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Body Position-Dependent Shift in Odor Percept Present Only for Perithreshold Odors

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Abstract

We recently demonstrated that a supine position causes a decrease in olfactory sensitivity compared with an upright position. We pursued that initial finding in 3 separate experiments in which we explored the extent of, and mechanism underlying, this phenomenon. In Experiment 1, we replicated the decrease in olfactory sensitivity when in a supine compared with an upright position. In Experiment 2, we measured body position–dependent shifts in physiological variables and sniff measures while smelling suprathreshold odorants and performing a perithreshold odor intensity discrimination task. Olfactory performances were reduced while supine. However, no relationships between the shift in olfactory performances and either the physiological variables or sniff measures were found. In Experiment 3, we determined that there were no position-dependent shifts in ability to discriminate or identify suprathreshold odors or rate them for pleasantness, intensity, or familiarity. However, a drop in scores was observed, and performance was slowed, on a cognitive skill while supine. These results demonstrate a body position–dependent shift in olfactory sensitivity only for perithreshold odors that appears to be mediated by cognitive rather than physiological factors. Implications for olfactory imaging studies are discussed.

Key words: imaging, posture, sensitivity, sniffing

Introduction

We recently demonstrated that body position affects olfactory functions (Lundstrom et al. 2006). A reduced olfactory sensitivity to a pure odorant was observed when subjects were in a supine compared with an upright position. This finding expanded initial report of Mester et al. (1988) that body position modulates odor identification performance. When in an upside-down position, subjects' ability to identify odors was greatly reduced compared with when sitting up. This effect could not be explained by changes in physiological measures, such as blood pressure, heart rate, or nasal resistance.

Body position–dependent effects on sensory processing have in the past mainly been reported with reference to the auditory system (Miltich 1968; Macrae 1972, 1974; Lackner 1974; Daniel et al. 1985; Fukai et al. 2005). These findings have led to speculations whether the body position–dependent shift in sensory functions could be mediated by an increase in intracranial cerebral blood flow while lying down (de Kleine et al. 2001). Shifts in intracranial blood pressure seem, however, unlikely to be the mediating mechanism. Neither global cerebral blood flow (Pittet et al. 1989) nor regional cerebral blood flow (Ouchi et al. 2001) shifts in a noticeable degree between a sitting and supine position. Similarly, there have also been reports of body position–dependent effects for the visual system (Marendaz et al. 1993; Mast et al. 2003). Body position–dependent changes hence appear to be present for most of our sensory systems, but the mediating mechanisms behind these changes are not known.

It has previously been speculated that the body position–dependent shift in sensitivity might be linked to a change in sniffing behavior between body positions (Mester et al. 1988). To date, several studies have investigated the relationship between respiratory variables and olfactory sensitivity, with contradictory results. Studies have demonstrated that there are no solid relationships between sniff duration and perceived intensity (Laing 1985), sniff volume and perceived intensity (Teghtsoonian et al. 1978; Hornung et al. 1997), or nasal resistance and odor sensitivity (Doty et al. 1988; Eccles et al. 1989). However, others have reported the opposite. Olfactory threshold has been shown to vary linearly with

nasal airflow (Le Magnen 1945; Laing 1983; Sobel et al. 2000), and a recent study demonstrated that a surgically induced increase in nasal airflow led to a heightened odor sensitivity and increased olfactory identification and discrimination performance (Damm et al. 2003). Interestingly, Laing (1986) showed that the duration of a sniff influenced identification performance only at perithreshold concentrations, indicating that sniff-induced modulation of the odor percept takes place only for weak odors (Laing 1986). From this, one might postulate that the body position–dependent change in olfactory sensitivity would be modulated by a change in sniffing behavior between body positions only for weak odors.

Posture is further known to alter several physiological variables. Cardiovascular variables (Tomaselli et al. 1987; Mester et al. 1988; Schondorf and Low 1992; Jones and Dean 2004), lung volume (Moreno and Lyons 1961), maximal expiratory pressure and expiratory flow (Badr et al. 2002), and hypothermia (Nakajima et al. 2002) all decrease in a supine position compared with when sitting up. Little is known of the impact these physiological variables may have on olfactory sensitivity. The reduction in olfactory sensitivity experienced in a supine position could thus be mediated by either a shift in the physiological state or a change in sniff behavior between the 2 body positions. In an effort to elucidate the potential mediating mechanisms behind our initial finding of decreased olfactory sensitivity when in a supine position, we here report 3 complementary experiments. In Experiment 1, we sought to replicate our initial effect of reduced olfactory sensitivity in a supine compared with a sitting-up position. In Experiment 2, we investigated whether shifts in physiological or sniff measures between body positions could explain the position-dependent effects on olfactory performance, and in Experiment 3, we explored potential body position–dependent effects on olfactory tasks using suprathreshold odors. All aspects of the studies were performed in accordance with the Declaration of Helsinki approved by the Montreal Neurological Institute's Research Ethics Board, and written informed consent was obtained prior to enrolment.

Experiment 1

Methods

Participants

Forty healthy subjects (20 women; mean age 23.6; range 19–35) participated in Experiment 1. Inclusion criteria were self-reported absence of nasal congestion, acute infection, or decreased olfactory function. Participants were asked not to wear perfume on the day of testing and not to eat or drink anything other than water 1 h prior to testing.

Materials

Olfactory thresholds for PEA were assessed using the Sniffin' Sticks threshold set (Hummel et al. 1997), which consists of felt-tip pens filled with phenyl ethyl alcohol (PEA) diluted in propylene glycol in 16 different concentrations. The set ranges from 16.3 μM (dilution 16) to 0.54 M (dilution 1) in a geometric series consisting of 16 steps with dilution ratio of 1:2. In addition, participants' ability to discriminate between odorants was assessed using the Sniffin' Sticks discrimination test, comprising 16 suprathreshold target odors, each of which is presented together with 2 identical lure odors (for a detailed description of the test, see Kobal et al. 2000). The Sniffin' Sticks were selected for odor delivery because they lack the volatile headspace that is present in bottles; that is, there would be no difference between the 2 body positions in how the odor was administered.

Procedure

Each participant's sensitivity for PEA and ability to discriminate between odors was tested twice, once lying down and once sitting up, in a pseudorandomized order. When lying down, participants were situated comfortably in a supine position and were allowed to rest for 3 min before testing to allow time for stabilization of cephalic circulation. When tested sitting up, participants were seated in a comfortable chair and also allowed to rest for 3 min before testing to prevent any dissimilarities between the conditions. Threshold tests were of an ascending staircase, 3-alternative, no feedback, forced-choice design, and similarly, the discrimination tests were of a 3-alternative, no feedback, forced-choice design. Each trial included 1 target (a pen with the odorant in propylene glycol) and 2 control stimuli (pens with only propylene glycol for the threshold test or pens with a distractor odorant in propylene glycol for the discrimination test). For the threshold test, odorants were presented in ascending concentrations until the participant correctly discerned the odorant in 2 successive trials, which triggered a reversal (Doty 1991). The threshold test ended after 7 reversals of the staircase. The mean of the concentration at the last 4 reversal points was calculated to estimate the olfactory threshold, and the total number of correct discriminations (maximum = 16) was calculated as the discrimination score. Values for power estimates for each analysis are given as Cohen's *d'* (Cohen 1977).

Results

Average olfactory thresholds for PEA were one dilution step higher (i.e., lower threshold) when participants were tested sitting up (11.58 ± standard deviation [SD] 2.4) than while lying down (10.59 ± SD 3.1). When in a supine position, 26 participants (65%) demonstrated a decrease in olfactory sensitivity, 6 an increase (15%), and 8 (20%) showed no difference compared with when in an upright position. A repeated-measures analysis of variance (rm-ANOVA) with "body position" as a within-subject variable and "sex" as a between-group variable indicated a significant main effect of body position on olfactory sensitivity, $F(1, 38) = 12.50$, $P < 0.01$, $d' = 0.93$; see Figure 1A. There were no main

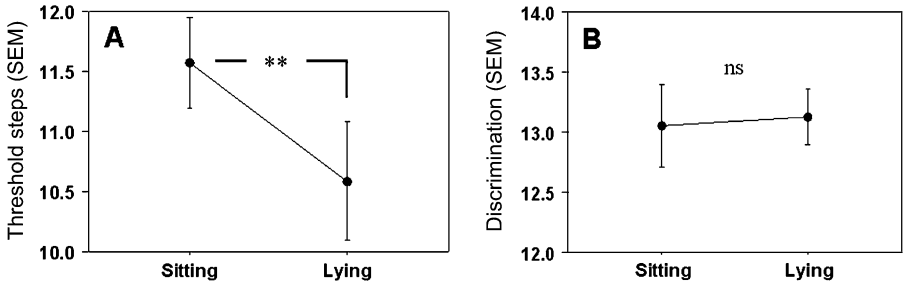

Figure 1 **(A)** Mean olfactory thresholds expressed in threshold steps and divided by body position when tested. **(B)** Mean discrimination scores shown separately for each body position when tested. Higher values mean better olfactory performance in both figures. ** significant difference ($P < 0.01$) and "ns" denotes a nonsignificant difference as indicated by a rm-ANOVA. Error bars symbolize SEM.

effects of the variables sex, $F(1, 38) = 1.73$, $P = 0.20$, $d' = 0.25$, or "starting position," $F(1, 38) = 0.82$, $P = 0.37$, $d' = 0.11$, as tested with rm-ANOVAs with body position as the within-subjects variable and either the variables sex or starting position as the between-subjects variable. There was no significant interaction between the variables sex and body position, $F(1, 38) = 0.16$, $P = 0.69$, $d' = 0.07$.

Although there was a body position–dependent shift in olfactory sensitivity, there was no such difference in discriminatory performance. The average discrimination score was 13.05 (SD ± 2.2) while sitting up and 13.13 (SD ± 1.4) while lying down. A rm-ANOVA with body position as within-subjects variable and sex as between-group variable indicated that there was no significant main effect of body position on discrimination, $F(1, 38) = 0.05$, $P = 0.83$, $d' = 0.06$; see Figure 1B. No significant main effects for the variables sex, $F(1, 38) = 1.58$, $P = 0.22$, $d' = 0.23$, starting position, $F(1, 38) = 2.51$, $P = 0.12$, $d' = 0.37$, or an interaction between sex and body position, $F(1, 38) = 0.87$, $P = 0.36$, $d' = 0.15$, could be detected for olfactory discrimination.

To conclude, participants were more sensitive to the odor of phenylethyl alcohol when sitting up than when lying down—a body position–dependent effect on olfactory sensitivity. A comparison between the result obtained in this study and our previous one (Lundstrom et al. 2006) demonstrates a remarkable similarity. In both studies, the mean difference in sensitivity between the 2 body positions was one dilution step. Similarly, the distribution of participants demonstrating an effect was almost identical to what we previously reported (Lundstrom et al. 2006). There was, however, no effect on the ability to discriminate among suprathreshold odors.

As discussed above, the reduction in olfactory sensitivity experienced in a supine position could be mediated by either a shift in the physiological state or a change in sniff behavior between the 2 body positions. To explore whether the documented changes in odor sensitivity between body positions is induced by altered sniff behavior or physiological states, in Experiment 2 we measured sniff-related variables, blood pressure and heart rate, while smelling perithreshold or suprathreshold odors in a sitting-up or a supine position.

Experiment 2

Methods

Participants

Thirty healthy subjects (15 women; mean age 22.9; range 18–33) participated, none of whom had participated in Experiment 1, with identical inclusion criteria and enrolment instructions as in the previous experiment.

Materials

Sniff parameters were recorded birhinally with a nasal cannula coupled with a pneumatotachograph that relayed changes in intranasal pressure to an amplifier (PowerLab 4SP, A. D. Instruments, Milford, MA). The transduced signal was displayed and recorded at 100 Hz, and measures of sniff amplitude and volume were extracted with commercially available software (CHART 5.0.2.26, A. D. Instruments). Blood pressure (systolic and diastolic) and heart rate were measured with an automatic blood pressure and heart rate monitor (3BXO-A, Thermor Inc., Markham, Ontario, Canada) using an inflatable arm cuff.

Olfactory thresholds, sitting up and lying down, were assessed as described above for Experiment 1 with the main exception that *n*-butanol was used as the target odorant. Subjects were additionally exposed to 16 suprathreshold odorants using the Sniffin' Sticks odor identification test (Kobal et al. 2000), while measuring sniff volume and amplitudes. Eight odorants were used randomly in each body position and subjects had to identify the odorant in a 4-alternative, forced-choice identification task.

Results from Experiment 1 suggest that only perithreshold odor sensations are affected by an individual's body position. Assessing sniff parameters while subjects perform a staircase detection threshold test would result in large individual differences in the number of sniffs needed to determine the threshold, yielding unbalanced sniff measures. To enable the assessment of sniff parameters while subjects smell odors at peri- and suprathreshold concentrations using a defined number of sniffs, we administered

the suprathreshold odors and a new perithreshold odor intensity discrimination test (POID) that we devised. The POID test allowed us to empirically assess performance differences between body positions for a perithreshold odor task and also, by allowing only one sniff per presentation, we could measure sniff variables during a defined number of sniffs. The POID consists of 2-alternative, forced-choice discriminations between an odor at the individual's threshold (target), as determined by the prior threshold test, and the same odor either just above or just below their assessed threshold (foil). For each pair, the participant is asked to identify which one is the "stronger" concentration. Two concentration steps above (+1 and +2) and 2 concentration steps below (−1 and −2) their identified threshold, that is, target, were used as foils. The 2 odors in each pair were presented in a similar fashion to that described above for the detection threshold, with a separation of at least 30 s between odor pairs to allow recovery of sensitivity. Only *n*-butanol was used in the POID because this was the odor used for the detection threshold test. Each concentration was repeated 4 times in each test, yielding a total of 32 sniffs: 16 sniffs of an odor at the subject's threshold, 8 sniffs at an odor above, and 8 sniffs at an odor below threshold odor concentration.

State and trait anxiety was measured using the well-validated Spielberg State Trait Anxiety test, which consists of 2 subscales, STAI-S and STAI-T. STAI-S is meant to measure situational anxiety and STAI-T a more underlying, or trait, anxiety (Spielberger et al. 1970). Although we did not expect a body position–dependent modulation of trait anxiety, STAI-T was included as a control task to give the vascular and cephalic circulation systems additional time to stabilize before measures were taken while still keeping the participant active.

Procedure

The experiment was a repeated measures, within-group design in which all participants underwent all measures in both body positions (see Figure 2). Thresholds for *n*-butanol were initially assessed in each body position, with a randomized starting order for body position, using identical procedures as in Experiment 1. Participants then placed themselves in the a priori selected starting body position and were fitted with a nasal cannula. The STAI were administered followed by measures of blood pressure and heart rate.

Sniff amplitudes and volumes were determined while participants performed the POID and smelled the suprathreshold odors in both body positions in a pseudorandomized fashion. After the POID, the suprathreshold odors were administered. Participants were asked to identify the odor after each presentation and, as for the POID, allowed to take only one sniff of each pen to ensure consistency among participants. The suprathreshold odors were always administered at the end of the session to avoid olfactory adaptation, which could potentially influence the POID test.

Data processing and reduction

The data obtained from the sniff measures were analyzed on an individual and group level for each of the sniff conditions. A marked increase in amplitude directly after stimulus presentation, lasting longer than 0.5 s, was considered a sniff (Mainland and Sobel 2006). Sniffs deemed to be extreme values due to their maximum peak amplitude or because they were extremely short were removed based on outlier analyses using a cutoff value of 3 SDs from the mean. Sniffs were truncated at 2.5 s and standardized by dividing each individual value within a measured time unit from the sum of all values obtained within that time unit. One subject was removed completely from the individual level analyses of the maximum peak amplitude and area under the curve due to too few remaining nonoutlier recordings. Area under the curve and maximum peak amplitude value was calculated from the averaged sniff for each subject and condition. For the sniff measures in the POID test, we only analyzed sniffs obtained during smelling the target odor. This measure ensured that only data obtained during a perithreshold sensation were collected. rm-ANOVA with body position (sitting up, lying down) as a within-subject factor and sex (men, women) as between-subject factor were used to assess main effects.

Results

Behavioral measures

Contrary to previous findings, there was no difference between body positions in olfactory threshold for *n*-butanol, $F(1, 28) = 1.07$, $P = 0.31$, $d' = 0.17$; see Table 1 for mean values of behavioral and physiological measures. There was, however, a significant interaction between the variables body position and sex with respect to threshold for *n*-butanol, see Figure 3, $F(1, 28) = 4.93$, $P = 0.03$, $d' = 0.57$. Men became less sensitive while lying down (7.12 ± SD 2.3) compared with when sitting up (8.22 ± SD 1.5; $t(14) = 2.21$, $P = 0.04$, $d' = 0.55$), whereas the sensitivity of women did not change significantly (lying down: 9.18 ± SD 2.9; sitting up: 8.78 ± SD 2.5; $t(14) = 0.94$, $P = 0.37$, $d' = 0.14$). There was no significant difference between body positions in ability to identify the odors, $F(1, 28) = 0.24$, $P = 0.63$, $d' = 0.08$, nor was there a significant interaction between the variables body position and sex, $F(1, 28) = 1.30$, $P = 0.26$, $d' = 0.20$.

Although there was no significant main effect of body position on sensitivity to *n*-butanol, there were significant differences between body positions for the POID test, $F(1, 28) = 5.88$, $P = 0.02$, $d' = 0.65$, see Figure 4. Seventeen participants (59%) demonstrated a reduction in the lying down position, 4 (14%) did not change their performance, whereas 8 (27%) participants demonstrated a slightly increased performance while lying down compared with when sitting up. These results are again consistent with the previously reported body position–dependent reduction in odor sensitivity

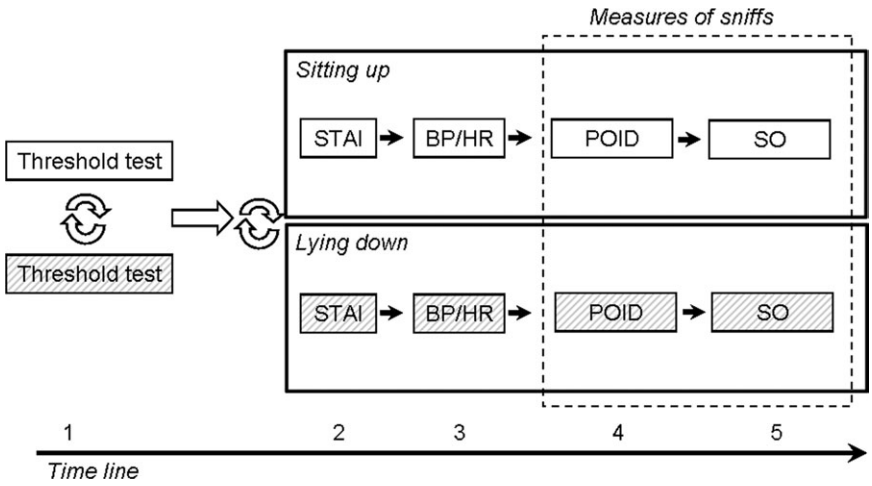

Figure 2 Figure depicts temporal order of the experimental design in Experiment 2. Colored boxes indicate measures obtained in a supine body position and the dotted enclosure marks tasks in which sniff parameters were measured. Circular arrows indicate repeated measures. STAI, state trait anxiety inventory; BP/HR, blood pressure and heart rate; POID, perithreshold odor intensity discrimination; SO, suprathreshold odorants.

Table 1 Mean scores and SD for each variable and body position

Variable	Body position	Mean value (SD)
Threshold test (ns)	Sitting up	8.50 (2.07)
	Lying down	8.15 (2.81)
Identification test (ns)	Sitting up	6.63 (1.13)
	Lying down	6.63 (0.91)
POID test[a]	Sitting up	10.93 (2.01)
	Lying down	10.01 (1.85)
Heart rate[a]	Sitting up	64.04 (12.43)
	Lying down	58.03 (11.25)
Systolic blood pressure (ns)	Sitting up	118.23 (12.75)
	Lying down	119.13 (12.11)
Diastolic blood pressure[a]	Sitting up	73.67 (1.52)
	Lying down	68.07 (1.66)
STAI-S (ns)	Sitting up	31.60 (8.26)
	Lying down	31.17 (6.89)
STAI-T (ns)	Sitting up	39.47 (10.36)
	Lying down	38.43 (10.19)

ns, no main effect of body position.
[a]Main effect of body position ($P < 0.05$).

(cf. Experiment 1, Lundstrom et al. 2006). There was also a significant interaction between sex and performance for the POID test, $F(1, 28) = 4.68$, $P = 0.04$, $d' = 0.55$. Compared with when sitting up, men performed the intensity discrimination task less accurately when lying down, whereas women did not demonstrate a similar change in accuracy.

No body position–dependent effects could be found for either the state anxiety (STAI-S), $F(1, 28) = 0.15$, $P = 0.69$, $d' = 0.07$, or the trait anxiety (STAI-T) measures, $F(1, 28) = 2.03$, $P = 0.17$, $d' = 0.28$. Likewise, no interactions between the factors body position and sex could be found, all Fs < 0.27; all Ps > 0.60. The lack of body position–dependent effects on self-reported anxiety indicates that participants did not find lying down more stressful than the upright position. There was, however, a main effect of sex, independent of body position, on the state anxiety measure. Women felt overall less anxious than men, reporting a mean score of 27.9 (standard error of the mean [SEM] ±1.6) compared with the men's score of 34.8 (SEM ±1.6). No sex-related difference was found for the trait anxiety measure.

Physiological measures

There was a significant body position–dependent shift in measured heart rate, $F(1, 28) = 17.07$, $P < 0.01$, $d' = 0.98$. The heart rate dropped almost 6 units from sitting up to lying down. A similar shift was seen in blood pressure. The measured diastolic blood pressure was significantly lower when in the supine position compared with when sitting up, $F(1, 28) = 9.89$, $P < 0.01$, $d' = 0.86$. No such difference was found for the systolic blood pressure, $F(1, 28) = 0.26$, $P = 0.61$, $d' = 0.08$, and no significant interactions between the variables body position and sex was found for any of the physiological variables, all Fs < 3.2; all Ps > 0.10.

Sniff measures

There were large differences between body positions for all measured sniff variables independently of whether the odors were of a perithreshold or suprathreshold concentration. For sniffs obtained while smelling the suprathreshold odors, the peak amplitude value while lying down was

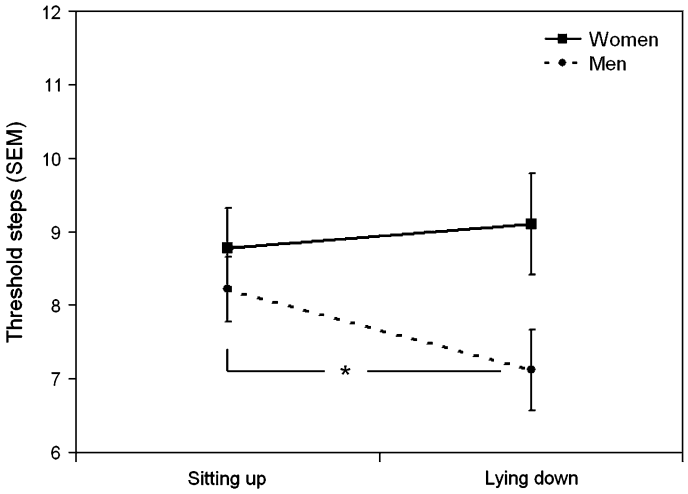

Figure 3 Mean olfactory thresholds for *n*-butanol expressed in threshold steps and shown separately for each body position when tested and sex of participants. Higher values mean higher sensitivity. * significant difference ($P < 0.05$) as indicated by a rm-ANOVA. Error bars symbolize SEM.

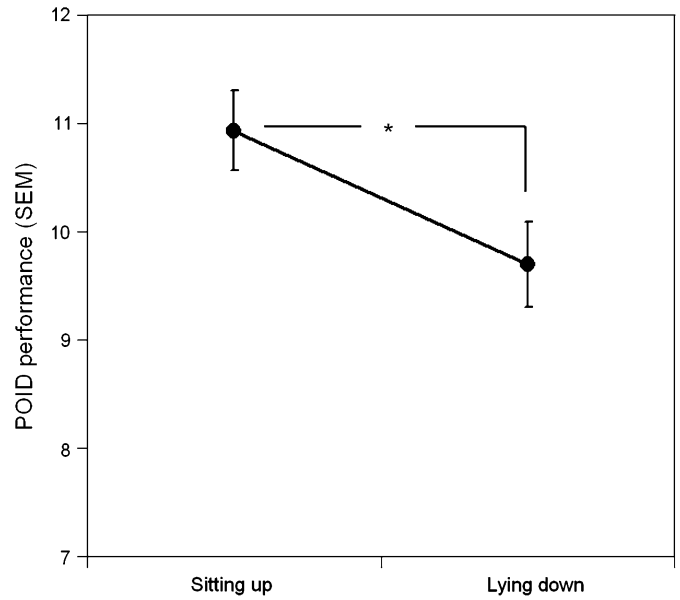

Figure 4 Mean POID performance shown separately for each body position when tested. Higher values mean better performance. * significant difference ($P < 0.05$) as indicated by a rm-ANOVA. Error bars symbolize SEM.

0.20 (SEM ± 0.021) measuring units and 0.31 (SEM ± 0.030) units while sitting up, a significant difference, $F(1, 27) = 35.15$, $P < 0.01$, $d' > 0.99$. Similarly, sniff volumes were significantly larger (3421.59, SEM ±356.8) when sitting up compared with lying down (1948.41, SEM ±242.9), $F(1, 27) = 48.24$, $P < 0.01$, $d' > 0.99$.

There were also significant differences in sniff behavior for the perithreshold odors of the POID in both sniff volume and peak amplitude. The peak amplitude of the sniff while lying down was 0.22 (SEM ± 0.026) measuring units and 0.33 (SEM ± 0.032) units while sitting up, constituting a significant difference, $F(1, 27) = 90.23$, $P < 0.01$, $d' > 0.99$. Similarly, sniff volumes were significantly larger (3399.35, SEM ±368.9) when sitting up compared with lying down (2736.30, SEM ±398.3), $F(1, 27) = 78.10$, $P < 0.01$, $d' > 0.99$.

Sniff-dependent relationships

Although a clear difference in both sniff volume and peak amplitude between body positions was observed, it is not clear whether the differences in behavioral performance on the POID test and physical measures is directly related to the change in sniff behavior. To elucidate the relationship between the measured body position–dependent changes in sniff behavior and the physiology of behavioral performance, separate bivariate Pearson correlation analyses were performed between individual changes. For each individual and variable, a score was calculated by subtracting the obtained value while lying down from the corresponding value while sitting up. This gave us individual change scores that indicated the effect body position had on each individual for each variable; these change scores were subsequently used as dependent variables in the correlation analyses.

Change between body positions for the POID test correlated significantly with the change in sniff behavior for only one variable. There was a significant negative correlation between the change in POID performance and the change in sniff volume while performing the task, $r(29)$ −0.49, $P < 0.01$, see Figure 5. No other significant correlations between sniff measures and behavioral measures were observed, all rs < -0.27 and Ps > 0.17. Further, there were only 2 statistical tendencies for correlations between changes in sniff variables and physiological measures, both related to the significant drop in diastolic blood pressure. These were relationships between change in diastolic blood pressure and the difference in peak amplitude, $r(29)$ −0.37, $P = 0.05$, and sniff volume, $r(29)$ −0.37, $P = 0.05$. However, no significant correlation was evident between changes in POID and diastolic blood pressure, $r(29)$ −0.09, $P < 0.61$. No other significant correlations between behavioral and physiological measures were observed, all rs < -0.06 and Ps > 0.74.

To conclude, Experiment 2 demonstrates that performance in a perithreshold odor task is affected by body position. However, the body position effect on odor sensitivity is not primarily mediated by a change in either sniff behavior, physiological variables such as blood pressure or heart rate, or levels of self-reported anxiety. Experiment 1 indicated that performance in tests using suprathreshold odors are not affected by shifts in body position. Moreover, contradictory to the result previously reported by Mester et al. (1988), the result of the identification test in this experiment indicated that there was no effect of body position on a participant's ability to identify strong odors. Hence, it is possible that body position–dependent effects in odor perception are limited to tasks involving perithreshold odors. To test whether body

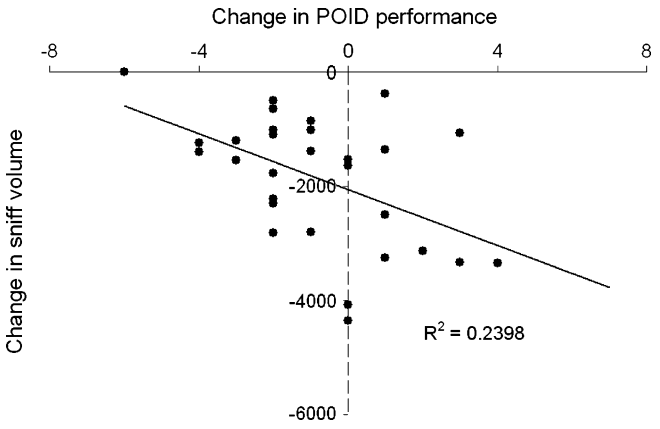

Figure 5 Correlation between the shift in sniff volume from sitting up to lying down and the shift in performance on the POID from sitting up to lying down. Circles represent individual participants and solid line indicates the regression line.

position affects either our ability to identify suprathreshold odors or our general odor perception, in Experiment 3 we measured identification performance once again using more odorants and we measured subjective perception of intensity, pleasantness, and familiarity of suprathreshold odors.

Experiment 3

Methods

Participants

Forty healthy subjects (20 women; mean age 22.8; range 18–39) participated with identical inclusion criteria as in the previous 2 experiments, and none had participated in either Experiment 1 or 2.

Materials

Odor identification was assessed using 40 common odors placed inside Sniffin' Sticks felt-tip pens (Kobal et al. 2000). Sixteen of the odors emanated from the Sniffin' Sticks validated olfactory identification set, and to enable a repeated testing design without repetition of odor stimuli, 24 other unique odors were added. In addition to identification performance, ratings of perceived pleasantness, intensity, and familiarity were obtained for each odor using 100-mm visual analog scales (VAS). Cognitive performance was assessed using the Raven's Standard Progressive Matrices test (Raven et al. 2000), designed to measure the ability to form visual-based perceptual relations, a so-called logical reasoning task. In order to avoid repetition of single test items, the test was divided into 2 halves with an equal progression in difficulty, yielding a total of 18 test items for each position.

Procedure

Each participant was tested twice for the ability to identify odors, once lying down and once sitting up in an identical manner to Experiment 1. In this task, participants were allowed one sniff of each odor, which they then attempted to identify (free odor identification). Next, they rated the pleasantness, intensity, and familiarity of the odor on 3 separate VAS. The anchors for pleasantness ratings were "extremely unpleasant" and "extremely pleasant"; for intensity, "not perceivable" and "extremely intense"; and for familiarity ratings, "extremely unfamiliar" and "extremely familiar." Following the rating task, cued identification was tested using a cue card containing the name of the target odor and 3 foils. This sequence was repeated for each odor with roughly 40 s between odor presentations. Twenty unique odors were presented in each body position in a completely randomized order.

For the Raven's Standard Progressive Matrices (cognitive test), the individual problems were presented by the experimenter and subjects were given a maximum of 30 s to solve each one, after which the next item was presented. The total number of correct responses and total time in seconds to completion were recorded. The starting body position and order of the olfactory and cognitive tests was pseudorandomized and a 3-min pause between body positions was imposed to allow for stabilization of circulatory systems.

Results

The general influence of the variable body position was initially assessed by multivariate analysis of variance (MANOVA) with all 7 dependent variables included: free odor identification, cued odor identification, perceived intensity, familiarity, pleasantness, correct responses on the cognitive test, and time taken to complete the cognitive test. The MANOVA revealed a borderline statistical significance for the overall influence of body position when all dependent variables were considered, $F(7, 33) = 2.24$, $P = 0.05$, $d' = 0.74$.

Separate rm-ANOVAs indicated, however, that there were no main effects of body position on either free odor identification, $F(1, 39) = 2.11$, $P = 0.16$, $d' = 0.29$, or cued odor identification, $F(1, 39) = 0.04$, $P = 0.84$, $d' = 0.05$. Further, no significant main effects of body position were observed on the subjective ratings of the odors for ratings of familiarity, $F(1, 39) = 0.03$, $P = 0.87$, $d' = 0.05$; pleasantness, $F(1, 39) = 0.02$, $P = 0.90$, $d' = 0.05$; or intensity, $F(1, 39) = 0.38$, $P = 0.54$, $d' = 0.09$. See Table 2 for descriptive values of all variables. In contrast, a significant difference was observed on the cognitive test accuracy score: subjects performed better while sitting up than while lying down, $F(1, 39) = 8.88$, $P < 0.01$, $d' = 0.83$; see Figure 6a. There was in addition a statistical tendency that subjects required less time to complete the test in an upright compared with a supine position, $F(1, 39) = 3.52$, $P = 0.07$, $d' = 0.45$; see Figure 6b. No interaction effects

between the factors body position and sex were observed, all Fs > 0.69 and all Ps < 0.41.

General discussion

The body position–dependent shift in odor sensitivity for the odorant PEA seems to be a stable finding. In 2 consecutive experiments (Experiment 1 and Lundstrom et al. 2006), the reduction in sensitivity from sitting up to a supine position was one scale step, corresponding to a 50% decrease in odor concentration. As discussed below, this seems to be an odorant dependent effect because we did not find a similar effect for the odorant *n*-butanol. There were no effects on either the ability to identify suprathreshold odors, as indicated by Experiments 2 and 3, or on perceptual ratings of the same. The lack of a body position effect on odor identification in our experiments is contradictory to the findings of Mester et al. (1988), who reported that odor identification was affected by body position. This discrepancy can, however, be explained by 2 major differences between the studies. Mester et al. assessed identification performance for only 10 odors in each position using a mere 16 participants, and the body position–dependent effect in their case was a marked reduction in identification while subjects were suspended upside down. We used more odorants and more subjects, reducing the likelihood of type 1 error. Furthermore, we found no body position–dependent effects on olfactory identification in either Experiment 2 or 3. We therefore conclude that body position does not influence the ability to identify odors in suprathreshold concentration.

The shifts between body positions in measured sniff amplitude, sniff volume, heart rate, and blood pressure were quite substantial. There were, however, no significant correlations between these changes and the observed change in perithreshold odor intensity discrimination performance other than the negative correlation between performance and sniff volume. No straightforward link between olfactory performance and sniff volume exists (Teghtsoonian et al. 1978). Although one study has demonstrated that nasal patency decreases in healthy subjects when in a supine compared with upright position (Kase et al. 1994), others have failed to find this connection (Rundcrantz 1969; Hasegawa and Saito 1979; Haight and Cole 1984; Cole and Haight 1986; Riechelmann and Krause 1994; Lal et al. 2006). Moreover, most studies to date have found that neither nasal patency (Doty et al. 1988; Eccles et al. 1989) nor sniff volume (Teghtsoonian et al. 1978; Hornung et al. 1997) affects olfactory functions. However, studies that do demonstrate a connection have indicated that greater volume leads to a better performance (cf. Mainland and Sobel 2006). To the best

Table 2 Mean scores and SD for each variable and body position

Variable	Body position	Mean value (SD)
Free odor identification (ns)	Sitting up	5.00 (2.21)
	Lying down	5.60 (1.82)
Cued odor identification (ns)	Sitting up	14.98 (1.25)
	Lying down	15.05 (1.69)
Familiarity rating (ns)	Sitting up	7.04 (1.31)
	Lying down	7.01 (1.21)
Pleasantness rating (ns)	Sitting up	6.22 (0.97)
	Lying down	6.24 (0.85)
Intensity rating (ns)	Sitting up	6.31 (1.17)
	Lying down	6.37 (1.02)
Cognitive test[a]	Sitting up	15.63 (1.76)
	Lying down	14.65 (2.17)
Time to complete cognitive test[b] (seconds)	Sitting up	198.68 (42.31)
	Lying down	211.03 (44.16)

The scores for Familiarity ratings range from 0 extremely unfamiliar to 10 extremely familiar, Pleasantness ratings range from 0 extremely unpleasant to 10 extremely pleasant, and Intensity ratings range from 0 "not perceivable" to 10 extremely intense. ns, no main effect of body position.
[a]Significant main effect of body position (P < 0.01).
[b]Denotes a statistical tendency for main effect (P < 0.10).

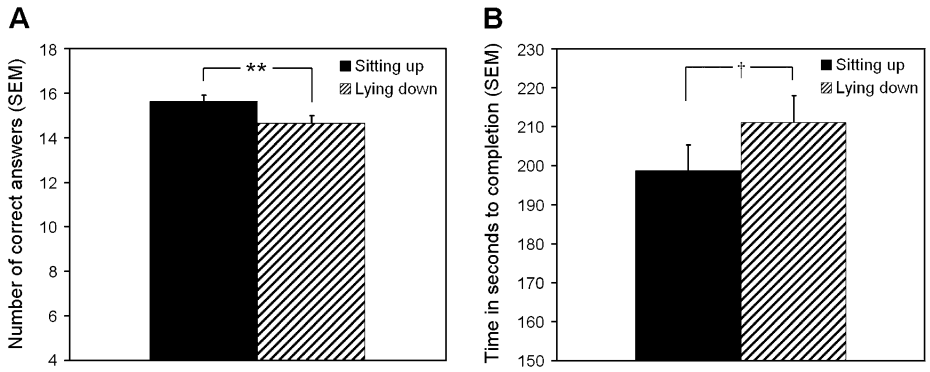

Figure 6 **(A)** Mean accuracy scores on Raven's Progressive Matrices divided by body position when tested. Graph is scaled at the chance value of 4. **(B)** Mean total time in seconds required to complete all items on Raven's Progressive Matrices divided by body position when tested. ** significant difference (P < 0.01) and † statistical tendency (P < 0.10) as indicated by a rm-ANOVA. Error bars symbolize SEM.

of our knowledge, no previous data exist that demonstrate a negative relationship between sniff volume and behavioral performance. We therefore conclude that the observed reduction in POID performance, and with that the shift in olfactory sensitivity when lying down, was not solely mediated by either sniffing behavior or any one of the measured physiological variables.

We found in Experiment 3 that there was a body-dependent shift in the ability to solve a logical reasoning task. Participants found fewer correct solutions and needed more time to complete the task while in the supine compared with the sitting-up position. Posture related effects on other cognitive variables have been reported in the past. As mentioned above, there is a dissociation in the visual system between perceptual and cognitive tasks in how they are affected by a shift in body position (Mast et al. 2003). Body position is also known to modulate cognitive performance (Rand and Wapner 1967; Dijkstra et al. 2007). Whether the reduced performance in the logical reasoning test in the supine position is indicative of a reduction in subjects' general cognitive function or an alteration of attention/vigilance still remains to be elucidated. However, recent data indicate that olfactory sensitivity is greater to attended stimuli than to unattended stimuli (Marks 2002), supporting the latter mechanism.

In line with the notion that an alteration of attention could mediate the demonstrated reduction in sensory functions when in a supine position is the finding that body position alters the measured levels of midday salivary cortisol (Hennig et al. 2000; however, not the cortisol response upon awakening Hucklebridge et al. 2002). Cortisol is one of the main regulators of the state of alertness and vigilance. One might postulate that a supine position leads to a reduction in circulating cortisol. This in turn would alter attention and, subsequently, performance on tests demanding a high degree of attention such as our cognitive test and the attention demanding threshold and POID tasks. Thus, it is conceivable that the mediating mechanism is an alteration of circulating cortisol. Changes in attention while lying down would have a potentially large impact on imaging experiments due to the forced supine position in the scanner. Functional imaging experiments often correlate perceptual and cognitive measures obtained outside the scanner (normally in an upright position) with the acquired functional data. If attention is reduced inside the scanner, 2 different states would be compared. One of our initial concerns was that imaging paradigms would be compromised by the demonstrated reduction in odor sensitivity due to the often forced supine position inside the scanner. However, we have now demonstrated that only perithreshold odors are affected by a shift in body position, with no noticeable effects on suprathreshold odors. Whether general cognitive functions are altered by body position remains to be elucidated.

There was no main effect of body position on olfactory sensitivity in Experiment 2 when assessed with *n*-butanol rather than PEA as the target odor. This seems to be dependent on differences between the sexes. Men demonstrated a clear body position–dependent change in their sensitivity but women did not. Similarly, although there was a main effect of body position on the POID test, men demonstrated a larger effect than women did. Identical methods and similar populations were used in the previous studies with the exception of target odorant. The main difference between the 2 odorants is that PEA (Experiment 1) is considered a pure odorant with little to no stimulation of the trigeminal system, whereas *n*-butanol (Experiment 2) is considered to be a bimodal odorant (Doty et al. 1978; Savic et al. 2002); that is, in higher concentrations the odorant activates both the olfactory and the trigeminal system (Cometto-Muniz et al. 1999). Recent data indicate that there is a sex difference in the cortical processing of bimodal odorants. Large differences in hemispheric processing (Savic et al. 2002; Lundstrom and Hummel 2006) have been reported for bimodal odors, whereas similar comparisons for pure odorants show no sex specific effects (Bengtsson et al. 2001). We are not inferring that the stimuli used here were perceived as either pungent or irritating by the participants. However, low *n*-butanol concentrations clearly activate the cortical trigeminal system (Savic et al. 2002). Hence, one might speculate whether bimodal odorants are processed differently from pure odorants also at concentrations below a conscious trigeminal percept. Future experiments using a wider range of odorants, concentrations, and behavioral measures are needed to fully understand this discrepancy between studies.

The effect distribution between experiments, that is, percentage of participants demonstrating a body position–dependent change in sensitivity (cf. Lundstrom et al. 2006, Experiment 1, and Experiment 2—POID [see Figure 5]), seems very consistent with an interesting small subgroup of participants who exhibit an effect opposite to the main one. Although this is expected in behavioral experiments, and especially so in olfactory sensitivity experiments as they are known to exhibit a large intersubject variability (Stevens et al. 1988), the consistency between experiments in the proportion of this group warrants some attention. Understanding of the common often comes from studying the uncommon. Hence, future studies on body position–dependent effects would benefit from focusing on individuals whose sensitivity is affected by changes in body position in an opposite direction to that of the general population.

To conclude, in 3 consecutive experiments we have demonstrated that body position affects olfactory sensitivity and olfactory performance, but only for weak perithreshold odors. No discernable effects were observed on suprathreshold odors. In addition, although the ability to discriminate between perithreshold odors was affected by body position, no clear relationships between heart rate, blood pressure, or sniff behavior were observed. In Experiment 3, we demonstrated that the ability to perform a cognitive task was affected by body position. This effect, paired with the

previously reported effects on auditory threshold, indicates that the body position–dependent effects on sensory performance demonstrated by us and others might not be mediated solely by changes in the peripheral sensory and nervous systems. Rather, it seems that the body position effects are mediated by a complex interplay between both the peripheral and more central cognitive variables.

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