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ABSTRACT

Background: When you smell an odorant, your first reaction will certainly be either I like it or I dislike it. This primary reaction is a reflection of what is called the "hedonic value" of the odor. Very often, this hedonic value dominates the olfactory percept, more than olfactory identification or intensity. This component of olfactory perception is of primary importance for guiding behavior: avoiding danger (the smell of smoke, gas, etc.), consuming food, or seduction. Olfactory hedonics can be assessed using a large number of methods in humans, including psychophysical measures, autonomic responses, measurement of facial expressions or peripheral nervous activity. All of these techniques have their limitations: subjectivity, invasiveness, need for expertise, etc.
A new method: The olfactory system is closely linked to the reward system, the role of which is to mediate motivated behavior. In this context, we propose that the capacity odorants have of recruiting the reward system and thus inducing motivated behavior can be used to identify new behavioral parameters to assess odor hedonic value in humans.
Results: We recorded freely moving human participants exploring odors emanating from flasks, and showed that five parameters linked to motivated behavior were closely linked to odor hedonics: speed of approach to the nose and withdrawal of the flask containing the odorant, distance between flask and nose, number of samplings, and withdrawal distance (maximal distance between nose and flask after odor sampling).
Conclusions: We highlighted new non-verbal and non-invasive parameters to evaluate olfactory hedonics in humans based on the assessment of odor-motivated behavior.

1. Introduction

Olfactory perception includes different dimensions such as identity (What am I smelling?), familiarity (Do I know that smell?), intensity (Is the smell strong or weak?) and hedonics (Is the smell pleasant or not?). Of all these dimensions, odor hedonics appears to be the most important in humans. It is the primary odor feature spontaneously used by humans to perform olfactory discrimination tasks (Schiffman, 1974), categorize odorants into groups (Berglund et al., 1973; Schiffman et al., 1977) and verbally describe odorants (Khan et al., 2007; Moskowitz and Barbe, 1977; Zarzo, 2008). Odor hedonics has major implications in a large array of everyday life situations: feeding, social communication, awareness of environmental hazards, and experiencing pleasure (Stevenson, 2010; Walliczek-Dworschak and Hummel, 2017).

Emotional responses to odorants are expressed at different levels (e.g., verbalization of emotional feelings, changes in physiological state or motor behavior) and thus hedonic perception can be assessed by a large number of methods, depending on the level to be explored. The most direct approaches use psychophysical measures, with measurement scales or verbal responses (Poncelet et al., 2010; Stevens, 1958). The limitation of these techniques is that they require the active participation of the subject, making the hedonic evaluation subjective.

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Autonomic responses that are known to be modulated by odor hedonics can also be used: electrodermal response (Brauchli et al., 1995), heart rate (Alaoui-Ismaïli et al., 1997b, 1997a; Bensafi et al., 2002), or motor startle reflex (Ehrlichman et al., 1995, 1997; Miltner et al., 1994). The motor sniff response can also be assessed as a reflection of odor hedonics (Bensafi et al., 2003; Bensafi et al., 2007; Ferdenzi et al., 2015). These responses have the advantage of being more objective, since they are not based on verbal reports by the subject. However, they are more invasive, in that various types of sensors are placed on the subject's body and/or face, which may inhibit spontaneous behavior in response to odorants. Facial expression can also be measured to assess olfactory preferences. This includes "mouthing" behavior (Soussignan et al., 1997; Mennella and Beauchamp, 1998; Delaunay-El Allam et al., 2010), slight smile, and expressions of disgust (Soussignan et al., 1997; Schaal et al., 2000; Danyang et al., 2020). These assessments are, however, dependent on the expertise of the investigator in recognizing and categorizing facial expressions. Finally, recent software is able to measure peripheral vasomotor activity to assess emotional response to a stimulus; but results are not completely reliable and head movement is required to be limited (Bousefsaf et al., 2016).

Olfactory emotional responses are a valuable source of information for decision-making and guiding motivated behaviors, leading to attraction or aversion in response to an odorant source. This particularity can be explained, at least partly, by the anatomo-functional organization of the olfactory system and its close connections to the reward system (Midroit et al., 2021; Wesson and Wilson, 2011; Ikemoto, 2007; Xiong and Wesson, 2016). The olfactory bulb is the first cortical relay of the olfactory information which carries the neural signature of odor hedonics (Kermen et al., 2016, 2021) and projects directly onto the olfactory tubercle (Wesson and Wilson, 2011; Xiong and Wesson, 2016; Price, 1973). This is part of the ventral striatum (with the accumbens nucleus) and is the target of dopaminergic projections from the ventral tegmental area, constituting the key structures of motivated behaviors (Ikemoto, 2007, 2003; Fitzgerald et al., 2014; Kornetsky et al., 1991). In this context, we propose that the capacity of odorants to recruit the reward system and thus induce motivated behavior can be used to identify new behavioral parameters to assess the hedonic value of odorants in humans. The aim of the study is thus to investigate new non-verbal non-invasive parameters to evaluate olfactory hedonics in humans based on the assessment of odor-motivated behavior.

2. Material and methods

2.1. Participants

Data were collected and processed according to the ethical guidelines of the Declaration of Helsinki and approved by a French ethics committee (#CPP- IdF-IV). Twenty-four participants (12 women and 12 men) between the ages of 18 and 28 years (mean ± SD, 21 ± 2.1 years) were tested in March 2018. All were recruited from the Lyon area in France. Their olfactory performances were checked using the European Test of Olfactory Capabilities (Joussain et al., 2016). Participants received financial compensation for the experiment and provided written informed consent prior to participation.

2.2. Perceptual rating

Twenty-three monomeric odorants (Table 1) were selected to cover the olfactory perceptual space as fully as possible: edible and non-edible odors, body odors, flower odors, decay odors, etc. The odorants were diluted to reach similar vapor pressures (1 Pa, diluted in mineral oil) on a piece of polypropylene, and were presented in 15 mL flasks (opening diameter, 1.7 cm; height, 5.8 cm; filled with 5 mL of liquid) (Licon et al., 2018) (Table 1). Participants were allowed to freely smell each odorant for 1 min. The order of odorant presentation was randomized between participants. During the 1-minute period devoted to odorant exploration, participants were asked to rate each odorant in terms of liking ("Is the smell pleasant?"), wanting ("Do you want to smell it again?"), intensity ("Is the smell intense?"), familiarity ("Is the smell familiar?") and irritation ("Is the smell irritating?"). Participants evaluated each odorant on Pie-Pie software (Licon et al., 2018), which involves rating on a continuous scale from 0 to 1. Using this software, all perceptual criteria, presented on a pie, were evaluated at the same time for a given odorant. No further instructions were given to participants, meaning that they could sample the odorant and next perform the ratings or perform the ratings during odorant sampling. Participants could not switch to the next odorant before the end of the trial (duration: 1 min).

Table 1
Odorant names, abbreviations, CID and dilution for the experiment.

Odorant name	Abbreviation	CID #	Dilution in mineral oil (vol/vol)
Thioglycolic acid	THIO	1133	1.55%
Butanoic acid	BUT	264	0.11%
3-hydroxy-3-methylhexanoic acid	HMHA	16666688	1%
Propanoic acid	PROA	1032	0.04%
p-cresol	CRE	2879	1.84%
3-methyl-3-sulfanylhexan-1-ol	MSH	10130039	1%
Guaiacol	GUA	460	2.09%
Eugenol	EUG	3314	13.44%
1-propanol	1-PRO	1031	0.007%
Cis3hexenol	CIS3	5281167	0.24%
(-)-terpinen-4-ol	TER	5325830	8.003%
D-limonene	LIM	440917	0.2%
(+)-camphor	CAM	159055	0.46%
Citronellal	CITRA	7794	1.42%
b ionone	ION	668014	7,27%
Citronellol	CITRO	8842	17.85%
Trans-2-hexenylacetate	TRANS	2733294	0,16%
Cineole	CIN	2758	0,17%
2-phenylethanol	PEA	6054	2,66%
Geraniol	GER	637566	11,29%
L-carvone	CAR	439570	1.93%
Isoamyl acetate	ISO	31276	0.03%
Benzaldehyde	BEN	240	1,54%

2.3. Assessment and analysis of odor-motivated behaviors

During the odorant exploration and rating phase, participants were filmed with a webcam (Logitech C920) positioned beside them. Video measurements were made using Volcan software developed under LabVIEW (National Instruments) (Richard et al., 2017; Hegoburu et al., 2009). Each recording was stored in AVI file format with jpeg codec. Offline, the video recordings could be replayed using Volcan (A2V module) software, and video track analyses were performed. Using this procedure, behavior was encoded per session and trial in a data-file by manually defining on each frame (25 frames/seconds) the location of the flask containing the odorant and participant's tip of the nose. Distances in the video analysis process were calibrated by measuring the size of the flask in real and on the videos. We performed this calibration on each video. Then, trajectory of both odor flask and participant's nose were automatically calculated by Volcan software to enable measures of speeds and distances. More specifically, we measured the speed of approach to the nose and withdrawal of the flask containing the odorant, the distance between the flask and the nose ("odorant sampling distance"), and withdrawal distance (maximal distance between nose and flask after odor sampling) (Fig. 1). These measures were performed on the first sampling of the odorant to avoid any effect of the subjective ratings on motor behavior. In addition, we measured the number of odorant sampling performed during the entire trial. Each odorant sampling was defined as an approach of the flask within 5 cm around the tip of the participant's nose.

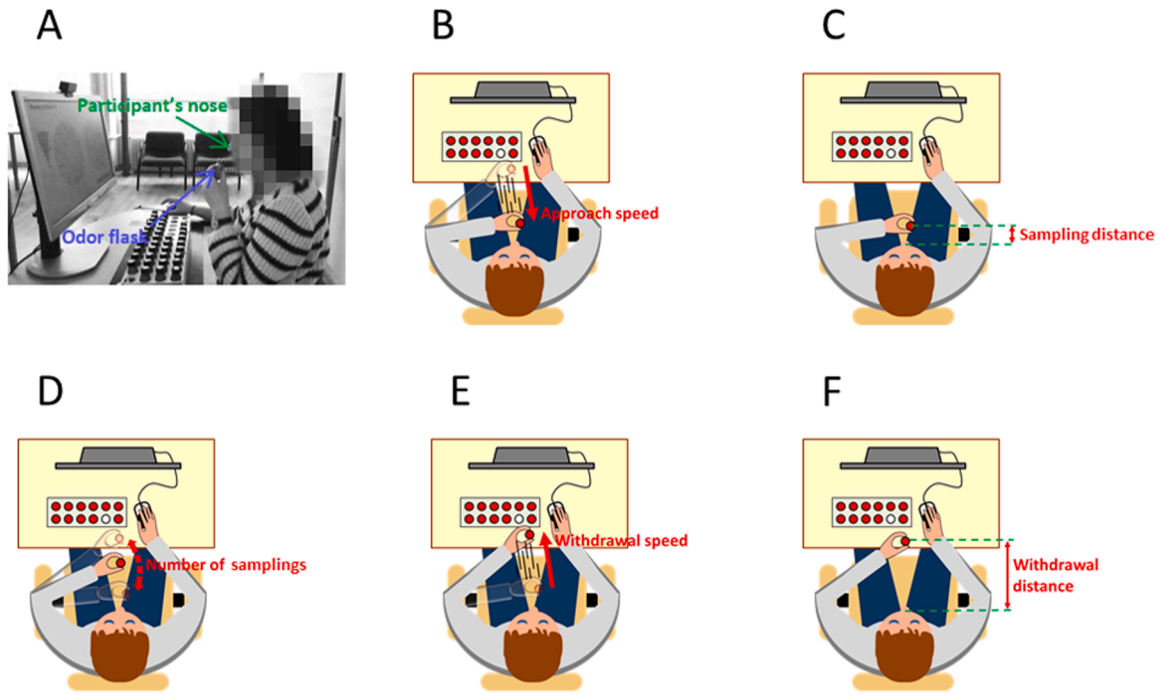


Fig. 1. Motor parameters. A. Example of a participant exploring odor flask. We measured the B. speed of approach of the flask containing the odorant to the nose C. the distance between the flask and the nose (called sampling distance), D. the number of odorant samplings, E. the withdrawal speed and F. the distance of withdrawal corresponding to the maximal distance between the nose and the flask after odor sampling.

2.4. Data analysis

All statistical analyses were performed using Statistica software with α risk set at 5%. For all experiments, we checked normality (Kolmogorov-Smirnov) and variance (Levene Test), and parametric or non-parametric tests were performed accordingly.

For perceptual rating analyses (explicit assessments), we performed Friedman tests for comparison of odorant and Spearman tests for correlations. A principal component analysis (PCA) was carried out on odorants ratings (a data matrix with 23 columns for the 23 odorants, and 24 lines for the ratings of the 24 participants). The first principal component (PC1, explaining maximum data variance) accounted for 71.4% of the total variance and underlay liking and wanting on the one hand, and the irritation dimension on the other hand. The second principal component (PC2) accounted for 24.99% of the total variance and underlay, to a lesser extent, the intensity and familiarity dimensions.

Based on the PC1 and PC2 coordinates, we defined two hedonic groups of odorants (highly pleasant and unpleasant) and compared 5 independent behavioral responses induced by these odorants, using two-tailed paired *t*-tests. Finally, we performed Pearson correlations between PC1 and the various behavioral parameters.

3. Results

Explicit assessments and relationships between ratings.

To use of motivational behavior to assess the hedonic value of odorants, it first needs confirming that pleasant odorants are indeed also motivating. One simple way to assess this motivational component is to directly ask participants whether they want to smell the odorant again (Triscoli et al., 2014) (Fig. 2A). Analysis of verbal reports first showed that both liking (Odorant effect Friedman $F_{24,22} = 263.542$, $p < 0.001$; Fig. 2Bi) and wanting ratings (Odorant effect Friedman $F_{24,22} = 230.823$, $p < 0.001$; Fig. 2Bii) varied between odorants. Importantly, there was a significant correlation between the two ratings: the more an odorant was liked, the more it was wanted (Spearman $r = 0.979$, $p < 0.001$; Fig. 2Biii).

We then explored other perceptual dimensions: intensity (Odorant effect Friedman $F_{24,22} = 213.513$, $p < 0.001$; Fig. 2C), familiarity (Odorant effect Friedman $F_{24,22} = 156.008$, $p < 0.001$; Fig. 2D) and irritation (Odorant effect Friedman $F_{24,22} = 217.639$, $p < 0.001$; Fig. 2E), all of which were found to vary between odorants.

Thirdly, we considered human olfactory perception in its complexity by applying a PCA to the 23 olfactory stimulations, showing that the liking and wanting dimensions were very close in the perceptual space (Fig. 3A). We then built an odor space formed by the first two PCs, into which the 23 odorants were projected (Fig. 3B). Within this odor space, odorants that were close on the X axis were also found to be close in term of hedonics and reinforcement properties (Fig. 3B).

Overall, we showed that odorants that were perceived as pleasant were also described as wanted. This suggests that pleasant odorants possess rewarding properties such as those that are involved in guiding motivated behavior.

We next analyzed the impact of the odorants that were the most liked/wanted (highly pleasant odorants) and the least liked/wanted (unpleasant odorants) on various parameters of motivated behavior. This determined whether odorants with different hedonic values differently impacted motivated behavior.

Odor motivated behavior.

We first selected the odorants that were the closest on PC2 (to control for intensity and/or familiarity effects on behavior) but were the most distant on PC1 (the most different in terms of hedonics and reinforcement capacity). ISO, CAR and GER were the most "liked/wanted" odorants ("highly pleasant odorants": see right side of PC1 axis, Fig. 3B), and BUT, THIO and CRE were the most "unliked/unwanted odorants" ("unpleasant odorants": left side of PC1 axis, Fig. 3B). In the odorant rating experiment, the participants had 1 min to freely smell each odorant of the panel. During this time, their movements were video-tracked; this technique avoided the use of devices that could affect movements (Fig. 2A). Using Volcan software, we analyzed 5 independent steps of the exploration kinetics of the 6 selected odorants: odor source approach and withdrawal speed, number of odorant samplings,

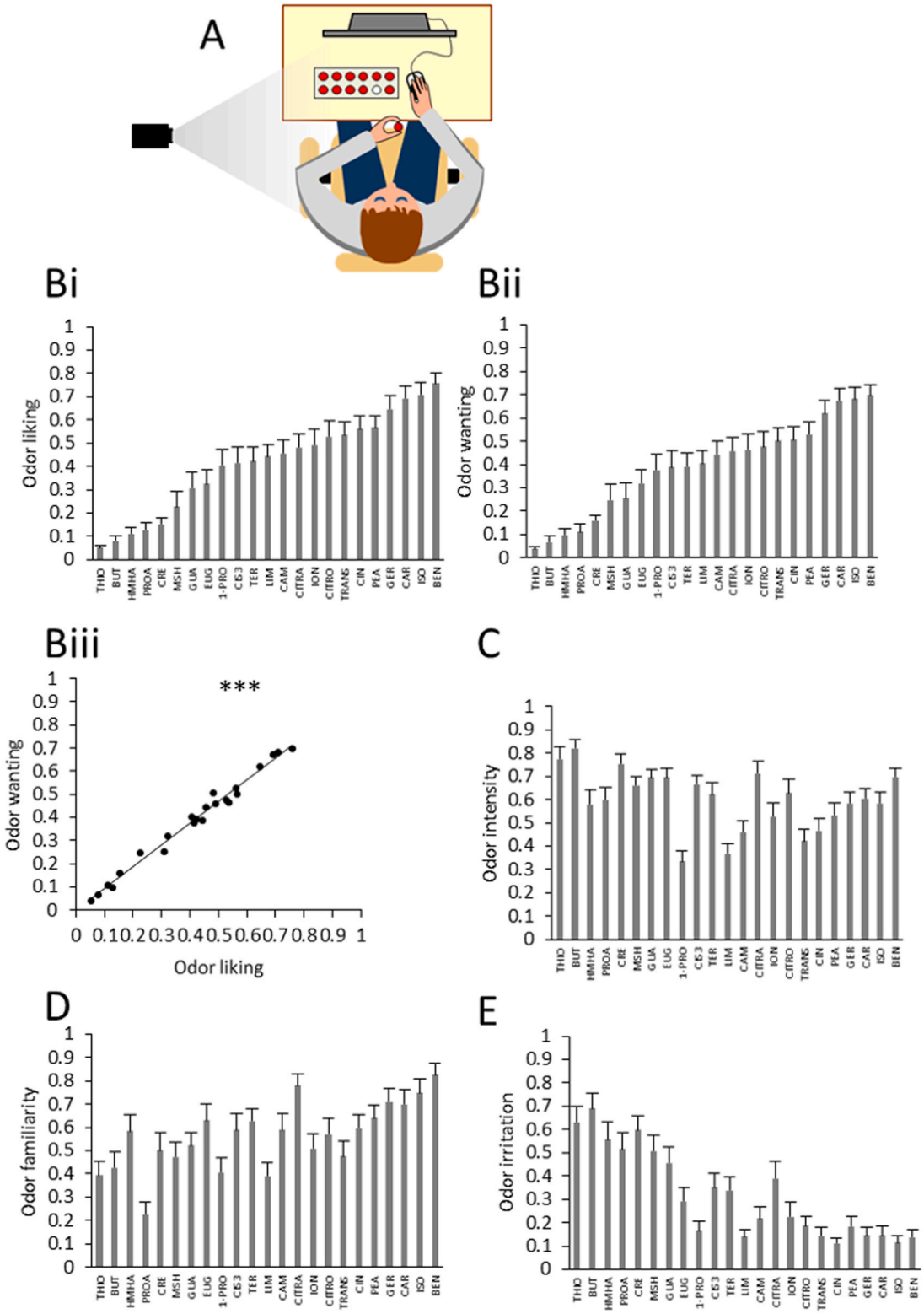
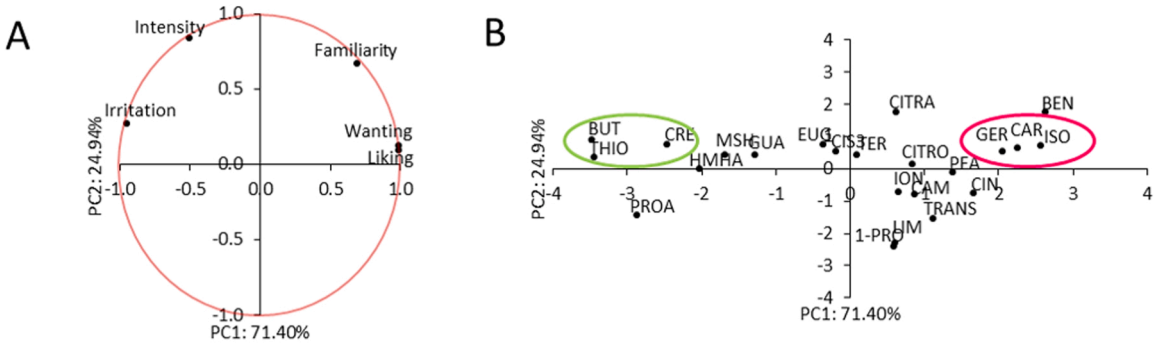


Fig. 2. Subjective assessment of odorant perception by rating. A. Subjects (n = 24) were instructed to rate the pleasantness, intensity, familiarity, irritation and desire to smell again of 23 odorants in one session. All odorant compounds were presented at the same vapor pressure and in random order during 1 min Bi. Liking and Bii. Wanting were assessed for the 23 odorants (Friedman Odorant effect; Liking $F_{(24,22)}$= 263.542 $p < 0.001$, Wanting $F_{(24,22)}$= 230.823 $p < 0.001$). Biii. There is a positive correlation between Liking and wanting (Spearman correlation r = 0.979, $p < 0.001$). C. Intensity, D. Familiarity and E. Irritation ratings varied among odorants (Intensity $F_{(24,22)}$= 213.513 $p < 0.001$, Familiarity $F_{(24,22)}$= 156.008 $p < 0.001$, Irritation $F_{(24,22)}$= 217.639 $p < 0.001$). * **$p < 0.001$.
BEN: Benzaldehyde, ISO: Isoamylacetate, CAR: L-Carvone, GER: Geraniol, PEA: 2-phenylethanol, CIN: Cineol, TRANS: Trans: trans-2-hexenylacetate, CITRO: Citronelol, ION: β-Ionone, CITRA: Citronelal, CAM: Camphor, LIM: R-Limonene, TER: (-)Terpinen-4-ol, CIS3: Cis-3-hexenol, 1-Pro: 1-propanol, EUG: Eugenol, GUA: Guaïacol, MSH: 3-methyl-3sulfanylhexan-1-ol, CRE: p-Cresol, PROA: Propanoic acid, HMHA: 3-hydoxy-3-methylhexanoic acid, BUT: Butanoic acid, Thio: Thioglycolic acid.



	PC1	PC2
Liking	0.984	0.091
Intensity	-0.506	0.835
Wanting	0.984	0.126
Familiarity	0.690	0.673
Irritation	-0.950	0.269

Fig. 3. PCA on odorant ratings. A. The correlation coefficients between the two first principal components of the PCA (PC1 and PC2) and each of the five olfactory perceptual dimensions. B. The 23 odorants projected into a two-dimensional space made of the first and second PCs. For motor behavior analyses, we selected the 3 most extreme odorants on PC1 and closest on PC2 (pink: high pleasant; green: low pleasant).
BEN: Benzaldehyde, ISO: Isoamylacetate, CAR: L-Carvone, GER: Geraniol, PEA: 2-phenylethanol, CIN: Cineol, TRANS: Trans: trans-2-hexenylacetate, CITRO: Citronelol, ION: β-Ionone, CITRA: Citronelal, CAM: Camphor, LIM: R-Limonene, TER: (-)Terpinen-4-ol, CIS3: Cis-3-hexenol, 1-Pro: 1-propanol, EUG: Eugenol, GUA: Guaïacol, MSH: 3-methyl-3sulfanylhexan-1-ol, CRE: p-Cresol, PROA: Propanoic acid, HMHA: 3-hydoxy-3-methylhexanoic acid, BUT: Butanoic acid, Thio: Thioglycolic acid.

closest distance between odor source and nose (odorant sampling distance), and greatest distance between odor source and nose after odor sampling (withdrawal distance). We found that participants exhibited different motor behaviors depending on the odorant group (high versus low pleasantness) (interaction between odorant group and motor parameters $F_{4115} = 5.7$, $p < 0.001$). Participants approached the odor source faster (Fig. 4 Ai, paired *t*-test $t_{23} = -2.363$, $p = 0.027$) and closer to their nose (Fig. 4 Aii, paired *t*-test $t_{23} = 2.692$, $p = 0.013$) for the highly pleasant than for the unpleasant odorant group. They smelled the odor source longer (Fig. 4 Aiii, Wilcoxon $W_{23} = 20.500$, $p = 0.003$), and removed it more slowly (Fig. 4 Aiv, paired *t*-test $t_{23} = 2.247$, $p = 0.035$) for the highly pleasant than for the unpleasant odor group. Finally, the odor flask was held closer to the nose after sampling for highly pleasant than unpleasant odorants (Fig. 4 Av, paired *t*-test $t_{23} = 2.563$, $p = 0.015$). Using permutation tests (100,000 permutations), we found that the probability of the 5 motor parameters being significantly different between 2 odorant groups (constituted of 3 odorants each) was $p < 0.00002$.

To confirm that these results can be applied to the whole range of odorants, and not only to the extreme cases, we performed correlations between PC1 including the 23 odorants and the 5 individual motor parameters. There was no correlation between speed of approach and PC1 coordinates (Fig. 4Bi, Pearson correlation $r = 0.240$, $p = 0.269$), whereas odorant sampling distance (Fig. 4 Bii, Pearson correlation $r = -0.478$, $p = 0.021$), number of samplings (Fig. 4 Biii, Pearson correlation $r = 0.627$, $p = 0.001$), speed of withdrawal (Fig. 4 Biv, Pearson correlation $r = -0.510$, $p = 0.013$) and withdrawal distance (Fig. 4 Bv, Pearson correlation $r = -0.490$, $p = 0.018$) were significantly correlated to PC1 coordinates. These results showed that highly pleasant and unpleasant odorants elicited different motivated behaviors (Fig. 4C) that could be implicitly assessed, without external intervention or and invasive method.

Taken together, these results showed that odor source approach and withdrawal speed, number of samplings, smallest distance between flask and nose and greatest distance between odor source and nose after odor sampling depended on the odor's hedonic value. In other words, this strongly suggests that motivated behavior reflects odor hedonic value and can thus be used as an objective non-invasive measure of odor hedonics.

4. Discussion

In the present study, we sought to identify new measurements of odor hedonics based on motivated-approach behavior. Odor hedonics is the most salient aspect of olfactory perception. In affective neurosciences, the hedonic value of a stimulus and its induced motivation have been dissociated based on their respective neural bases (Berridge and Aldridge, 2009). We found here, in accordance with Berridge's observations concerning food, that odorant liking and wanting ratings were positively correlated: the more the odorant was liked, the more it was wanted. These findings highlight the close link between affective response and the motivation to smell an odorant, and encouraged us to use odor-induced motivated behavior to assess odor hedonics.

From a behavioral point of view, odor hedonics is a major source of information about the environment, and triggers approach or avoidance. Here, we found that participants approached pleasant odorants faster, held them closer to their nose, smelled them longer and removed them more slowly and less far than unpleasant ones. These findings open up a new possibility of measuring odor-driven behaviors in freely moving humans. Such an approach constitutes real added value to the paradigms that are currently used and that suffer from limitations such as invasiveness (assessment of skin conductance, heart rate, sniffing, etc.), subjectivity (measurement scales or verbal responses) or a requirement of high expertise (facial expressions).

The difference in motor behavior induced by pleasant and unpleasant odorants may allow adaptive behavior (Scherer, Ekman, and Schorr 1994; Keltner and Gross 1999). In animals, pleasant odorants can signal pleasant stimuli such as palatable food or sexual behavior. In this case, it seems relevant to quickly approach food before a congener eats it or to quickly approach a congener of the opposite sex to increase the likelihood of mating. Interestingly, in our procedure, while speed of approach differed between pleasant and unpleasant odorants, it did not correlate with olfactory perception (PC1). This can be explained by the fact that the odorant cannot be sampled before it is close enough to the nose, and that some participants may slow down their movement before odor detection. However, when odor intensity is sufficiently high to allow detection at a sufficient distance, speed of approach has been successfully used in rodents to assess odor hedonics (Kermen et al., 2016). In the present study, during the entire trial, the participant was allowed to

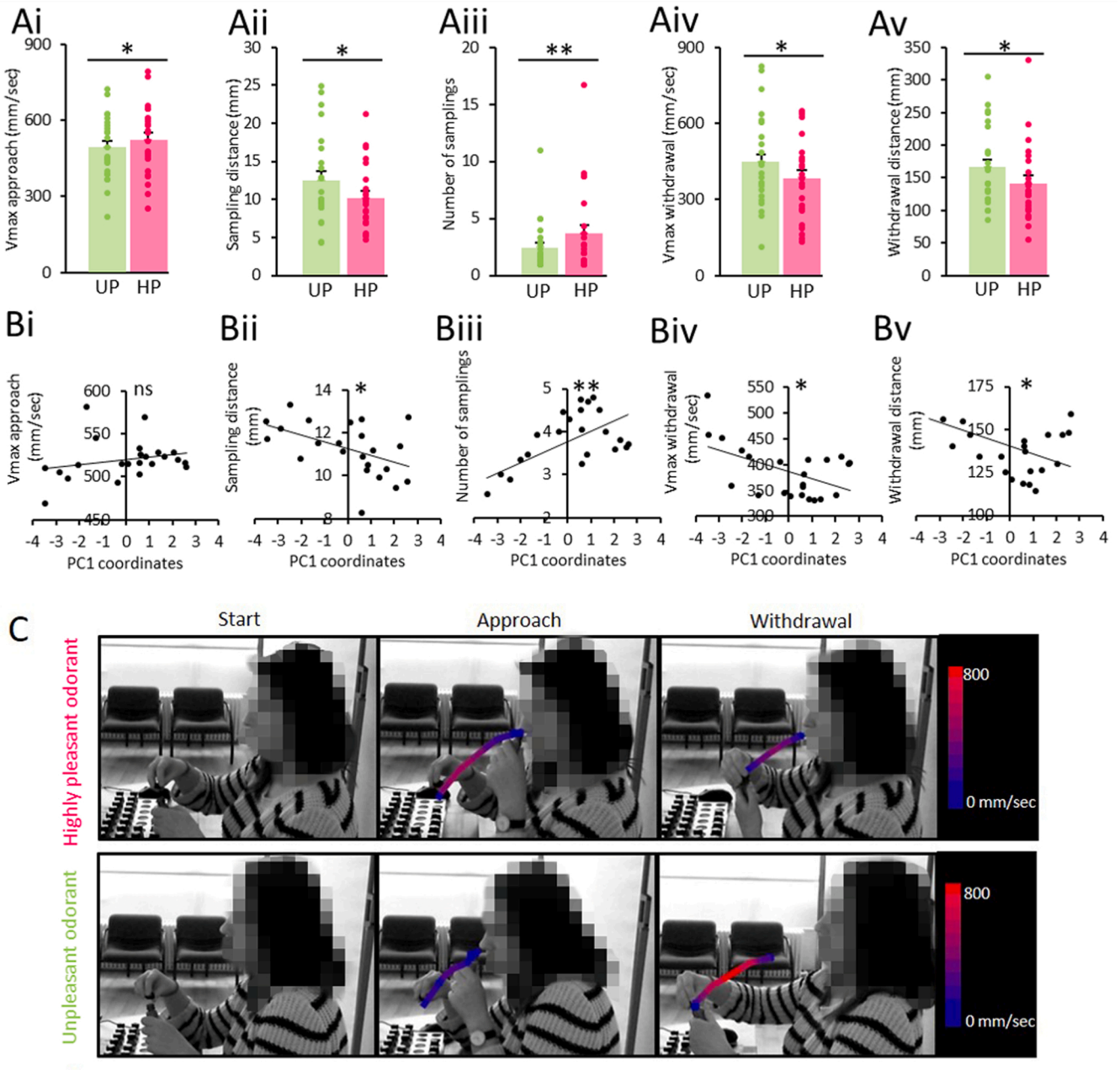


Fig. 4. Pleasant odorants induce motor motivated behaviors. A. We compared motor behavior between highly pleasant (HP) and unpleasant (UP) odorant groups. Ai. Speed of approach toward subjects (n = 24) is higher for HP compared to UP odorants (Two-Tailed paired T-Test, p = 0.027). Aii. The distance between the nose and the odor source is shorter for HP compared to UP odorants (Two-Tailed paired T-Test, p = 0.013). Aiii. HP odorants are sampled more time than UP ones (Two-Tailed paired T-Test, p = 0.003). Aiv. Speed withdrawal is slower for HP than UP odorants (Two-Tailed paired T-Test, p = 0.035). Av. Withdrawal distance is shorter for HP than for UP odorants (Two-Tailed paired T-Test, p = 0.017). B. Correlations between motor behavior and PC1 coordinates. Bi. There is no correlation between the speed of approach and PC1 coordinates (Pearson correlation, R=0.240 p = 0.269). Bii. The sampling distance (Pearson correlation, R=−0.478 p = 0.021), Biii. the number of samplings (Pearson correlation, R=0.627 p = 0.001), Biv. the speed of withdrawal (Pearson correlation, R=−0.510 p = 0.013) and Bv. the withdrawal distance (Pearson correlation, R=−0.490 p = 0.018) are correlated to PC1 coordinates. C. Example of odor exploration kinetic for HP and UP odorants. Bars represent means of individual data points. *p < 0.05, * *p < 0.01.

approach the flask to the nose as many times as they wanted. We measured the number of times they did so (number of odorant samplings), and found that this was greater for pleasant odorants, in line with previous studies showing that sniff volume and duration are larger/longer for appetitive smells (Warren et al., 1994; Bensafi et al., 2003; Bensafi et al., 2007; Johnson et al., 2006). Note that since odorant subjective ratings could occur throughout odorant exploration in our experiment, it is likely that ratings could affect the number of odorant sampling. Indeed, rating odorant liking and wanting could constrain the subsequent decision to perform additional sampling during the remaining exploration period. Beside the number of odorant samplings, we identified other novel motor parameters which are measured during the first odorant sampling and thus are not affected by any additional instructions given to the participant or participant's ratings: withdrawal speed, distance between flask and nose, and withdrawal distance (maximal distance between nose and flask after odor samplings). These motor behaviors were strongly correlated with hedonics and occurred after sampling. They reflect the need to get further away and faster from aversive odorant sources, or to stay longer and closer when the odor source is pleasant.

To sum up, the present methodological contribution suggests that measurements of motivated behaviors can be used to assess human odor hedonics. This could be achieved with a simple webcam placed next to the participant in order to evaluate the speeds and trajectories of the odor flask and the participant's nose. In these conditions, the participant's motor behavior is not constrained by any sensors. An originality of our approach concerns the way in which participants were stimulated. Whereas most previous studies in the field used a stimulation mode managed by an automaton (olfactometer) or another person (experimenter), our method allows measurement of the emotional response to odorants in more ecological or naturalistic conditions, since participants stimulate themselves. Thus, the collected response is closer to real conditions, and much less influenced by the experimental setting. Another advantage is the cost of the experiment, requiring only a standard webcam. One limitation may be that the participant has to stay in range of the camera and that the use of only one lateral camera do not consider any possible movements in depth dimension, although this can be solved by a more powerful camera system enabling flask and nose trajectories to be tracked in 3D. Finally, as a perspective, one may consider the use of these measures in populations with language impairment or when the use of sensors is difficult to implement.

CRediT authorship contribution statement

LC, MB and NM designed the study. LC performed the experiments. MT and NN provided technical support. LC, MB, MT and NM analyzed the data. LC, MB and NM wrote the manuscript in consultation with MT.

Declaration of Competing Interest

The authors have no conflicts of interest to disclose.

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