-trimethylthiazoline in four species of mammals*. Physiol. Behav., 84, 211–215.

Laska, M., Miethe, V., Rieck, C. and **Weindl, K.** (2005b) *Olfactory sensitivity for aliphatic ketones in squirrel monkeys and pigtail macaques*. Exp. Brain Res., 160, 302–311.

Laska, M., Rivas Bautista, R.M. and **Hernandez Salazar, L.T.** (2005c) *Olfactory sensitivity for aliphatic alcohols and aldehydes in spider monkeys,* Ateles geoffroyi. Am. J. Phys. Anthropol.

Mattioli, M., Galeati, G., Conte, F. and **Seren, E.** (1986) *Effect of 5-alpha-androst-16-en-3-one on oxytocin release in estrous sows*. Theriogenology, 25, 399–403.

McClintock, M.K. (2002) *Pheromones, odors, and vasanas: the neuroendocrinology of social chemosignals in humans and animals.* In Pfaff, D. (ed.), Hormones, Brain and Behavior. Academic Press, San Diego, CA, pp. 797–870.

Morofushi, M., Shinohara, K., Funabashi, T. and **Kimura, F.** (2000) *Positive relationship between menstrual synchrony and ability to smell 5-α-androst-16-en-3-ol*. Chem. Senses, 25, 407–411.

Pause, B.M. (2004) *Are androgen steroids acting as pheromones in humans?* Physiol. Behav., 83, 21–29.

Rouquier, S., Blancher, A. and **Giorgi, D.** (2000) *The olfactory receptor gene repertoire in primates and mouse: evidence for reduction of the functional fraction in primates*. Proc. Natl Acad. Sci. USA, 97, 2870–2874.

Shepherd, G.M. (2004) *The human sense of smell: are we better than we think?* PLoS Biol., 2, 572–575.

Sirota, P., Davidson, B., Masheva, T., Benhatov, R., Zohar, J. and **Gross-Isseroff, R.** (1999) *Increased olfactory sensitivity in first episode psychosis and the effect of neuroleptic treatment on olfactory sensitivity in schizophrenia*. Psychiat. Res., 86, 143–153.

Smith, T.D., Siegel, M.I. and **Bhatnagar, K.P.** (2001) *Reappraisal of the vomeronasal system of catarrhine primates: ontogeny, morphology, functionality and persisting questions*. Anat. Rec., 265, 176–192.

Stephan, H., Baron, G. and **Frahm, H.D.** (1988) *Comparative size of brains and brain structures.* In Steklis, H. and Erwin, J. (eds), Comparative Primate Biology. Alan R. Liss, New York, Vol. 4, pp. 1–38.

Stevens, J.C., Cain, W.S. and **Burke, R.J.** (1988) *Variability of olfactory thresholds*. Chem. Senses, 13, 643–653.

Voznessenskaya, V.V., Wysocki, C.J., Chukhrai, E.S., Poltorack, O.M. and **Atyaksheva, L.F.** (1999) *Is there a time during neonatal development for maximal imprinting for odor?* In Johnston, R.E., Müller-Schwarze, D and Sorensen, P.W. (eds), Advances in Chemical Signals in Vertebrates. Kluwer, New York, pp. 563–571.

Wyatt, T.D. (2003) Pheromones and Animal Behaviour: Communication by Smell and Taste. Cambridge University Press, Cambridge.

Wysocki, C.J. and **Beauchamp, G.K.** (1984) *Ability to smell androstenone is genetically determined*. Proc. Natl Acad. Sci. USA, 81, 4899–4902.

Wysocki, C.J. and **Preti, G.** (2004) *Facts, fallacies, fears, and frustrations with human pheromones*. Anat. Rec., 281, 1201–1211.

Yee, K.K. and **Wysocki, C.J.** (2001). *Odorant exposure increases olfactory sensitivity: olfactory epithelium is implicated*. Physiol. Behav., 72, 705–711.

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