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Psychophysical evaluation of responses to pleasant and mal-odour stimulation in human subjects; adaptation, dose response and gender differences

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Abstract

A psychophysical detection test was used to measure the response of human subjects to 'good' and 'bad' smells. Different intensities and frequencies of odour stimulation were delivered by an olfactometer and the responses to a group of malodours (valeric acid, skatol, butyric acid) and pleasant smells (amyl acetate, *cis*-3-hexenol, linalool) were compared. A mathematical model, a power equation, was used to fit the three-dimensional data plots (dose vs. stimulus frequency vs. response). The model was able to distinguish between malodours and pleasant odours on the basis of the values of parameters describing dose–response and adaptation/habituation. We show that the olfactory system adapts/habituates more rapidly to malodours than to pleasant smells, but is much more sensitive to changes in stimulation by malodours than pleasant odours. The degree of adaptation is inversely proportional to stimulus strength. The response profile for women was different to that of men for certain odours, in particular valeric acid, skatol and *cis*-3-hexenol. The difference lay in their sensitivity and the slope and range of the dose response. Thus, we have shown for the first time that the olfactory system adapts more readily to 'bad' smells than 'good' smells, and that it has a broader range of adaptation for bad smells. As a consequence, the olfactory system is specially responsive to changes in potential olfactory warning signals.

Keywords: Smell; Olfactory system; Odour; Psychology of smell

1. Introduction

As adults we display distinct odour preferences and, allowing for some minor individual and gender differences, readily discriminate between pleasant smells and malodours. Unfamiliar smells are generally judged as unpleasant (Engen, 1991), and it is believed that odour hedonics are acquired (Engen, 1988) and context-dependent (King, 1988). However, there is still debate as to whether there are innate odour preferences (Porter and Schaal, 1995). Steiner (1979) demonstrated that 1-day-old infants exhibited 'attraction' or 'rejection' of pleasant and unpleasant odours, respectively, as judged by their facial expressions but

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Engen (1982), using a similar experimental protocol, failed to find differences elicited by pleasant (amyl acetate) and unpleasant (butyric acid) odour stimuli. The situation is complicated by the fact that there is prenatal chemoreception and human foetuses learn odours from their pregnant mother's diet (Schaal et al., 2000).

Discrimination between 'good' and 'bad' smells is important since pleasant and unpleasant smells require different behavioural responses. Bad smells warn us of danger, poor air quality, 'off' food, poisons, even illness—each of which requires some immediate decision to be made and action to be taken, for example avoidance or withdrawal. Pleasant smells, on the other hand, do not necessitate immediate actions or decisions. In fact, the biological significance of pleasant smells is not immediately obvious. Recent evidence suggests that malodours activate different areas of the brain from 'pleasant' odours (Kettenman et al., 1997; Levy et al., 1997; Zald and Pardo, 1997, 2000; Fulbright et al., 1998). Greater left than right frontal EEG activation was observed with a pleasant odour (vanillin) compared to an unpleasant odour (valerian) (Kline et al., 2000) in keeping with the observation that unpleasant emotions seem to be processed predominantly by the right hemisphere (Dimond et al., 1976). The detection and processing of malodours is more urgent, and therefore one might predict that the dose–response relationships and adaptation/habituation kinetics would be different for malodours vs. non-malodours. In particular, it would be important not to adapt too quickly to malodours and to be more sensitive to low concentrations of malodours. While previous studies point to neurophysiological differences in the handling of certain odour qualities, the psychological dimension of those differences—beyond the simple hedonic division, is unknown. The present study is the first step in identifying processes that underlie these physiological differences and set out to test the hypotheses that the olfactory system would; (1) adapt more slowly, and (2) exhibit a shallower dose–response curve, to malodours compared to pleasant smells.

Gender differences in olfactory sensitivity have been reported. Thus, in order to determine such differences between odours with varying hedonic qualities, the responses of men and women were assessed separately.

To assess adaptation/habituation we used a repetitive odour pulse detection paradigm. Increasing the stimulus frequency causes the receptors to adapt and the central processors to habituate. At high pulse frequencies the stimulus tends towards a constant odour. Thus, by measuring responses to repetitive stimulation, we can obtain information about adaptation/habituation that is, by extrapolation, relevant to a constant stimulus.

2. Methods

2.1. Olfactometry

Odour stimulation was achieved using an olfactometer based on a design by Lorig et al. (1999). Air was pumped by a microprocessor controlled pump (J.D. Technical Services, Old Ynysybwl, Wales, UK), split two ways and connected in parallel to two flow meters (Platon Flowbits, Basingstoke, UK) set to 1 l min^{-1} and 2 l min^{-1}. The outputs of the flow meters were connected to Teflon-lined solenoid three-way valves (Cole Palmer, Bishops Stortford, UK) via Teflon tubing (2 mm i.d., 3 mm o.d., The Hose Centre, Cardiff, UK). The solenoid valves were switched by Darlington drivers under computer control via the digital output of an A/D converter (CED 1401, Cambridge, UK). At the output of the valves, air from the two parallel lines was fed to 25-ml glass reservoirs, containing either warm water, to humidify the air, or odour. The reservoirs were seated in a water bath maintained at 40 °C. The air emerged from the olfactometer at 24 °C (room temperature) and 70% humidity. One continuous flow air line acted as the dilution line (2 l min^{-1}), and this was recombined with the control air line (1 l min^{-1}) in parallel with an odour line just before the two lines reached the nose (final flow rate = 3 l min^{-1}). Under normal conditions the odour line was closed (by solenoid valves). The odour vapour was fed into the continuous flow line by switching off the control line and switching on the odour

line simultaneously, thus ensuring no change in flow rate or pressure. The rise time of the odour pulse was ≈10 ms.

A single tube, inserted through a self-expanding bung (ear protector, Aearo Ltd., Stockport, UK), entered the nose. When fully expanded, the foam bung completely blocked the nose, preventing backflow, and forcing the air to pass through the nasopharynx into the oral cavity. The control air was switched to the odour reservoir when a stimulus was required. Pulses of odorised air could therefore be injected into a continuous airstream without altering the flow rate. This arrangement prevented the activation of thermo- or mechanoreceptors. Subjects were instructed to breathe through their mouths.

2.2. Odorants

Chemicals used were of the highest purity (minimum 99%); *N*-amyl acetate (Sigma, Poole, Dorset, UK), linalool (DL-3,7-dimethyl-3-hydroxy-1,6-octadiene, from Sigma) and *cis*-3-hexen-1-ol (BBA, Blackhorse Lane, London[1]) were used as pleasant odours and *n*-butyric acid (Sigma), *n*-valeric acid (Sigma) (1% in dipropylene glycol) and skatol (BBA), [1% in dipropylene glycol (Sigma)] were used as malodours. The odour chemicals were added to the reservoirs. Odour stimuli were presented in a series of between 10 and 15 pulses of the saturated vapour in the reservoirs for each concentration. The stimulus dose was varied by altering the duration of the odour pulse. This has the advantage over standard air-dilution techniques (where the pulse length is kept constant and the concentration varied) in that the flow rate of odorant molecules over the receptors is maintained constant for all stimulus intensities. The dose is the same since, as stated by the Bunsen–Roscoe law (Bunsen and Roscoe, 1855), the biological effect is dependent only on the product of the stimulus intensity and duration of exposure (Intensity × Time = Constant), irrespective of the absolute values of either quantity.

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The concentrations of the odorants in the reservoirs, determined from their vapour pressure at 20 °C, were as follows:

	Concentration (ppm)
Amyl acetate	5263
Linalool	66
cis-3-Hexenol	5132
Butyric acid	921
Valeric acid	1.3
Skatol	0.03

These concentrations were chosen empirically to give a detection rate on the rising phase of the dose response curve (a non-zero second derivative). In this way the range of responses were between 0 and 30% correct at the low concentration end of the curve to near 100% correct at the high concentration end.

The total flow rate was 3 l min^{-1} and the odour line was diluted 1:3, thus 16.6 ml s^{-1} of each odorant was delivered to the nostril. Pulse widths were 35, 50, 75, 100 and 200 ms, allowing 1.75, 2.5, 3.75, 5 and 10 ml of the air-diluted odorants of the concentrations given in the table to enter the nose.

2.3. Subjects

Subjects, 10 for each odour (five males and five females) except amyl acetate ($n=12$), were between 18 and 25 years old from the student population of the University and none had a history of olfactory dysfunction or respiratory disease. The protocol was explained and informed consent obtained. During the experiment the subjects were seated in a comfortable chair in a test booth with a controlled environment. They were given a visual stimulus (silent cartoons on a 12-cm TV screen) that maintained alertness. The subjects wore headphones through which a white noise was played to eliminate auditory cues. They were given a button to press for the psychometric test so they could record odour pulse detection and instructed to breathe through their mouths.

2.4. Psychophysical tests

Subjects were presented with a series of odour pulse stimuli, referred to as 'blocks'. Within a block each pulse had the same duration and inter-stimulus interval (ISI). Blocks of different stimulus strengths were given with varying inter-stimulus intervals (2.5, 5, 10 and 60 s) in random order and with a 2-min break between each series to allow for recovery from adaptation/habituation. Each experiment lasted approximately 90 min. The timing and number of pulses was stored on the computer. The stimulus blocks were randomised in order to prevent learning and anticipation on the part of the subjects. The subjects were asked to indicate when they detected an odour pulse by pressing a button. This sent a signal to a computer via the laboratory interface and these signals, along with the pulse information, were stored for off-line analysis using SIGNAL software (CED, Cambridge, UK). The results were expressed as the percent of correctly detected odour pulses.

2.5. Regression analysis of data

The dose (pulse duration), ISI and detection rate (% correct) were plotted as three-dimensional graphs. Non-linear regression analysis was performed using three-dimensional curve fitting of a model (Eq. (1)) to the data. The curve fitter (SigmaPlot, SPSS Science, Chicago) uses the Marquardt–Levenberg algorithm to find the parameters of the independent variables that give the best fit between the equation and the data. This alogorithm seeks the values of the parameters that minimise the sum of the squared differences between the observed and predicted values of the dependent variable by an iterative process.

$$z = y_0 + a(1 - b^x) + c(1 - d^y) \quad (1)$$

where z is the percentage of odour pulses correctly identified, y is stimulus strength (pulse width) and x is the inter-stimulus interval (ISI). The term y_0 determines the sensitivity of the subjects to the odour, the larger (less negative) the value the more sensitive the subjects. The fitted parameters 'a' and 'b' define the effects of ISI on the dependent variable, and the parameters 'c' and 'd' define the effects of pulse length on the dependent variable.

While this empirical model makes no assumptions about the processes underlying olfactory transduction, it reflects the previous observation that the perception of odour increases as a power function of increasing concentration (Cain, 1978). We have used this approach previously (Wang et al., 2001, 2002) to compare perceptual and physiological responses to a single odorant.

2.6. Statistics

Comparison of responses to different odours; a 3-factor [ISI (4) × pulse duration (5) × odour (6)] analysis of variance, ANOVA, was performed where pulse width and ISI were repeated in the same person for a given odour (within subjects factors), but different sets of people were used for each odour (between subjects factor).

The mean values of the fitted parameters generated by Eq. (1) from data in Figs. 1 and 2 were compared using the Ryan–Einot–Gabriel–Welsch multiple step-down procedure (R–E–G–W post hoc Q-test) based on the Studentized range.

3. Results

The detection rate for all odours declined as the stimulus frequency increased, a process known as adaptation (a peripheral process) or habituation (a central phenomenon). In addition, for most odours there was a clear relationship between stimulus dose (duration of the odour pulse) and detection rate; the detection rate increased with increasing odour dose. The percent detection rate therefore depended upon both the duration of the odour pulse and the stimulus frequency (Figs. 1 and 2). The data obtained from different odorants was compared by fitting an empirical model (Eq. (1)) to the data (see Table 1).

3.1. Comparisons between pleasant and unpleasant odours

The data for the pleasant (Fig. 1) and malodours (Fig. 2) were compared. From these comparisons it emerged that firstly, there were no differences

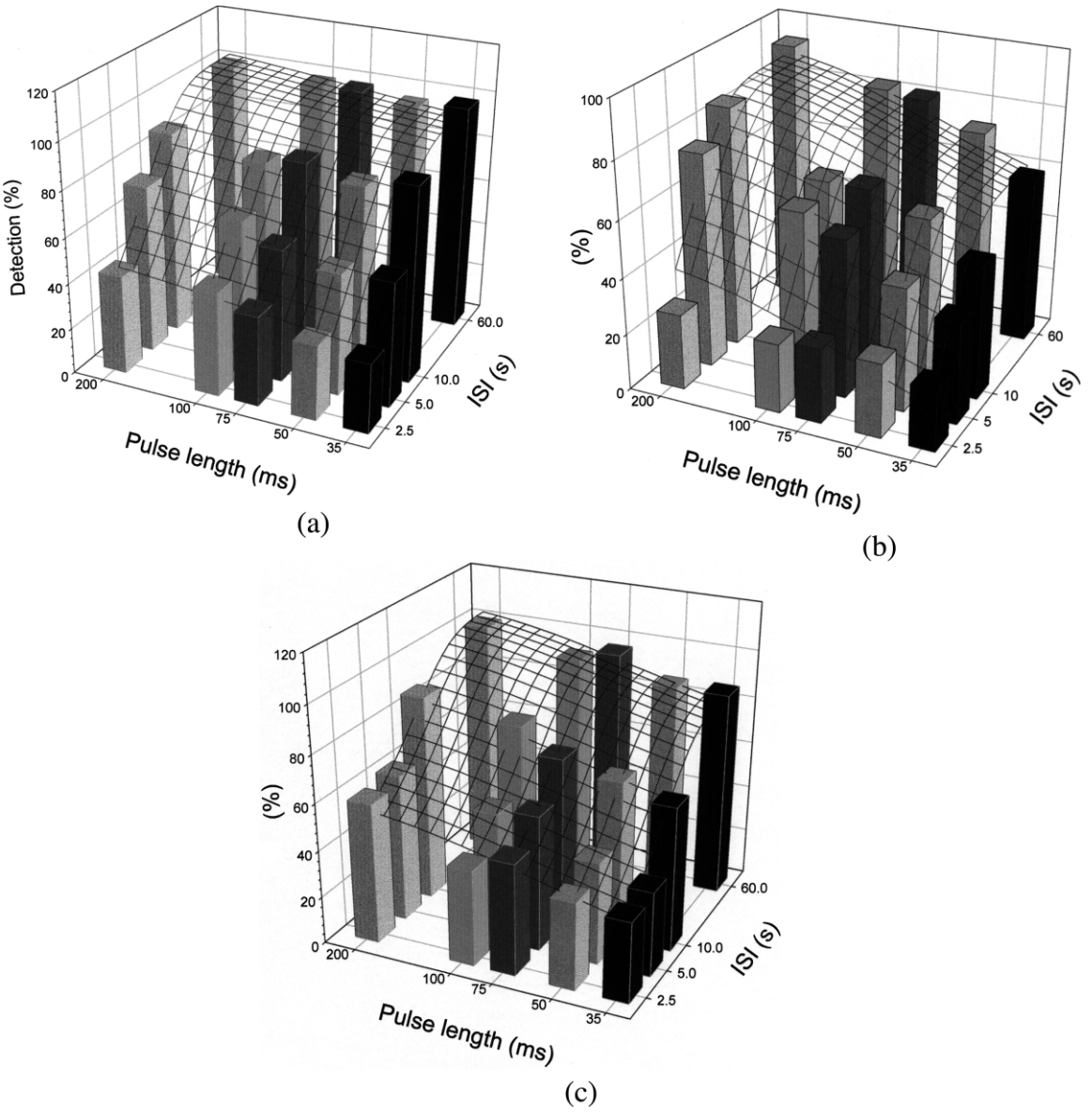

Fig. 1. Dose–stimulus frequency–response plots for 'pleasant' odours. Odour pulses of different durations [pulse length (ms)] and interstimulus intervals [ISI (s)] were delivered by olfactometry and subjects were required to press a button when they detected an odour pulse. The detection rate is expressed as the number of correctly detected odour pulses as a percentage of the total number of pulses delivered. For each odour, five females and five males were tested unless otherwise indicated. The mesh plot is a regression fit of Eq. (1) to the data. The values of the fitted parameters are: (a) *cis*-3-hexenol, $y_0 = -11.6 \pm 8.6$, $a = 98.9 \pm 5.5$, $b = 0.821 \pm 0.015$, $c = 18.6 \pm 4.5$, $d = 0.989 \pm 0.010$; (b) amyl acetate ($n = 12$), $y_0 = -60.0 \pm 22.9$, $a = 100.5 \pm 16.4$, $b = 0.752 \pm 0.046$, $c = 51.1 \pm 12.0$, $d = 0.984 \pm 0.008$; and (c) linalool, $y_0 = -3.77 \pm 11.2$, $a = 68.9 \pm 5.0$, $b = 0.889 \pm 0.015$, $c = 41.5 \pm 8.0$, $d = 0.985 \pm 0.007$.

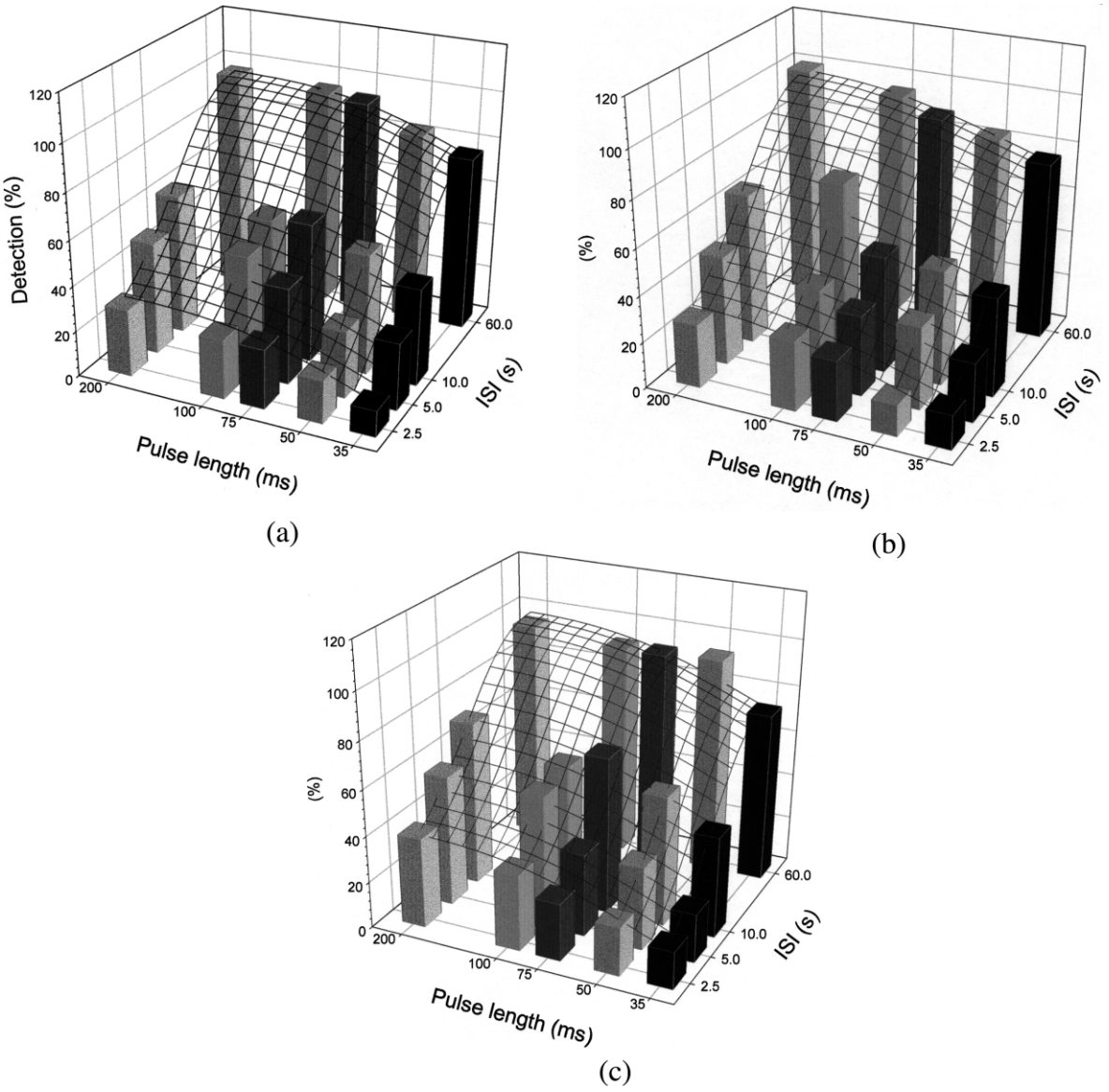

Fig. 2. Dose–stimulus frequency–response plots for malodours. Odour pulses of different durations [pulse length (ms)] and inter-stimulus intervals [ISI (s)] were delivered by olfactometry and subjects were required to press a button when they detected an odour pulse. The detection rate is expressed as the number of correctly detected odour pulses as a percentage of the total number of pulses delivered. For each odour, five females and five males were tested unless otherwise indicated. The mesh plot is a regression fit of Eq. (1) to the data. The values of the fitted parameters are: (a) butyric acid, $y_0 = -55.6 \pm 21.9$, $a = 82.7 \pm 3.1$, $b = 0.910 \pm 0.007$, $c = 67.1 \pm 20.8$, $d = 0.967 \pm 0.009$; (b) skatol, $y_0 = -37.6 \pm 18.2$, $a = 85.0 \pm 4.8$, $b = 0.907 \pm 0.011$, $c = 51.8 \pm 16.1$, $d = 0.976 \pm 0.009$; and (c) valeric acid, $y_0 = -48.7 \pm 25.0$, $a = 80.3 \pm 5.0$, $b = 0.905 \pm 0.012$, $c = 68.3 \pm 23.1$, $d = 0.971 \pm 0.010$.

Table 1
Odour differences; comparison of the 3-D fits of detection rates for different concentrations and interstimulus interval (ISI) of odorants of odorants using regression analysis [see Eq. (1)]

	Butyric acid	Valeric acid	Skatol	*cis*-3-Hexenol	Amyl acetate	Linalool
Butyric acid	–	ns[c]	ns	a^a, b^b	b^a	$y_0{}^b$
Valeric acid	–	–	ns	a^a, b^b	b^a	ns
Skatol	–	–	–	b^b, c^a	b^b	a^a
cis-3-Hexenol	–	–	–	–	$y_0{}^a$, c^a	a^b, b^a
Amyl acetate	–	–	–	–	–	$y_0{}^a$, b^a

Parameters are included in the table if a significant difference was found. Significance tested by R–E–G–W post hoc *Q*-test for multiple comparisons (see Section 2). The degree of significance is indicated for each parameter as appropriate. Parameters '*a*' and '*b*' relate to the interstimulus interval, '*c*' and '*d*' related to pulse duration, and 'y_0' relates to sensitivity.
[a] Significant, $P<0.01$.
[b] Significant, $P<0.05$.
[c] ns = not significant.

between the responses to the malodours. There were, however, differences between the malodours and the other, pleasant odours (with the exception of valeric acid and linalool).

Secondly, the main differences between pleasant and malodour responses were in the values of the parameters which relate to stimulus frequency and adaptation/habituation ('*a*', '*b*').

A 3-factor analysis of variance (see Section 2.6) found no significant difference between any of the malodours, but that each malodour was different from each non-malodour with a significance of $P<0.05$, or less, with one exception; valeric acid vs. linalool (the reason for this exception is explained below).

3.2. Analysis of gender differences in odour detection

There were significant gender differences in the detection rates for valeric acid, skatol, and *cis*-3-hexenol (Table 2). In particular, the parameter '*c*' was different between the genders for valeric acid and skatol (as well as for the pooled malodours). The parameters which determine the range ('*c*') and steepness ('*d*') of the slope of the dose–response curve, were generally lower in women because they were at the top of their dynamic range. In each case where there was a gender difference, women had less negative sensitivity parameter 'y_0', but unless indicated in Table 2, the

Table 2
Gender odour differences; comparison of the gender responses determined by 3-D regression fits of detection rates for different concentrations and stimulus frequencies of odorants

	Women ($n=5$) vs. men ($n=5$)
Pooled malodours	$y_0{}^b$ (women $= -14.8 \pm 9.2$, men $= -77.5 \pm 21.7$) c^a (women $= 30.8 \pm 7.9$, men $= 93.7 \pm 20.2$)
Butyric acid	ns
Valeric acid	$y_0{}^a$ (women $= -9.3 \pm 16.1$, men $= -113.0 \pm 45.5$) c^a (women $= 37.6 \pm 10.8$, men $= 131.4 \pm 43.0$)
Skatol	c^a (women $= 32.3 \pm 32.3$, men $= 71.4 \pm 10.0$)
Pooled pleasant odours	ns
cis-3-Hexenol	a^a (women $= 90.7 \pm 8.8$, men $= 113.6 \pm 5.3$)
Amyl acetate	ns
Linalool	ns

The degree of significance (Student's *t*-test) is indicated for each parameter as appropriate. Parameters '*a*' and '*b*' relate to the interstimulus interval, '*c*' and '*d*' related to pulse duration and 'y_0' relates to the sensitivity. Means ± S.D. are given in brackets.
[a] $P<0.05$.
[b] $P<0.01$.

standard error was too large and the means were not significantly different.

The degree of adaptation/habituation (described by parameters '*a*' and '*b*') did not vary significantly between genders except in the case of *cis*-3-hexenol where there was a slight difference; $'a'_{(\text{women})} = 90.7 \pm 8.8$ vs. $'a'_{(\text{men})} = 113.5 \pm 5.3$. This means that women adapted less than men.

While there were apparent differences in both the sensitivity parameter ('y_0') and the stimulus dose parameter ('*c*') for valeric acid vs. linalool, significance was nearly, but not quite achieved ($P = 0.1$). Upon further analysis it was apparent that men and women responded very differently to these two odours in particular. There was a significant difference for the sensitivity parameter 'y_0' when the genders were analysed separately. The response of the men was significantly different (valeric acid vs. linalool: $y_{0\ (\text{men})} = -112 \pm 45.6$ vs. 10.6 ± 8.8, $P < 0.01$), but although there was a difference in the means for the response of women ($y_{0\ (\text{women})} = -9.3 \pm 16.1$ vs. 36.7 ± 31.4), this was not significant. This result was due to one female subject producing erratic responses (detection rate and odour dose inversely correlated). When this subject was omitted the results achieved significance ($P < 0.05$).

3.3. Analysis of malodour and pleasant odour differences

The differences between odours emerges in the parameter plots (Fig. 3). In this figure pairs of parameters, obtained from fits of Eq. (1) to the data, are plotted against each other. It is immediately clear that the malodours group together. This is not the case for the pleasant odours. In the plots of the sensitivity, y_0, vs. parameters '*a*', '*b*' (both relating to ISI) and '*c*' (relating to dose response) the malodours cluster away from the pleasant smells (Fig. 3a,b,c,d). The three malodours cluster very close together in the plot of the ISI parameters ('*a*' vs. '*b*') (Fig. 3c) indicating the importance of ISI in malodour/pleasant odour discrimination. In the plot of other dose–response parameters ('*c*' vs. '*d*') the malodours form a looser cluster but are still well separated from the pleasant odours (Fig. 3f).

The clustering of the malodours away from non-malodours in this manner in Fig. 3, both in terms of factors relating to ISI and concentration, suggests that the olfactory system responds to malodours as a group in a different way to that which it responds to non-malodours. This may enable the olfactory system to identify malodours more rapidly, a point that is returned to in the discussion.

3.4. Adaptation/habituation

From the foregoing analysis it appeared that the rate of adaptation/habituation discriminated between malodours and pleasant smells. We therefore measured the degree of adaptation/habituation for each odour and compared them. To do this we used the pulse frequency that gave a 50% detection rate—borrowing from the concept of the 'IC_{50}' (the concentration of inhibitor giving 50% inhibition) in receptor pharmacology. In Fig. 4, the interstimulus interval (ISI) is plotted against detection rate (%correct) for each pulse duration for a malodour (butyric acid, Fig. 4a) and a non-malodour (amyl acetate, Fig. 4b). From these plots the ISI at which the subjects achieved 50% detection, ISI_{50}, was determined by fitting a two-parameter, single exponential equation ($y = a(1 - e^{-bx})$ – Eq. 2) to the data. The ISI_{50} is then plotted as a function of pulse duration (Fig. 5a). From this plot it can be seen that there is a distinct difference between the malodours (solid symbols/lines) and the pleasant smells (open symbols/dashed lines). The ISI_{50} changed as a function of odour strength far more for malodours than for pleasant smells. As odour strength increased, more rapid pulses were needed to reduce the detection rate to 50%. This separation between the two categories of odour is demonstrated further by plotting the ISI_{50} for each odour (Fig. 5b). For amyl acetate there is very little change in the ISI_{50} with stimulus strength, whereas there is a very large change of ISI_{50} with stimulus strength for valeric acid. Thus, the detection curves for the malodours, from being quite shallow, become steeper with increasing stimulus strength, whereas for pleasant smells the curve starts relatively steep and does not alter a great deal (see Fig. 4b). However, at low stimulus strengths, there is much more adaptation in malo-

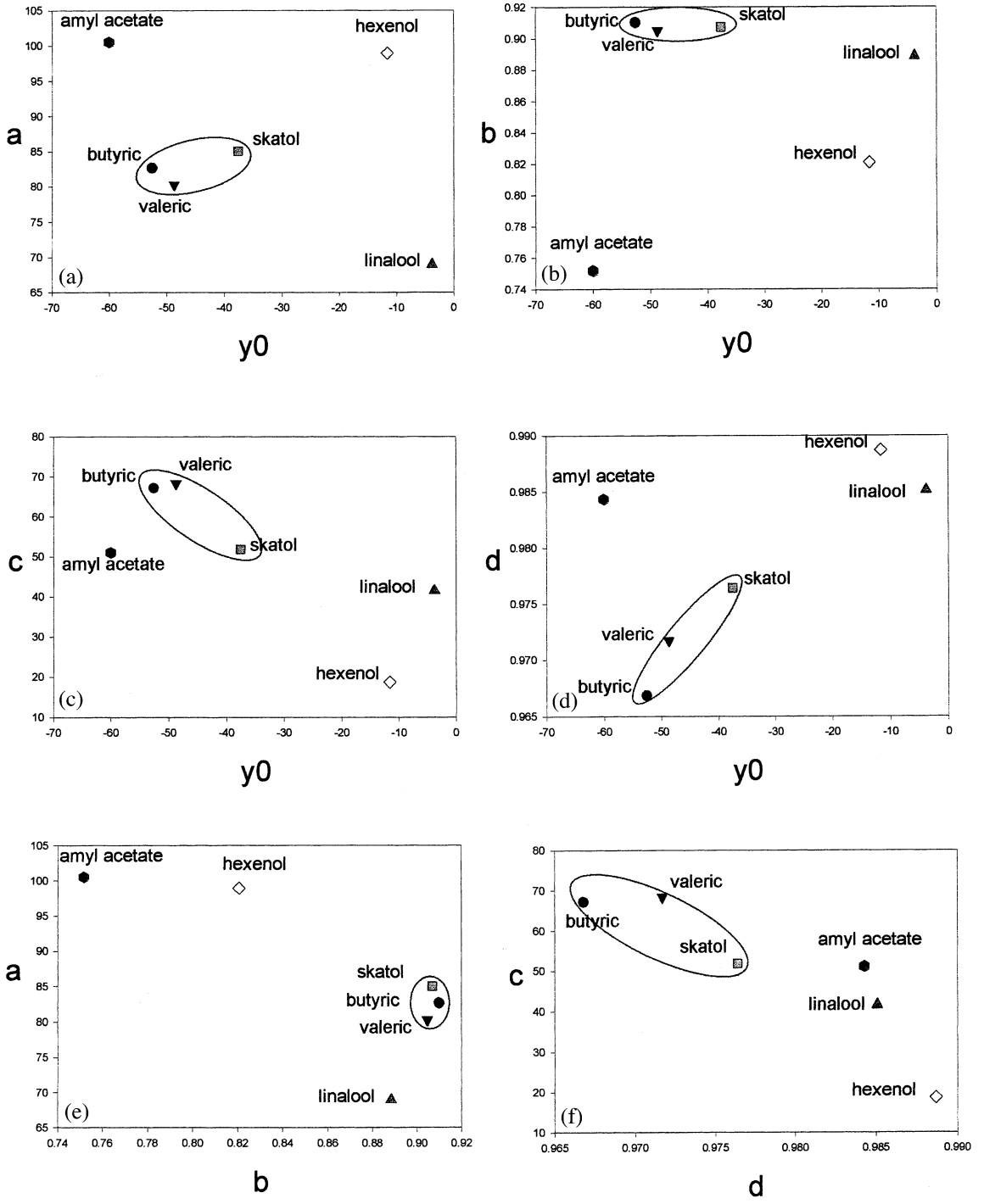

Fig. 3. Plots of parameters generated by fitting the model [Eq. (1)] to the data. Sensitivity ('y_0') is plotted against the parameters '*a*' (a), '*b*' (b), '*c*' (c) and '*d*' (d). The parameters '*a*' and '*b*' (e) relate to adaptation/habituation, and the parameters '*c*' and '*d*' (f) relate to dose response (see text for further explanation). The ellipses indicate the clustering of the malodours (butyric acid, valeric acid and skatol).

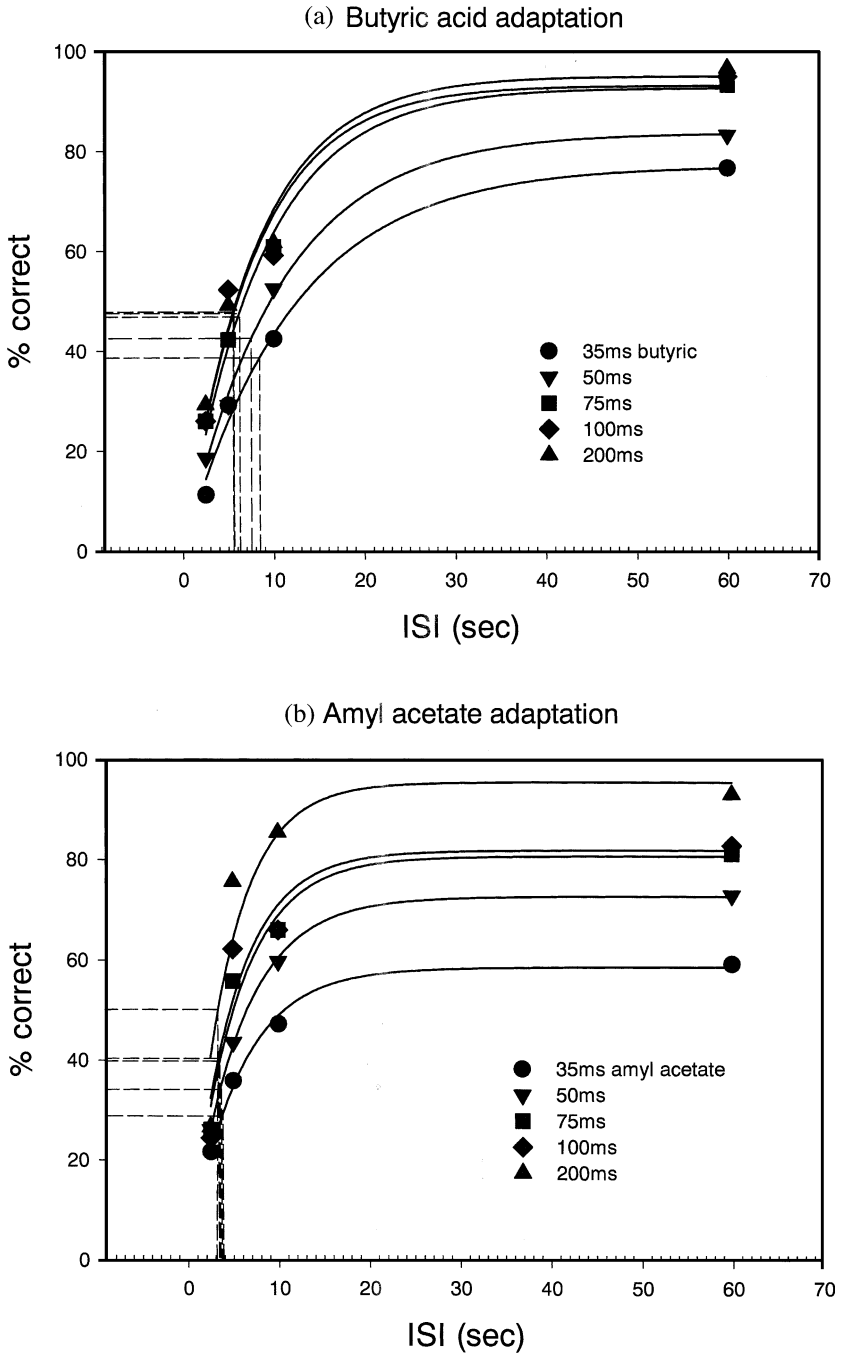

Fig. 4. Adaptation curves for (a) butyric acid and (b) amyl acetate. Each curve represents a different stimulus strength (pulse width) and the solid lines are fits of a 2-parameter single exponential equation, $y=a(1-e^{-bx})$ [Eq. 2], to the data. The dotted lines represent the frequencies at which detection is 50% of maximum (ISI_{50}).

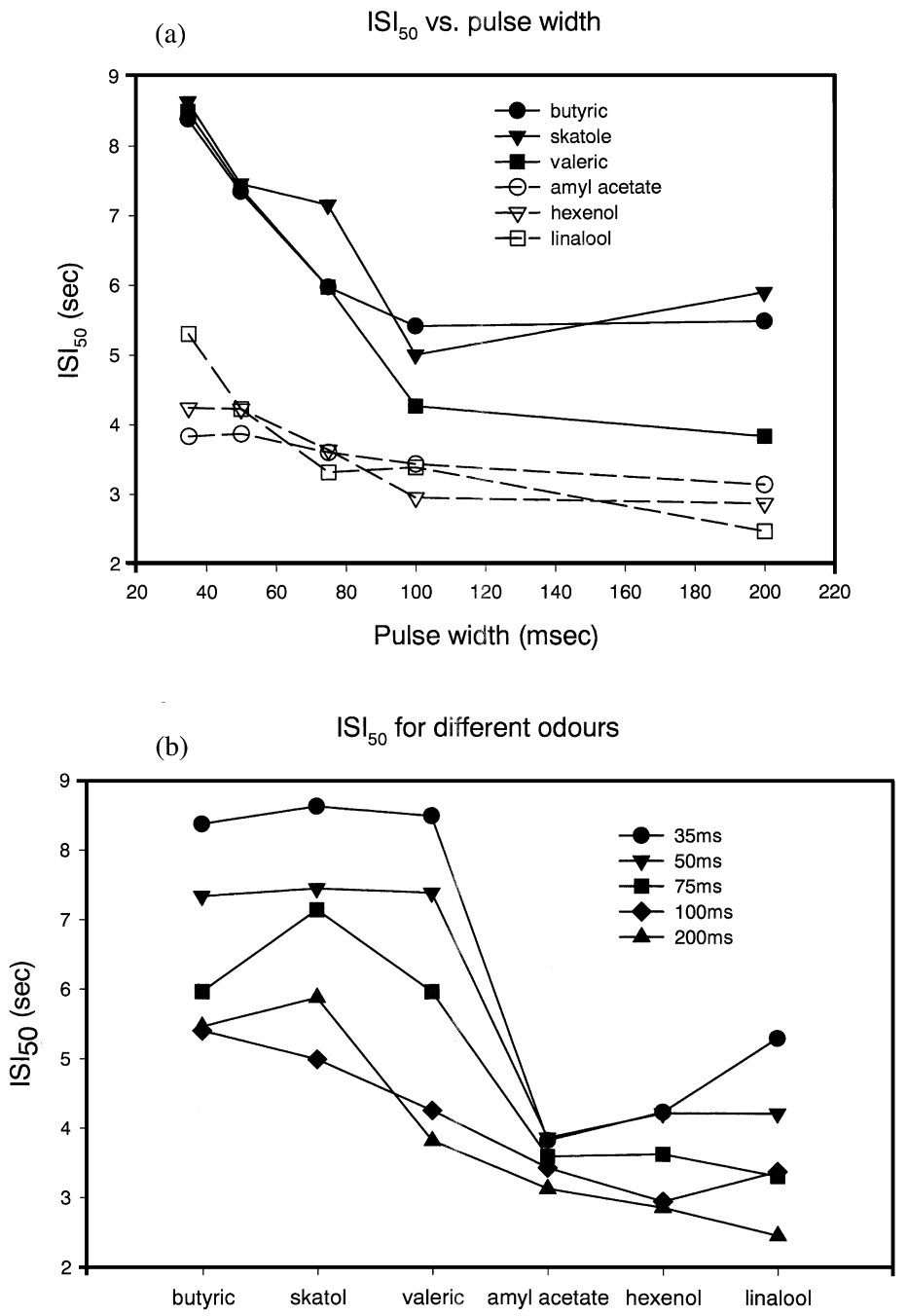

Fig. 5. Adaptation curves for different odours. (a) Adaptation plotted for different odours. The stimulus frequency at which the detection rate is 50% (ISI_{50}) gives the degree of adaptation of the olfactory system. The ISI_{50} values were obtained from the fits of Eq. 2 as illustrated in Fig. 4. The equation was fitted to the ISI vs. detection (%) data for each odorant ($n=10$ for all odours except amyl acetate where $n=12$). There is an inverse relationship between adaptation and stimulus strength, which is steeper for malodours than for pleasant smells. (b) Adaptation curves plotted as a stimulus strength (pulse width). There is a large change in the degree of adaptation (ISI_{50}) in malodours (solid symbols/lines), but much less for pleasant odours (open symbols/dashed lines)—almost none in the case of hexenol.

dours than pleasant smells (see 35 ms line in Fig. 5b). For example, the ISI_{50} for valeric acid is 8.5 s for the 35 ms pulse, whereas it is 3.8 s for amyl acetate. Only when the pulse width is increased to 200 ms do valeric and amyl acetate exhibit a similar degree of adaptation (3.8 s and 3.1 s, respectively). The consequence of this is that the olfactory system would be much more sensitive to changes in malodour stimulation than changes in stimulation with pleasant smells.

4. Discussion

The first hypothesis, that the olfactory system would adapt/habituate more slowly to malodours than to pleasant smells was not sustained. In fact, the reverse proved to be the case; the olfactory system adapts more rapidly to malodours, at least on the basis of a psychophysical test of perception.

The second hypothesis, that there would be a steeper dose–response to malodours than to pleasant smells was also not sustained. There were no major differences in the dose–response curves between these two broad classes of odour.

4.1. Responses to malodours and pleasant odours are different

Human subjects responded differently to malodours and pleasant smells. The three malodours used in this study (valeric acid, butyric acid and skatol) had similar dose and frequency response histograms (Fig. 2). The individual malodour data can be clearly separated from the pleasant odours on the basis of the fit of an empirical model to the data using regression analysis (Fig. 3) and the slopes of the frequency–response curves (Fig. 4). The malodour parameters were very similar to one another and significantly different to the non-malodours (see Table 1) in every case (with the exception of valeric acid vs. linalool, the reason for which is given in Section 3).

When the parameters, generated by the model [Eq. (1)], were plotted (Fig. 3), pleasant odours were widely distributed in two-dimensional space no matter which combination of parameter pairs was chosen. Malodours on the other hand, tended to cluster in most of the plots. In particular, it was the parameters controlling adaptation/habituation ('a', 'b') and sensitivity ('y_0'), which discriminated best between malodours and the rest of the odours. Odour concentration, while it segregated valeric and butyric acids, did not always produce such a close association of all malodours. Thus, it is not odour concentration which distinguishes malodours from pleasant odours, but the sensitivity of the olfactory system and the degree and rate of adaptation/habituation. This is clearly demonstrated when considering the stimulus frequency at which pulse detection was 50% (ISI_{50}). At this frequency the olfactory system is 50% adapted. Adaptation is inversely proportional to stimulus strength and is far greater for malodours. Smaller stimuli (small pulse width) caused greater adaptation in malodours than pleasant smells. Then, further increasing the stimulus strength reduced the degree of adaptation (see Fig. 5b). This occurred over a greater range in malodours. Thus, the adaptation vs. stimulus strength curves were much steeper for malodours than for pleasant smells (Fig. 5a).

4.2. Gender differences in olfactory sensitivity and discrimination

Men and women respond differently to malodours. In general, women show a greater degree of brain activation in specific regions (frontal and perisylvian) compared to men in fMRI experiments (Yousem et al., 1999). Women tend to outperform men on tests of identification, detection, discrimination, and suprathreshold intensity and pleasantness perception (reviewed by Doty, 1991). However, using electrophysiological testing these differences have been more equivocal. Geisler and Murphy (2000), using amyl acetate as the olfactory stimulus, and Pause et al. (1996) using citral, found no differences between the olfactory event-related potential (OERP) amplitudes in men and women, but there were differences in latency and these were correlated with peripheral cortisol levels (Pause et al., 1996). Whereas Evans et al. (1995), also using amyl acetate, and Hummel et al. (1998) using vanillin, found that females exhibited larger mean chemosensory event-related potentials (CSERPs) than males. Opatz et al.

(2000) reported that on a psychophysical and electrophysiological level there was no difference between young, healthy men and women in relation to short-term adaptation to suprathreshold chemosensory stimulation.

We found that women have a greater sensitivity for valeric acid and skatol. Surprisingly, in view of the gender differences with valeric acid and skatol, and given its biological significance (it is an ingredient of sweat and vomit), there were no gender differences in the response to butyric acid. A close inspection of the data showed that, although there were large differences (for example in sensitivity; $y_{0\ (men)} = -86.4 \pm 49.0$, $y_{0\ (women)} = -23.6 \pm 18.4$), these failed to reach significance because of large standard deviations. The responses to butyric acid exhibited large individual variability that masked gender differences.

Where there were gender differences it was not because of differences in the degree of adaptation/habituation—in almost all cases (except *cis*-3-hexenol) this was very similar. The differences lay mainly in the sensitivity to the odour (the parameter 'y_0' in the model) and the range of the dose–response curve (parameter 'c'). This would correspond to olfactory threshold differences reported in other studies. This is in agreement with the findings of Opatz et al. (2000). It therefore appears that gender differences have to be explained by some other mechanism; perhaps by (1) changes in attentional performance (Dye, 1992), (2) an increased number of receptors, (3) differences in the viscosity/thickness of the nasal mucosa (Mair et al., 1978) or (4) increases in sensitivity that occur at ovulation during the menstrual cycle (Le Magnen, 1952; Doty et al., 1981) that may be hormonally regulated (Gandelman, 1993). It tends to argue against the hypothesis that men have lower sensitivity to certain malodours, for example valeric acid (an ingredient of sweat), because they have larger apocrine glands (Doty, 1981), produce more odorous secretions and are therefore experiencing long-term adaptation.

4.3. Biological significance

This study represents the first step in quantifying the physiological differences in the olfactory system underlying psychological distinctions of odour hedonics.

The clustering of the malodours in Fig. 3, suggests that the olfactory system treats malodours, as a group, differently to other, non-malodorous compounds. The significance of this, in evolutionary terms, could be that the olfactory system developed a specific response to possible toxins or poisons (different to other, non-malodorous compounds) that enabled it to identify potential olfactory warnings more rapidly.

That the olfactory system should adapt more rapidly to malodours is counterintuitive. These odours have a greater biological significance than pleasant odours. This study shows why this may be the case. The olfactory system adapts more rapidly and to a greater degree to malodours, but there is a steep inverse relationship between concentration and adaptation. Thus, if the system is exposed to a change (increase) in the malodour strength, some adaptation is removed and sensitivity is increased. The olfactory system thereby achieves a greater sensitivity to changes in malodour concentration than to changes in pleasant smells.

Thus, by virtue of this system, continuous exposure to a malodour will result in rapid adaptation/habituation until it is no longer perceived (or perceived at a greatly reduced level), but an increase in malodour concentration will be detected very readily. The same recovery from adaptation/habituation will not occur for non-malodours.

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