to total unresponsiveness to any stimulus. Three spontaneously active units had response characteristics similar to cold receptors i.e. a regular spontaneous discharge which was excited by a cold stimulus, inhibited by heat and unaffected by mechanical stimulation. The remaining 50 units were completely abnormal in their discharge and response characteristics. They were recorded from the beak stump at 5–83 days after the initial amputation with their receptive fields located on the distal tip of the stump and at varying distances (up to 12 mm) proximal to it. This spontaneous activity is markedly similar to that observed in the experimental neuroma preparation developed initially by Wall, Devor and coworkers[15–17] in the rat and later extended to the mouse and cat[18,19].

Beak trimming results in both cutting and cauterizing the beak, and a significant but variable amount of the remaining beak was damaged by the cautery. The nerves in the beak were damaged by the high temperature of the cautery blade for a distance of 2–3 mm from the cut end. By 6 days after trimming the damaged portion of the nerve had been completely degenerated. At 10 days there was evidence of nerve regrowth with some enlargement of the end of the nerve. This regeneration and regrowth of the nerve fibers continued so that by 15 days clear neuroma was present at the end of the nerve stump together with numerous bundles of regenerating fibers. These regenerating fibers continued to grow but, because of the adjacent scar tissue, were unable to innervate dermal structures and consequently the fibers grew back on themselves to form a complex mass of intertwining regenerating nerve fibers together with the surrounding tissue. In some nerves there was a simple terminal neuroma. In others a neuroma was formed at the original stump of the nerve (fig. 2A, B) in association with a large and complex neuroma formed adjacent to the scar tissue which forms the end of the beak. Some nerves did not appear to have a neuroma at the original stump but, instead, had a complex neuroma adjacent to the scar tissue (fig. 2C, D).

The activation of specific nociceptors in humans[20] and spontaneous discharges originating from stump neuromas are implicated in acute and chronic pain syndromes. From previous work[1] it is clear that the process of beak trimming results in the activation of specific nociceptors in the beak at the time of surgery. From the work presented here it is clear that neuromas are formed as a result of the amputation and that these neuromas probably give rise to abnormal spontaneous nervous activity.

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Axillary 5α-androst-16-en-3-one in men and women: relationships with olfactory acuity to odorous 16-androstenes[1]

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Summary. Axillary 5α-androst-16-en-3-one (5α-androstenone) levels were found to be significantly higher in men than in women but do not vary between left and right axillae, are not related to age, handedness or degree of hirsutism (in women) nor to anosmia to this steroid. In men (but not in women), levels are related linearly to axillary cholesterol concentrations but not to squalene. Olfactory thresholds for 5α-androstenone varied widely, the lowest recorded being 0.2 ppb, but there was no difference in thresholds between men and women. Women (70%) found the smell 'repellant' but anosmia did not differ greatly between men and women (9–20%). Anosmia to the smell of 5α-androst-16-en-3α-ol was most marked in women (90%) rather than in men (45%). Axillary 5α-androstenone values were generally consistent with the 'musky' or 'strong' smells of male axillary extracts, compared with the 'sweet' smell of those from female subjects.

Key words. Axilla; 5α-androst-16-en-3-one; 5α-androst-16-en-3α-ol; anosmia; cholesterol; squalene; olfactory threshold.

The subject of olfactory communication in humans has always been of interest but especially so now that many of the odors emitted have been characterized, and also because these odors might possibly act as olfactory cues in social behavior (for review, see Doty[4] and Gower[5]). One of the obvious sources of such volatile substances are the axillae, and recent research has focused on the components of axillary sweat. At least two odorous steroids are known to be present, 5α-androst-16-en-3-one (5α-androstenone) and 5α-androst-16-en-3α-ol (an-α)[6–8], the former being generally thought to have a urine-like smell and an-α a

musk-like smell. These compounds are formed in large quantities in boar testes (see Gower[9]) and, to a lesser extent, in human testes[10] and give rise to the characteristic 'taint' of the meat of entire boars[11,12]. Further studies have shown that freshly-secreted apocrine sweat is odorless and contains little or no 5α-androstenone[13,14] but that cholesterol, dehydroepiandrosterone sulphate and androsterone sulphate are present[13]. Incubation of apocrine sweat with coryneform bacteria, isolated from the skin, produced the typical axillary odor[15], suggesting that 5α-androstenone is a product of bacterial action[14]. Recent work indicates that axillary odor is associated with a coryneform-dominated axillary microflora[16,17].

The olfactory acuity of men and women to urine – and musk-smelling substances has been studied intensively[4,5,18,19] and 5α-androstenone, the primary urinous odor[20], has proved to be a useful tool in this regard.

Several studies have revealed specific anosmias to this steroid[18,20] and detailed experiments have shown that the mean olfactory threshold is as low as 0.18 parts per billion[20]. 46% of subjects were anosmic, showing that this is the most common form of anosmia so far encountered, and no difference was found between men and women in the frequency of 5α-androstenone anosmia or in olfactory threshold[20].

Similar studies have been performed using exaltolide (the primary musk odor) and an-α, and earlier reports (see Gower[5]) suggested that the olfactory acuity of women varied with the stage of the menstrual cycle and was greater than the acuity of men. However, olfactory acuity of women to furfural, although roughly correlated to changes in plasma oestrogen levels, is not related to such levels in women taking oral contraceptives[4,21].

As far as exaltolide is concerned, specific anosmia is documented, which is inherited as a simple recessive autosomal characteristic[22,23]. The olfactory thresholds for exaltolide and an-α were, respectively, 1.8 and 6.2 parts per billion[20].

With the finding of 5α-androstenone and an-α in human axillary secretions[6-8] and saliva[24], further interest has been stimulated in this group of steroids with regard to the possibility of them being concerned in human social communications. Several reports have so far indicated alteration of judgements[25,26] or effects on choice of location in others' presence[27].

In view of data showing the ability of humans to detect gender from axillary odors (see Doty[4] and Schleidt[28] and references therein), we present findings on possible relationships in human subjects between acuity to 5α-androstenone or an-α and the extent to which the former steroid occurs in the subject's own axillary secretions. Some earlier findings concerning description of odor of 5α-androstenone and an-α and of olfactory acuity have been confirmed[4,18-20].

In this study, 11 healthy men (aged 20–41 years) and 16 healthy women (aged 18–40 years) were investigated.

Axillary secretions (24 h) were collected[8] from right and left axillae separately and the concentrations of 5α-androstenone, cholesterol and squalene measured[14]. Before extraction, the smell of the collecting pads was recorded by the female analyst.

Tests on the ability of the subjects to smell 5α-androstenone and an-α were performed using a series of screw-cap vials containing distilled water (5 ml) plus an ethanolic solution (100 µl) of the substance under study (1 pg to 100 ng). After solutions had been thoroughly mixed, the bottles were kept at 37 °C in a thermostat. Bottles containing distilled water (5 ml), ethanol (100 µl in distilled water, 5 ml) and ethyl acetate (100 µl in distilled water, 5 ml) were included in a numbered sequence. Subjects were asked to open the bottle, smell the liquid immediately, record their first impression and replace the cap. After the bottle had been replaced in the thermostat, the subject waited for 60 sec before proceeding to the next one. The sequence of bottles was known only to the analyst, who changed this at intervals to obviate the possibility of learning smells, since the tests were performed several times for a particular subject. Bottles containing the 16-androstenes were always arranged in ascending order and were interspersed with bottles containing water or ethanol and ethyl acetate to obviate saturation and learning effects.

Each subject was allowed two adjectives to describe the smells, e.g. pleasant, fruity; strong, urinous, etc., although the male subjects preferred to use only one (see table). For the female subjects the tests were performed, as far as possible, on the same day of their cycle, most of these being 28–32 days in length; only 3 women had cycle lengths of 35–38 days.

Analysis of variance and regression calculations were performed using the GENSTAT package.

Axillary 5α-androstenone: Levels in men varied widely (5.2–1019 pmole/24 h) but were uniformly lower in women (1.2–16.6) with the exception of one normal woman (551.0 pmol/24 h). There was a highly significant difference in 5α-androstenone levels, the geometric means being 51 and 9.5 pmol/24 h for men and women, respectively ($p = 0.0054$).

For men and women, either as a group or separately, there was no difference between 5α-androstenone levels from left and right axillae. There was no relationship between leading or non-leading hand and the corresponding axillary 5α-androstenone. Total levels did not vary significantly with age of subjects, or with the degree of hirsutism of some of the female subjects.

Smell of axillary extracts: For men, 50% were considered 'musky' and 'strong' with only 20% as 'sweet'. For women, far more (57%) extracts were considered 'sweet' with only 11% 'musky' and 21% as 'strong' (one of these was subsequently shown to have a high value (550 pmol/24 h) on analysis).

Olfactory thresholds: For 5α-androstenone, these varied from 0.2 parts in a billion to 0.2 parts in 100 million; there was no significant difference between men and women.

Description of smell of 5α-androstenone: For the men tested, the adjectives 'strong', 'musky' or 'urinous' summed up the responses. Only 15% rated the smell as unpleasant and none recorded 'pleasant'. For the women, 70% found the smell repellant with a further 20% recording 'unpleasant'. 'Musky' and 'urinous' largely summed up the response using the other adjective (table).

Incidence of anosmia to 16-androstenes: The percentage incidence of anosmia to 5α-androstenone was 9 and 20 for men and women, respectively, and for an-α, 45 and 90 for men and women, respectively.

No significant relationship was found between total axillary 5α-androstenone and anosmia to this steroid.

Axillary cholesterol and squalene levels: No significant differences were observed between male and female subjects or between left and right axillae. The geometric means and ranges were:

Cholesterol (µmol/24 h), 2.84 (0.82–4.76) and 3.03 (1.34–5.58) for men and women, respectively;

Squalene (µmol/24 h), 1.52 (0.26–9.23) and 1.90 (0.49–7.57) for men and women, respectively.

There was a linear relationship between axillary 5α-androstenone and cholesterol in men but not in women:

$\ln$ 5α-androstenone = 1.9+0.72 cholesterol ($p = 0.02$).

No such relationship occurred with squalene either in men or women.

The marked sex-difference for axillary 5α-androstenone has

Description of the smell of 5α-androst-16-en-3-one

	Men*	Women**	
		a	b
Unpleasant	15 (%)	10 (%)	20 (%)
Pleasant	nil	–	10
Musky	23	36	–
Urinous	23	54	–
Sweat-like	9	–	–
Repellant	nil	–	70
Strong	30	–	–

*Only one adjective used; **two adjectives used; a, first adjective; b, second adjective.

been noted earlier[6,8] but the differences between left and right axillae were not significant for men or women in this study. Previously[14] in men we recorded a 'superior' axilla, but the intra- and inter-individual variation found in the present work may have obscured this.

Axillary 5α-androstenone levels were found to be un-related to age, handedness or degree of hirsutism (in women) and to anosmia to 5α-androstenone. A significant linear relationship exists, in men, between this steroid and cholesterol, but not with squalene. As squalene is not found in apocrine secretions[17] but in sebum[28], this suggests that 5α-androstenone does not correlate with sebum secretion, a finding that compares favorably with our earlier studies[14]. Olfactory thresholds to 5α-androstenone varied widely but the lowest recorded in several subjects (0.2 parts per billion) was as found earlier[18,20]. There was no difference in thresholds between men and women (as noted earlier[20]). Women largely (70%) found the smell repellant or unpleasant (20%). Anosmia to the smell of 5α-androstenone did not differ greatly between men and women but the incidence (9–20%) was much lower than the values reported before[18,20]. In this study, a very high proportion (90%) of women were anosmic to the smell of an-α, and this is difficult to explain in relation to data obtained from larger studies[18].

5α-Androstenone is now known to be a product of microbial action in the axilla[14,16,17]. Coryneform bacteria are present especially in the axillae of men and this could explain the higher levels of 5α-androstenone found compared with those in women. Results are also consistent with the more pronounced 'musky' or 'strong' smells of male axillary extracts compared with the 'sweet' smell of those from the female subjects[4] (except for one, recorded as 'strong', with 550 pmol/24 h). Sex discrimination of adult humans by odor is well-documented (see Doty[4] and Schleidt[28] and references therein), and axillary 5α-androstenone may well be involved.

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Bilateral lesions of suprachiasmatic nucleus eliminate circadian rhythms of oxygen consumption and the respiratory quotient in rats

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Summary. Bilateral lesions of the suprachiasmatic nucleus of the hypothalamus of rats abolished circadian rhythms of oxygen consumption and of the respiratory quotient (RQ). The RQ remained constant at a level intermediate between the maximum (about 1.0) and minimum (about 0.9) values in control animals.
Key words. Circadian rhythm; oxygen consumption; respiratory quotient; suprachiasmatic nucleus; rat.

Previously we found that the circadian rhythm of feeding behavior of rats disappeared after bilateral lesions of the suprachiasmatic nucleus (SCN) of the hypothalamus[1,2]. Since oxygen (O_2) consumption and the respiratory quotient (RQ) are closely related to food intake, and both are reported to show a daily rhythm[3], we next examined the effects of bilateral lesions of the SCN on these rhythms.

Materials and methods. Male Wistar strain rats, initially weighing 150–200 g, were used. Animals were housed in stainless steel cages with free access to water and powdered laboratory diet (type M, Oriental Yeast Co., Osaka), which contained 25 g of protein, 5.5 g fat and 58.6 g of carbohydrate per 100 g (359.9 Cal) of diet. The animal room was maintained at 24 ± 1 °C and 60 ± 10% relative humidity, and illuminated by fluorescent