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HUMAN EXPOSURE TO PUTATIVE PHEROMONES AND CHANGES IN ASPECTS OF SOCIAL BEHAVIOUR

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Summary—Student volunteers (38 of each sex) were exposed unknowingly overnight to the vapour of pheromonally active substances and compared with controls. The substances were either 5α-16-androsten-3α-ol (androstenol, occurring in human underarm sweat, and known to be pheromonally active in pig and man), or a mixture of short-chain fatty acids (occurring in human vaginal fluid, and known to be sexually attractive to the male rhesus monkey). The following morning, the subjects provided information about their social exchanges since rising, by recording on a standardized test diagram the number, depth, duration and direction of initiation, of all verbal exchanges with other individuals.

Irrespective of treatment, males returned significantly higher scores than did females for all exchanges and also for some exchanges initiated by other males. Neither exposure to androstenol nor to the fatty acids had any significant effects on any of the scores of males interacting with either sex, nor on any scores of females with other females. However, exposure of females to androstenol, but not to the fatty acids, resulted in significantly higher scores of exchanges with males, in terms of all parameters for all exchanges. Findings are considered in relation to the origin and maintenance across species of pheromonal communication: evolutionary conservation is seen in terms of the utilization of substances that have provided the means of controlling the social milieu.

INTRODUCTION

The likelihood of pheromones acting on human behaviour was argued forcibly by Wiener [1–3] and by Comfort [4, 5]. In this paper we are not only addressing, by psychological experiment, the question of whether pheromones affect human behaviour, but also considering whether substances (pheromones) over the course of evolution come to exert a controlling influence on physiological systems, development, and behaviour in animals and man. The focus here, unlike that of the ethologist, is not on characteristics which humans have in common with other species, but rather the way that they respond, by means of pheromones, to differences in each other.

Studies on human pheromonal communication may be undertaken with a range of psychological and physiological techniques: changes in heart rate, in respiration, or in electrical skin-resistance can be combined with behavioural observations of parallel changes in movement patterns and social interactions. By providing human subjects, at least in selected sophisticated samples, with novel tasks that require adherence to simple instructions, information can be elicited about the subjects own interpersonal interactions (exchanges) in a natural, if structured, setting. We will assess these in terms of number, duration and intensity. The problem of controlling variables in any social situation are immense, and it is possible to attribute endless reasons for people behaving in the way they do [6, 7]. The test we have used here, involving assessment of all exchanges after overnight exposure of subjects to pheromones, attempts to overcome some of these limitations.

A comprehensive and widely documented account of the research on human olfactory communication over the past decade is given by Schaal and Porter [8]; see [9] for a review of earlier human studies. General reviews of pheromonal studies on vertebrates in recent years include [10–13].

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METHODS

Composition of sample

The test was performed on 116 student volunteers, during the first week of their enrolment for a first degree in Psychology or Biology. In order to exclude more immediate interactive effects of the pheromones during the exposure period, the results with students who were sharing rooms were subsequently excluded from the analysis. The remaining sample consisted of 76 students (38 males and 38 females). They were all drawn from three successive intake years and the majority (79% of the males, 72% of the females) were aged 18–21 years, with a minority of mature students (21% of the males, 28% of the females) aged over 21 years. The mean ages of all subjects were 19.9 years (range 18–30 years) for males and 20.9 years (range 18–42 years) for females. Students were randomly assigned to treatment groups, and the numbers in each group are shown in Table 2.

The students were asked to wear a necklace continuously from the late afternoon (16.30 h) of one day until the morning (09.30 h) of the following day. They were told that the necklaces were impregnated with different but harmless substances and that they would, after completing the experiment, be informed about its purpose and the nature of the substances. Participation was voluntary and students could withdraw from the experiment at any stage; they were not paid. The necklaces and test booklets (see below) were coded, and students were assured that the information provided would be kept anonymous. They were asked not to compare necklaces and to return them.

The necklace was made up of a short length (4.5 cm) of hard plastic tubing (Alkathene, ICI Plastics), and was loosely tied around the neck with elastic thread passed through two holes punched near each end of the tube. The tube had two rows of slits (0.2 cm wide), spaced at regular intervals (approx. 0.4 cm) along about two-thirds of its length, and a dental swab of cottonwool was secured inside it. The slits and the open ends of the tube allowed the volatile components, injected into the cottonwool, to circulate freely into the atmosphere and without the substances having immediate contact with the skin. The tube was worn close to the Adam's apple. The cottonwool swabs were injected on the day before being inserted in the tubing and distributed as necklaces to the subjects, thus allowing time for evaporation at ambient temperature of the solvent vehicle, and there was nothing to suggest that the substances used reacted with the Alkathene tubes.

The substances used were as follows. Androstenol: 5α-16-androsten-3α-ol, 0.25 ml of a 1 mg/ml solution in chloroform. Fatty acids: acetic, propanoic, methylpropanoic, butanoic, methylbutanoic and methylpentanoic acids (in the proportions, 35:10:0.9:2.4:2.3:0.3; see [14]), 0.25 ml of a 1% (v/v) solution of this mixture in chloroform. The control swabs were treated with 0.25 ml chloroform alone.

As students returned their necklaces, after having worn them for 17 h, they were provided with a booklet, containing a diagram of a wheel-like figure and instuctions for entering information on the diagram, and also a questionnaire about themselves, their living circumstances and mode of travel to the college. In particular they were asked whether they lived at home or in student residence, and whether they shared a bedroom with others. A short mood questionnaire was included with the booklet, but the findings do not form part of the present report.

The figure was in the form of a wheel-like circle (20 cm dia), with a central "hub" (3 cm dia), representing the subject, and an outside "rim" (1 cm in width), the circular figure being divided into two clearly demarcated halves by a vertical broken line. The left semicircle was assigned to the recording of interactions (exchanges) with female individuals the right those with males. The individuals with whom the subjects interacted are here referred to as "exchangees". The rim of the "wheel" was divided into 22 equal segments, each segment being labelled to indicate some category of relationship between people. Close relatives, other relatives, close friends and partners were allocated to segments on top of the figure; other friends and fellow-students to mid-segments and acquaintances and strangers to the lower segments.

The students were asked to recall, as best they could, the persons to whom they had spoken from the time they got up that morning and until they received the test booklet. It was suggested that recall might be facilitated by running through, in the mind, the events of the morning, including the rooms and places the subject had been in. It was emphasized that all persons spoken to should be included, those in college, at home, in "digs", as well as those en route to the college.

In relation to the diagram, the subjects were required to: (i) draw one straight line, a "spoke" on the "wheel", between the "hub" (inner circle) and the "rim" (outer circles) for each exchange he/she had had with another person, irrespective of whether it was a greeting or a conversation of some length; (ii) indicate the depth of the exchange, i.e. the extent to which he/she felt the exchange encompassed personal involvement, by making a mark on each of the lines he/she had drawn, at a point, working outwards from the inner circle, to represent the degree of depth of the exchange, from one of a superficial nature (mark near the inner circle) to one of a deep nature (mark near the outer circle); the mid-point would represent an exchange that was average on this continuum; (iii) estimate the time spent (in min, <1 min to be recorded as 1 min) for each exchange, and to record their estimate in the space between the two outer rings; and (iv) indicate whether the exchange was initiated by the subject or by someone else (an exchangee), by adding an arrow-head to the line; the apex of the arrow-head should point outward if the exchange was self-initiated, and inward if the exchangee had initiated it.

Scoring

The numbers of lines drawn on the left half (female) and right half (male) side of the wheel diagram were counted, and their combined score constituted the total number of interactions (exchanges) for that subject. Similarly we recorded for each subject whether they or another had initiated the exchange (i.e. "outward" or "inward" exchanges), as well as whether the initiators were directing their exchanges to males or females. When the arrow-heads were placed at both ends of a line, presumably indicating that the exchange had been simultaneously initiated by both individuals and/or that the subject was uncertain as to who initiated the exchange, a half point was assigned as "outward" and a half point as "inward".

The estimates of the duration of the exchanges were also assessed in the same way, in terms of the exchange with males or with females and the direction of initiation of the exchange. Finally, scores for depth of the exchange were obtained by measuring the relative distance of the marks placed by the subject along the line away from the inner circle, and these scores were again calculated in respect to the sex of the exchangee and of the subject. Subsequently, in order to attempt to obtain further measures of the "intensity" of the exchanges, the derived parameters, number $\times$ depth and depth $\times$ duration, were calculated for each exchange. The scores for each parameter (number of exchanges, depth, duration and the two derived parameters) were broken down and analysed in terms of whether the exchanges originated from the subject and were directed outwards ("Out" scores) or whether they originated from someone else and were directed inwards to the subject ("In" scores). The sum of the "Out" and "In" scores constitute the total score for that category, and are referred to as "All" in the Tables. (A further breakdown of the data in terms of relationships of the subjects to the exchangees, relative, close friend, stranger, etc., was not warranted, the number of exchanges for any particular category being too small to allow a valid statistical analysis.)

All statistical analyses were performed with the SPSS Statistical package (2nd edition). One- and two-way analyses of variance (ANOVA) were used to test the statistical significance of mean differences, and the data are reported as means ($\pm$SEM) in the Tables and text. *Post hoc* comparisons were made by using Scheffé's test and P values $\leqslant 0.05$ were considered significant.

RESULTS

Sex differences

There were marked sex differences (two-way ANOVA; Table 1) in scores relating to the number and depth of the exchanges; there was also some indication of sex differences in the duration of exchanges. The differences were most marked in terms of the overall number of exchanges with males ($P < 0.004$) and in the number of outgoing exchanges to males ($P < 0.002$). In both instances the mean number of exchanges recorded by the women was less than those by the men. The Table also shows that there were no differences between the male and the female subjects in their exchanges with people in general, i.e. when the variables of both treatment and sex of exchangee are removed.

The depth and the duration of all exchanges with males also differed as between the sexes ($P = 0.05$ in both instances), with the females reporting lower mean scores than their male counterparts. There was a similar trend, for females to return lower scores for depth of outward exchanges with males and for depth of

Table 1. Mean scores on each of the parameters of exchange between subjects and others encountered by the subject between rising and completing the standard diagram

Sex of Exchangee	Number			Depth			Duration			Number × depth			Depth × duration		
	Out	In	All	Out	In	All	Out	In	All	Out	In	All	Out	In	All
Males exchanges, irrespective of treatment															
Males															
Means	3.63*	2.29	5.92*	54.0	49.4	102*	15.4	11.6	26.0*	271*	154	426*	1790	1030	2790
±SE	0.421	0.285	0.538	7.79	7.84	14.1	5.00	2.80	7.11	76.3	40.3	101	886	423	1240
P of *F*	0.002	0.312	0.004	0.062	0.061	0.048	0.343	0.169	0.053	0.024	0.148	0.021	0.345	0.299	0.315
Females															
Means	2.87	1.97	4.84	46.0	39.3	80.2	11.5	11.7	20.5	169	105	264	948	829	1640
±SE	0.316	0.254	0.475	7.91	7.24	11.4	2.80	3.02	4.42	37.2	28.3	52.5	310	322	489
P of *F*	0.059	0.143	0.100	0.376	0.482	0.325	0.143	0.418	0.689	0.108	0.658	0.166	0.471	0.535	0.585
Females exchanges, irrespective of treatment															
Males															
Means	2.12*	1.88	4.00*	34.2	33.2	57.5*	8.69	6.81	13.4*	88.1*	81.2	167*	441	444	754
±SE	0.201	0.247	0.354	5.66	6.23	8.63	1.39	1.91	2.37	20.3	22.0	31.6	112	192	202
Females															
Means	3.71	2.49	6.20	60.6	44.7	102	16.3	8.89	24.5	275	131	406	1390	583	1920
±SE	0.309	0.204	0.421	8.37	6.87	12.8	2.41	2.11	3.29	53.3	25.1	68.9	368	207	417
Males and females exchanges, irrespective of treatment or of sex of exchangee															
Males															
Means	6.50	4.26	10.8	97.2	82.4	180	25.6	21.0	46.0	435	255	677	2650	1720	4370
±SE	0.574	0.423	0.820	12.4	11.7	21.8	6.22	4.38	9.86	89.1	50.9	124	985	542	1470
P of *F*	0.397	0.561	0.744	0.948	0.748	0.840	0.593	0.083	0.219	0.495	0.395	0.544	0.413	0.122	0.246
Females															
Means	5.83	4.37	10.2	89.3	67.4	157	23.6	13.6	37.4	363	214	493	1740	887	2630
±SE	0.384	0.306	0.560	12.1	8.14	18.0	3.20	2.48	4.42	65.8	31.2	83.3	417	234	505

Scores are separated according to whether the exchange was initiated by the subject ("Out") or by the exchangee ("In"); "All" represents the sum of "Out" + "In" scores; and *P* of *F* represents significance of main effect with respect to sex of subject.

*Means that are significantly different.

inward exchanges from males, although the differences were not quite statistically significant ($P = 0.06$ in both cases). However the women's reported number of inward exchanges from males (mean 1.88 ± 0.247) was actually marginally lower than the men's reported number of outward exchanges to females (mean 2.87 ± 0.316). On the other hand, with respect to female-to-female exchanges, there was a nearly significantly ($P = 0.06$) greater number of outward exchanges to females reported by women than by men.

There were also sex × treatment interactional effects in the statistical sense, with the number and depth of outward exchanges to males and the number and depth of all exchanges with males differing as between the sexes ($P < 0.02$ in both instances).

Treatment effects

Male subjects. The mean scores of the men exposed to the androstenol, the fatty acid or the control condition did not differ significantly as between treatment groups, nor were there any other F values that reached an acceptable level of statistical significance (one-way ANOVA). The results, which are included (Table 2a) for comparison with the scores returned by the female subjects (Table 2b), show that for male subjects neither the number of exchanges nor estimates of their depth and duration were modified by treatment, nor were there any significant differences between the parameters tested and the directions of the exchange, i.e. initiated by the subject or by the exchangee.

Female subjects. The mean scores of the women are shown in Table 2b. The sample sizes in each cell are shown, together with the P values for F with respect to the between treatment group differences; the corresponding means that were statistically different are underlined. Application of Scheffé's test showed that the differences lay between the androstenol and the control samples, although in some instances, of measures of duration and of number × depth and depth × duration, there were also significant ($P < 0.05$) differences between the fatty acid and androstenol samples. (These columns are marked "x" in Table 2b). There were no significant differences between the fatty acid and the control treatments.

The results also show that the women in their exchanges with other females did not differ on any of the parameters when exposed to either of the three treatments, and this is also true in relation to the direction of the exchanges. On the other hand, there were marked differences in the way the women interacted with males, and this was primarily associated with exposure to androstenol, although the results indicate that the fatty acids were also not entirely without effect. Androstenol thus increased the score in every case where females were interacting with males, and it increased the parameter score in a male direction, the score becoming more male-like.

When the female subjects were interacting with males, there are significant differences apparent in the mean scores on each of the basic parameters (number, depth and duration) between subjects exposed to androstenol and those in the control condition. One-way ANOVA further shows that many of the differences in exchanges were significant also for the derived parameters. Thus, the number of exchanges × depth of all exchanges with males ($P < 0.01$), as well as number × depth of inward exchanges with males were significant ($P < 0.02$). There was also a significant treatment effect in depth × duration for outward and for all exchanges ($P < 0.03$ and < 0.002, respectively) and this was seen with women exposed to androstenol, who showed an increase in scores in their exchanges with males (Table 2b).

With women exposed to the fatty acids, there were no significant treatment effects, in relation either to number or to depth, when they were interacting with males. However, in relation to duration of all exchanges and of exchanges directed outwards, there were significant differences between the subjects exposed to fatty acids and those exposed to androstenol ($P < 0.05$ in both cases), on both measures the scores of the subjects exposed to androstenol being much higher. In addition, the F value for number × depth of the combined ("All") score was significant ($P < 0.05$). On the other hand, the increase in mean scores of the subjects in the fatty acid condition relative to those in the control condition was not significant statistically in terms of any of the parameters.

Thus the exposure of female subjects to androstenol was associated with a marked alteration in their exchanges with males, the increase in mean scores being observed in relation to the number, depth and duration of the exchanges,

Table 2a. Mean scores on each of the parameters of exchange between subjects and others encountered by the subject between rising and completing the standard diagram

	Number			Depth			Duration			Number × depth			Depth × duration		
Treatment	Out	In	All	Out	In	All	Out	In	All	Out	In	All	Out	In	All
							Males' reported exchanges with males								
Control															
Means	3.64	2.55	6.18	57.6	65.7	123	22.0	16.3	38.3	316	213	529	3010	1940	4950
±SE	0.778	0.493	1.23	17.3	16.0	32.0	14.8	6.80	21.2	159	98.7	254	2550	1236	3752
n =	11	11	11	10	10	10	10	10	10	10	10	10	10	10	10
Androstenol															
Means	3.85	2.46	6.31	58.5	49.6	104	14.9	9.08	23.1	288	172	460	1740	601	2284
±SE	0.883	0.616	0.963	13.3	11.7	18.5	7.58	2.45	7.28	157	72.3	165	1312	222	1276
n =	13	13	13	11	10	11	11	10	11	12	12	12	10	9	10
P of F	0.921	0.634	0.733	0.792	0.293	0.508	0.683	0.545	0.554	0.869	0.454	0.668	0.604	0.344	0.496
Fatty acids															
Means	3.43	1.93	5.36	46.8	35.6	82.3	11.1	9.91	19.6	217	88.1	305	806	593	1400
±SE	0.571	0.370	0.700	11.2	12.5	23.0	4.04	4.56	8.00	83.9	35.7	115	312	313	616
n =	14	14	14	12	12	12	14	12	14	12	12	12	12	12	12
							Males reported exchanges with females								
Control															
Means	2.82	2.64	5.45	46.7	40.5	87.2	18.3	10.6	27.1	191	129	320	1580	745	2160
±SE	0.736	0.411	0.994	11.7	10.8	21.6	7.29	4.68	10.8	81.9	52.3	125	779	521	1197
n =	11	11	11	10	10	10	9	10	10	10	10	10	9	10	10
Androstenol															
Means	2.85	1.31	4.15	43.2	36.7	71.9	10.9	13.8	22.2	152	71.3	211	1090	706	1600
±SE	0.553	0.328	0.715	13.7	14.3	18.9	5.38	5.99	6.57	66.3	34.6	74.8	659	500	660
n =	13	13	13	9	9	10	9	9	10	11	12	12	8	8	9
P of F	0.990	0.111	0.551	0.976	0.973	0.876	0.261	0.907	0.503	0.919	0.698	0.724	0.266	0.919	0.736
Fatty acids															
Means	2.93	2.07	5.00	47.5	40.4	81.2	7.16	11.1	14.6	165	117	269	382	1010	1230
±SE	0.425	0.497	0.805	15.6	13.9	20.5	2.17	5.56	5.98	52.4	58.3	82.5	141	661	660
n =	14	14	14	12	10	12	13	10	14	12	13	13	12	10	12

Scores are separated according to whether the exchange was initiated by the subject ("Out") or by the exchange ("In"); "All" represents the sum of "Out" + "In" scores; and n = number of subjects returning scores for that parameter. P of F represents significance of main effect with respect to treatment.
None of the F probabilities was significant.

Table 2b. Mean scores on each of the parameters of exchange between subjects and others encountered by the subject between rising and completing the standard diagram

	Number			Depth			Duration			Number × depth			Depth × duration		
Treatment	Out	In	All	Out	In	All	Out	In	All	Out	In	All	Out	In	All
Females reported exchanges with males															
Control															
Means	1.77	1.31	3.08*	32.6	11.9*	34.2*	5.89*	2.00	6.09*	75.5	22.0*	91.3*	221*	42.9	208*
±SE	0.323	0.382	0.500	11.5	5.82	12.0	1.882	0.690	1.621	35.1	14.5	38.2	85.8	35.0	76.3
n =	13	13	13	9	7	11	9	7	11	11	12	12	9	7	11
Androstenol															
Means	2.75	2.67	5.42*	49.0	54.5*	97.4*	15.1*	13.0	26.7*	146	181*	327*	913*	1040	1840*
±SE	0.392	0.555	0.723	10.5	14.4	14.4	2.44	5.16	4.90	49.3	65.4	71.9	269	566	529
n =	12	12	12	9	8	9	9	8	9	10	10	10	9	8	9
Fatty acids															
Means	1.94	1.75	3.69	25.7	31.2	50.2	6.36*	5.36	10.6*	58.7	61.8	121*	279*	264	486*
±SE	0.309	0.323	0.506	7.88	6.93	13.2	1.999	1.816	3.34	23.6	19.7	38.5	144	126	234
n =	16	16	16	14	11	14	14	11	14	15	15	15	14	11	14
P of *F*	0.125	0.090	0.024	0.237	0.026	0.011	0.011	0.069	0.001	0.200	0.012	0.005	0.024	0.102	0.002
							x		x			x	x		x
Females reported exchanges with females															
Control															
Means	4.46	2.77	7.23	71.0	55.1	126	17.3	10.2	27.5	360	179	539	1460	946	2410
±SE	0.584	0.281	0.735	17.7	14.6	28.4	3.44	3.25	3.97	110	56.8	158	511	600	787
n =	13	13	13	11	11	11	11	11	11	11	11	11	11	11	11
Androstenol															
Means	4.00	1.92	5.92	65.1	36.4	97.9	14.7	11.9	25.4	302	73.7	376	1170	550	1660
±SE	0.564	0.417	0.839	10.8	12.0	19.2	3.45	7.18	8.95	88.6	24.8	110	343	302	533
n =	12	12	12	10	9	10	10	9	10	10	10	10	10	9	10
Fatty acids															
Means	2.88	2.69	5.56	49.1	42.1	87.9	16.7	6.14	21.7	195	135	329	1500	336	1730
±SE	0.417	0.338	0.619	13.9	9.91	19.0	4.99	1.04	4.63	80.1	39.2	94.3	817	114	761
n =	16	16	16	14	15	15	14	15	15	15	15	15	14	15	15
P of *F*	0.080	0.198	0.236	0.531	0.576	0.461	0.912	0.520	0.767	0.419	0.280	0.437	0.932	0.467	0.748

Scores are separated according to whether the exchange was initiated by the subject ("Out") or by the exchangee ("In"); "All" represents the sum of "Out" + "In" scores; and *n* = number of subjects returning scores for that parameter; and *P* of *F* represents significance of main effect with respect to treatment.

All differences found significant were for those between control and androstenol groups, except (by the Scheffé test) a significant difference ($P < 0.05$) also existed between fatty acid and androstenol groups, in those instances marked "x"; *differences that were significant. None of the differences for females exchanging with females was significant.

and to the parameters of number × depth and depth × duration. In relation to number it was the mean score of all exchanges that was differentiated from the control ($P < 0.02$), but the pattern and direction of the change was indicated in the mean score of both outward and inward parameters, albeit some of the differences were not statistically significant.

Overall there was a greater degree of interaction of males with males than of females with males. This behavioural sex difference was obliterated following exposure to androstenol (due to the increase in scores of the female subjects), and was observed to a very much lesser extent following exposure to the fatty acids. The results are shown in Table 3a, as a ratio of the means for the male subjects exchanges with males vs the means for the female subjects exchanges with males. The ratio for the subjects exposed to androstenol showed little deviation from unity, indicating that the presence of androstenol modified the exchanges in a direction more characteristic of the males, whereas the ratios of the control sample were greater and this in many instances was by a considerable factor (Table 3a). There was some suggestion also that exposure to fatty acids had diminished the sex difference in scores, but the effect was small and less consistent compared with that seen in the androstenol-exposed sample.

The ratios of the number, depth and duration of male subjects exchanges with females to that of female subjects with females was nearer unity. This suggested that these scores for exchanges with females had been unaffected by androstenol, although exposure to fatty acids was not entirely without effect (Table 3b). Likewise, the ratio of males exchanges with males to that of males with females also underlines the lack of effect of treatment of the male subjects on the exchanges (Table 3c). Finally it was also evident, as revealed by the ratio of the females exchanges with females to that of females with males (Table 3d), that in the control condition (as with males) the females reacted with other females more than they did with males, but that this difference in behaviour was obliterated by exposure to androstenol and often also to fatty acids.

Some meaning may be attached to the relative degree of outward to inward exchanges, that is to the extent to which exchanges reported as initiated by the subject differed from those initiated by the exchangee. These ratios of mean "Out" and "In" scores are set out in Table 4. They indicate that in terms of most of the parameters the women recorded much more outward than inward exchanges only in the control condition and this was much more so with male than with female exchangees. When the women were in the androstenol condition or in the fatty acid condition however, the ratios of exchanges with males fell to around unity. Exposure to fatty acids seems to have had a similar effect in decreasing the Out/In ratio in female subjects exchanges with males, and little consistent effect in exchanges with other females. As regards the Out/In ratios for male subjects, these did not differ greatly from unity in any of the conditions, and thus seem to have been unaffected by treatment.

Table 3. Ratios derived from mean scores set out in Tables 2a and b

	Number			Depth			Duration			Number × depth			Depth × duration		
Treatment	Out	In	All	Out	In	All	Out	In	All	Out	In	All	Out	In	All
(a) Ratio of males exchanges with males to females exchanges with males															
Control	2.06	1.95	2.01	1.77	5.52	3.60	3.74	8.15	6.29	4.19	9.68	5.79	13.6	45.2	23.8
Androstenol	1.40	0.92	1.16	1.19	0.91	1.07	0.99	0.70	0.87	1.97	0.95	1.41	1.91	0.58	1.24
Fatty acids	1.77	1.10	1.45	1.82	1.14	1.64	1.75	1.85	1.85	3.70	1.43	2.60	2.89	2.25	2.88
(b) Ratio of males exchanges with females to females exchanges with females															
Control	0.63	0.95	0.75	0.66	0.74	0.69	1.06	1.04	0.99	0.53	0.72	0.59	1.08	0.79	0.90
Androstenol	0.71	0.68	0.70	0.66	1.01	0.73	0.74	1.16	0.87	0.50	0.97	0.56	0.93	1.28	0.96
Fatty acids	1.02	0.77	0.90	0.97	0.96	0.92	0.43	1.81	0.67	0.85	0.87	0.82	0.25	3.01	0.71
(c) Ratio of males exchanges with males to males exchanges with females															
Control	1.29	0.97	1.13	1.23	1.62	1.41	1.20	1.54	1.41	1.65	1.65	1.65	1.91	2.60	2.29
Androstenol	1.35	1.88	1.52	1.35	1.35	1.45	1.37	0.66	1.04	1.89	2.41	2.18	1.60	0.85	1.43
Fatty acids	1.17	0.93	1.07	0.99	0.88	1.01	1.55	0.89	1.34	1.32	0.75	1.13	2.11	0.59	1.14
(d) Ratio of females exchanges with females to females exchanges with males															
Control	2.52	2.11	2.35	2.18	4.63	3.68	2.94	5.10	4.52	4.77	8.14	5.90	6.61	22.1	11.6
Androstenol	1.45	0.72	1.09	1.33	0.67	1.01	0.97	0.92	0.95	2.07	0.41	1.15	1.28	0.53	0.90
Fatty acids	1.48	1.54	1.51	1.91	1.35	1.75	2.63	1.15	2.05	3.32	2.18	2.72	5.38	1.27	3.56

Ratios >2, or <0.5 are underlined.

Table 4. Ratios of "Outward" to "Inward" exchanges, derived from mean scores set out in Tables 2a and b

Treatment	Number	Depth	Duration	Number × depth	Depth × duration
			Females with males		
Control	1.35	2.74	2.95	3.41	5.15
Androstenol	1.03	0.90	1.16	0.81	0.88
Fatty acids	1.11	0.82	1.19	0.95	1.06
			Females with females		
Control	1.61	1.29	1.70	2.01	1.54
Androstenol	2.09	1.79	1.24	4.10	2.13
Fatty acids	1.07	1.17	2.72	1.44	4.46
			Males with males		
Control	1.43	0.88	1.35	1.48	1.55
Androstenol	2.18	1.18	1.64	1.67	2.90
Fatty acids	1.42	1.31	1.12	2.46	1.36
			Males with females		
Control	1.07	1.15	1.73	1.48	2.12
Androstenol	2.18	1.18	0.79	2.13	1.54
Fatty acids	1.42	1.18	0.65	1.41	0.38

Ratios of >2 and <0.5 may be considered significant, and are underlined.

DISCUSSION

Interpretation of the present study

Considering the natural setting of the experiment, which inevitably meant that an almost infinite number of variables were not controlled, it is perhaps surprising that any positive findings were obtained. On the other hand, the fact that clear differences relating to sex and to treatment were elicited when human individuals were interacting under "real life" circumstances, lends considerable weight to the social significance of the results. In our view, this conclusion is more strongly warranted than was the demonstration of a sex-related pheromonal effect previously observed in our assessment-of-people test [15].

The scores returned by the subjects in the present study, i.e. on the number, depth and duration of the exchanges they had during the first 2–3 h of the morning after the pheromonal exposure, the direction of the exchanges, and the derived parameters, number × depth and depth × duration, were first subjected to two-way ANOVA with respect to sex and treatment of subject, respectively. The analysis revealed a marked sex effect, but also some significant sex × treatment interactions. The data were therefore also examined by one-way ANOVA, with respect to treatment, and highly significant differences were then elicited.

The sex differences (Table 1) show that, irrespective of treatment (i.e. exposure to pheromonally active substances), these young men were significantly more "socially active", in terms of their interactions (or exchanges) with other male individuals, and perhaps also to a marginal extent with females, than were the young women. This observation is in itself irrelevant to the question of the pheromonal influences on social behaviour, but accords with common observation and with scientific analysis of sex differences in human behaviour (see e.g. [16–18]). On the other hand, the ANOVA did not elicit any significant differences (irrespective of treatment) in the exchanges of male subjects with female individuals compared with those of female subjects with females. At first sight, this is perhaps not what would be expected, and may have been a chance artefact of the situation, although when outwardly and inwardly directed exchanges were compared separately, some sex-dependent differences were seen (see below). There were no significant differences between men and women in any of the scores when exchanges were compared irrespective of both treatment and of sex of exchangee.

The one-way ANOVA drew out findings (Table 2) that show clearly that with the young women subjects, but not with the men, there was a conclusive treatment effect, which is apparent in all of the five parameters measured (Table 2b). There were no significant effects when comparing the fatty acid condition with the control condition, and the few significant differences between certain scores in the fatty acid condition and those in the androstenol condition may be a statistical artefact; the mean scores in the fatty acid condition were in most of these instances only marginally higher than those in the control condition.

The fatty acids used in our experiments consisted of a mixture of volatile short-chain acids (Copulin), in the relative proportions reported to occur in the vaginal fluid of women and to be under hormonal control [14,19,20]. The

pheromonal properties of this mixture of fatty acids from the vagina of primates was well established in a series of studies by Michael *et al.* (reviewed in [21–23]) to have a female > male sex releaser action. In our earlier studies with the assessment-of-people test [15], the vapour of the mixture was found to affect (more than did androstenol) the assessment by women of written descriptions of fictitious male applicants for a job, while having only marginal effects on judgements by men in this test.

It seemed of interest to determine whether the fatty acid mixture would have any effect on interpersonal interactions in the present behavioural test. As it turned out, any effects of the fatty acid vapour proved to be relatively slight compared to those of androstenol vapour, albeit often in the same direction. In view of the lack of any obvious structural similarity between the steroid and fatty acid pheromones, it would be surprising if they did induce similar behavioural effects. Moreover, there are important differences between the present experiment and the experiment with the assessment-of-people test. In the earlier study, the relative proportions of the fatty acids was based on that reported by Michael *et al.* [23] as characteristic of rhesus monkeys, whereas in the present study the composition was made up to resemble that found in the human vagina; the pheromonal efficacy of such a mixture may depend on the relative volatility of the component acids. Secondly, the pheromones were administered for a relatively brief period of time while the subjects were completing their written assessments, rather than overnight before the written test, and the results of the earlier test were more dependent on cognitive processes than is the recording and rating of social exchanges.

By contrast, in the present study of the women's exchanges with other females, where often higher scores were returned than for their exchanges with males, there were absolutely no treatment effects elicited, nor were any treatment effects found in the data from the male subjects (Table 2a).

Thus it is evident that, compared with those in the control condition or those exposed to the fatty acid mixture, the women exposed to androstenol showed substantially higher scores in our five parameters of exchange when they were interacting with men. The two derived parameters, especially that of depth × duration, appear to enhance this difference due to exposure to androstenol, suggesting that exposure to androstenol altered the women's behaviour in such a way as to intensify exchanges with men. The pheromone might perhaps operate by making the women feel more at ease with men, and/or more attractive to them or more attracted by them. Unfortunately, no specific record could be kept of exchanges of the experimental subjects between each other, which might have given indications about the operation of these factors.

The effect of exposure to androstenol on the behavioural exchanges of female subjects with respect to males is shown also in terms of ratios of mean scores (Tables 3a and d). Thus the unmistakable propensity of both men and women to interact normally (under the control condition) more with their own sex is obliterated by androstenol exposure of female subjects. This observation underlines that of an effect of androstenol on the women in increasing their scores for exchanges with men (Table 2b). The ratios in Tables 3b and c, on the other hand, show the lack of effect of androstenol (or of the fatty acids) in altering men's exchanges with either sex or of women's exchanges with their own sex. The ratios of Tables 3a and d that are affected by androstenol also tend to be lower than control for the fatty acid condition, indicating that the fatty acids may have had some (lesser) effect analogous to that of androstenol, although examination of Tables 2a and b shows that the fatty acids had a tendency to decrease scores of men as well as to increase those of women. Any attempt to interpret these marginal effects of the fatty acids would be problematic, as already indicated.

Lastly, we thought it was possible that pheromonal treatment might make people more (or less) outgoing or attractive, and that this might be revealed by alterations in the scores returned by the subjects for the exchanges in terms of direction, i.e. whether they or the exchangee initiated the exchange, "Out" scores vs "In" scores. The scores reported were somewhat complicated by the failure of the subjects to recollect in many instances whether it was they or the other person who initiated the exchange. Perhaps partly for this reason there were few very obvious cases where the treatment effect on any one parameter was exerted differently on Out scores than on In scores. However, it does appear that with females exchanges with males (but not for their exchanges with other females, or for males exchanges with either sex), both androstenol and the fatty acids decreased the

ratio of means of Out and In scores, which was well above unity in the control condition (Table 4). This may be attributable to an increase of inward exchanges of males to females when the latter had been exposed to androstenol (and to a lesser extent to the fatty acids). It would be rash to attach too much importance to this observation, but it is not inconsistent with the idea that exposure of females to androstenol (and perhaps to the fatty acids) renders them more "approachable" or "attractive".

In general terms, the study has clearly demonstrated the capacity of a substance with known pheromonal properties, 5α-16-androsten-3α-ol, to affect the social behaviour in a natural setting of young women exposed to its vapour overnight. The women exposed to the 16-androstene pheromone exercise (not necessarily consciously) showed an increased responsiveness to men, and this is apparent in all three of the main parameters of the test scores on exchanges i.e. number, duration and depth. It appears from our present findings that the 16-androstene has a communicating function, and that the behaviour which finds expression is not just an increase in the general level of activity. Rather, the actions are specific changes relating to judgements made about duration and degree of involvement and about alterations in the direction of the exchanges. Both partners (male and female) may benefit from the transaction, but it is evident that the behavioural changes are restricted to females; clearly, from a sociobiological point of view the benefit would be to the male signaller as the source of the pheromone.

The 16-androstene steroid, 5α-16-androsten-3α-ol, along with its immediate metabolic precursor, 5α-16-androsten-3-one, were discovered 20 years ago to act as male > female sex releaser pheromones in the pig [24], and over the years several studies have provided evidence for pheromonal effects of one or both of these steroids in man [e.g. 15, 25–32], although others have failed to find an effect [33]. (For reviews on the 16-androstenes see [34–37]).

In spite of their established action in rousing oestrous sows to be sexually receptive, and in spite of their much greater concentration in human male than in female urine [38], blood [39], saliva [40] and exocrine secretions [37, 41, 42], we lack any firm knowledge, at least in humans, about the effects of 16-androstenes on female sexual receptivity [43, 44]; for reviews on relevant sexual behaviour in primates see [45, 46]. The mere fact that they do act as pheromones in man has, however, far-reaching implications for social behaviour.

General considerations

Pheromones (in the form of scents) have a long evolutionary history, and provide a means of recognition of self, kin and strangers. The role of pheromones in human sexual and social behaviour is filled with uncertainty [47], and the techniques for the assessment of behaviour we have used here and elsewhere [15, 26] remain exploratory. Nevertheless, man's phylogenetic and ontogenetic history suggests that there is much to be gained from a comparative approach, and human studies on pheromones are often modelled on work on other species [12, 22, 23]. The taxonomic diversity over which underlying structural and functional features have continuity is impressive, but there remains a reluctance to apply the same principles of continuity to behaviour. The conservation of biochemical elements across species [48], and their retention through the evolution of exocrine, endocrine and nervous systems, suggests the value of a similar comparative approach in relation to human behaviour.

With the retention of the structural and functional components of the olfactory system we would expect to see a maintenance, through the pressures of selection, of the molecular mechanisms involved in coding and transducing those selected substances that have proved effective outside the organism in fostering its own genetic enhancement. Foremost amongst such substances would be those pheromones which facilitate communication, and manipulation, between the sexes. The mechanism entails a biochemical system that provides feedback to the self about the self, and there would also be feedback from individuals that represented an extension of the self. (See studies by Yamazaki *et al.* [49, 50, 51].)

The evident restriction to females of the effects observed in the present experiment raises the question as to whether olfactory cues act differently in females from the way they do in males; Keverne [44] considers that they may indeed be less important in the sexual behaviour of the female. In most mammals, however, females are attracted to normal male urine in preference to that from castrates, but further attractivity is vested mainly in the female while males are the active pursuers. Differences in motor activity induced by pheromones in developing laboratory rodents depend on sex as

ɔn age [52–54], while adult human fe-
e more sensitive to the odour of an-
l than are men [55]. (The reader is
particularly to [8, 56, 57] regarding de-
ntal aspects in man). Furthermore,
marked changes in structure and in the
s of the glands of the axillae with the
puberty, as well as differences between
s in the increased production of se-
associated with gonadal changes which
e to some extent the characteristic di-
odours that remain through adulthood
l in [8, 58]). Thus, the concentration
drostene steroids is higher in axillary
men than in women [41, 42, 59]; indeed
pheromones may affect human men-
ycles [8, 27, 37, 60–62]. Moreover, the
androstenol can be shown to be long
16-Androstenes are implicated in the
ion of puberty in pigs [63], and in the
similar acceleration occurs with ex-
androstenol [64]. Jackson, working in
atory (unpublished) and using a cross-
gn in her experiments with the Bem [65]
sment inventory of subjects own sex
tity, was able to show that the effects
tial exposure to androstenol can influ-
sequent test scores after a two week
n the studies we have reported, it
that exposure to androstenol induces
:h" responses in females. Women,
ɔecause of the absence of the masculin-
ion of hormones on the brain early
are the responsive partners and the
r expressed can be cast in a diversity of

ements—The study was carried out at Hatfield
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