Social odors (even when masked) make you more emotional: behavioral and neural insights

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Keywords: moral decision-making, moral dilemmas, chemosignals, social odors, olfaction, social context

Highlights:

- Social odors modulate neural activity during the processing of moral dilemmas
- Social odors increase the recruitment of emotional areas during accidental dilemmas
- Social odors do not affect the processing of congruent and instrumental dilemmas
- Social odors mediate high-level decision-making by increasing emotional experience

Abstract

Moral rules evolved within specific social contexts that are argued to shape moral choices. In turn, moral choices are hypothesized to be affected by social odors as they powerfully convey socially-relevant information. We thus investigated the neural underpinnings of the effects that social odors operate on the participants' decisions. In an fMRI study we presented to healthy individuals 64 moral dilemmas divided in incongruent (real) and congruent (fake) moral dilemmas, using different types of harm (intentional: instrumental dilemmas, or inadvertent: accidental dilemmas). Participants were required to choose between deontological or utilitarian actions under the exposure to a neutral fragrance (masker) or social odors concealed by the same masker. Smelling the masked social odor while processing incongruent (but not congruent) dilemmas activates the supramarginal gyrus, consistent with an increase in prosocial attitude. When processing accidental (but not instrumental) dilemmas, smelling the social odor activates the angular gyrus, an area associated with the processing of people's presence, supporting the hypothesis that social odors enhance the saliency of the social context in moral scenarios. These results suggest that social odors can influence moral choices by increasing the emotional experience during the decision process, and further explain how sensory unconscious biases influence human behavior.

1. Introduction

Moral choices are most often explained as a result of emotional and cognitive processes¹⁻⁸. However, morality is primarily a social phenomenon, tightly dependent on the social context. In their Relationship Regulation theory (RR), Rai and Fiske⁹ highlight the role of social context in shaping moral choices and posit that people are led by moral motives to evaluate and guide one's own and others' judgments and behaviors, according to moral rules developed within specific social relationships. In other words, people build a particular moral motive allowing to live in a specific social context and moral transgressions are defined as the circumvention of such specific relational prescriptions⁹. Recent empirical evidence supports this theory: for instance, participants' moral acceptability of tradeoff scenarios can be affected by unconscious biases, such as intergroup prejudices and stereotypes, and the perception of different social groups influences the neural systems implicated in moral choices¹⁰.

Unconscious biases can influence moral decisions based on a variety of stimuli: for example attitudes (such as dispositions towards people or places), implicit stereotypes (such as judging a person as attractive or unintelligent because is a cheerleaders¹¹) or somatic reactions (such as endocrine release or psychophysical reactions¹²), but this investigation has yet to consider the possibility of evaluating the effects of social information transmitted via sensory subliminal cues, such as odors. Humans transfer socially-relevant information, such as age, gender, health status, sexual availability and personal predispositions, via body (or social) odors^{13,14}. Furthermore, odors – including people's odors – are everywhere, and we do not necessarily realize their presence consciously^{14,15}.

The idea of using olfactory stimuli to investigate moral choices is not entirely new. Landy & Goodwin¹⁶ argued how olfactory influences on morality are greater than those mediated by vision, the sense humans consider to mostly rely on. Additionally, Schnall et al.¹⁷ demonstrated that the presence of a disgusting odor toughens the judgment on vignettes without moral content. Also, we have previously shown that the subliminal exposure to a neutral (non-social) odor can bias moral

choices towards options characterized by harm avoidance (deontological options¹⁸). Generally speaking, a harm is justified (or to some extent forgiven) if it comes as the side-effect of a moral action carrying a greater benefit compared to an intentional harm with the same outcome^{19,20}. All in all, odors are able to transfer social information and their effect on moral choices seems to modulate harm avoidance.

To our knowledge, previous studies have only explored the behavioral effects of olfactory contextual stimuli on moral choices^{17,18}. However, whether and how the social context might impact moral decision making when induced via sensory subliminal stimulation, and the neural underpinnings of moral choices under the exposure of masked social odors are still unknown. In an meta-analysis it has been indicated that, in absence of odor stimulation, moral (vs. non-moral) choices were found to be associated with increased activations in primarily cognition-related areas (i.e., left and right middle temporal gyrus, MTG, right middle frontal gyrus, rMFG, right inferior frontal gyrus, rIFG) and primarily emotion-related areas (i.e., cingulate gyrus, left precuneus²¹). However, the way in which moral dilemmas are formulated modulates the competition between the fast, automatic emotional response and the slow, deliberative cognitive system. As previously shown, instrumental dilemmas (Footbridge-type dilemmas²²) present the recruitment of emotion-related brain areas such as medial prefrontal cortex, posterior cingulate cortex/precuneus, amygdala, and brain areas involved in “theory of mind” such as the temporoparietal junction (TPJ) and angular gyrus^{1,2,4}. On the other hand, accidental dilemmas (trolley-type dilemmas) are associated with activations in neural areas involved in working memory and cognitive control, such as dorsolateral prefrontal cortex and inferior parietal lobe^{1,2,4}.

If the impact of the exposure to social odors on the neural underpinnings of moral choices still remains unexplored, it has been shown that distinct neural pathways are responsible for the processing of social (vs. non-social) odors²³, in line with what found for social information presented through other sensory modalities (Schupp et al.,²⁴ for vision and Belin et al.,²⁵ for audition). Processing social odors recruits distinct brain regions including the occipital cortex, an

area that becomes active when either visual stimuli or socially-relevant stimuli are cross-modally presented²⁶; the angular gyrus, that activates in response to human body related information²⁷, but also to tasks involving social cognition and multisensory integration; and finally, the anterior and posterior cingulate cortex, an area involved in emotion regulation^{28,29} and self-reflective processes³⁰.

In the present work, we hereby tested whether and how introducing a social context through masked social odors impact the behavioral and neural correlates of moral choices. The aims of the study were the following: 1) to test whether subliminally presented social odors have a selective effect on incongruent moral dilemmas (real dilemmas) or generalize to different types of decision-making scenarios (congruent or fake dilemmas); and 2) to investigate whether and how social odors impact harm avoidance decisions. We designed a functional magnetic resonance imaging (fMRI) study in which participants were asked to answer to 64 moral dilemmas during the presentation of a fragrance neutral in pleasantness (masker) or to a social odor concealed by the same fragrance (masked social odor). The main dependent variable was the type of moral choice made, which could be *utilitarian*, if participants decided to execute harmful actions in order to save people, or *deontological*, if participants decided not to cause harm, even if the harm is meant for a greater good^{19,31}. To explore whether the effect of the masked social odor is modulated by the dilemmatic nature of the presented scenario, half of the dilemmas were designed to be congruent, meaning that cognitive and emotional processes converged in the same deontological action so that they were fake dilemmas, and half to be incongruent dilemmas, in which the two processes diverged, so they were real dilemmas³². Moreover, to clarify the modulation of the type of harm, half of the dilemmas were instrumental (dilemmas in which the harm is deliberate) and the other half were accidental (dilemmas in which the harm is a side effect).

We hypothesized that the effect of the masked social odor would be specific for the incongruent dilemmas (aka the real dilemmas). Since it has been shown that when dealing with incongruent (compared to congruent) dilemmas, individuals are more willing to provide utilitarian

answers, we expected such trend to be reduced in the presence of the masked social odor.

Moreover, if the social context, induced by the presence of masker social odor, makes people more prone to behave according to social rules, the presentation of the masker social odor should result in an increment of deontological answers for instrumental dilemmas.

With respect to the neural underpinnings, we hypothesized that the processing of incongruent (compared to the congruent) dilemmas would be associated with brain regions commonly implicated in this type of task, such as the amygdala, the ventro-medial prefrontal cortex (vmPFC)^{1,33}, the temporo-parietal junction³⁴ and the precuneus²¹. Additionally, we predict that the presence of the social odor would favor activations at the level of areas commonly associated with social information, including social odor processing, such as the angular gyrus, occipital cortex, and the anterior posterior cingulate cortex^{14,23}.

We further hypothesized that during the processing of dilemmas that describe intentional harm, emotional brain areas, such as the cingulate gyrus or precuneus, would be more strongly activated. However, given the innovative nature of this research, we do not have specific predictions on whether the masker social odor would recruit different brain areas to process instrumental or accidental dilemmas, and we will therefore explore whole-brain activations with respect to this contrast.

2. Materials and Methods

2.1 Donors

Ten healthy, heterosexual males donated their body odors in two different days (Age: M = 26.28 years old; SD = 3.63; range = 20 – 31 years old). Male donors were chosen based on the greater intensity of their body odor axillary secretions³⁵. The donors reported: i) to be non-smokers³⁶; ii) not to have health issues or to undergo drug treatment known to be related to olfactory alterations; iii) to have an age ranging from 18 to 35. Donors provided written consent and agreed to follow behavioral, nutritional (i.e., no alcohol, smoking, food altering the natural body odor) and

hygiene instructions throughout the collection session (adapted from¹⁴). The medium of body odor collection was a t-shirt, previously washed with an odorless detergent. T-shirts were worn by donors for 12 consecutive hours during the day, right after having taken a shower using fragrance-free body wash and having dried themselves with towels washed with the same odor-free detergent used to pre-wash the t-shirts. Donors collected their body odors on separate t-shirt for each day of collection. Odorless plastic bags were provided to each donor to store each of their t-shirts before bringing them to the lab, the day after each collection period^{23,37}. Samples were perceptually evaluated for odor contamination (e.g., alcohol, smoke, fragrance, food) and for body odor detectability by one to three trained experimenters. All samples were then stored in a -80°C freezer to prevent sample deterioration³⁸.

2.2 Participants

The original group of participants was composed of 30 women. The rationale for testing only women is based on the evidence that women show a greater preference for social emotional stimuli³⁹, also when presented in olfactory form⁴⁰. The participants followed the same criteria as the donors, and additionally they had to score at the 16-item Sniffin' Sticks Identification subtest of the Sniffin' Sticks Extended test above 10⁴¹ as well as presenting a regular menstrual cycle⁴².

No depression or heightened sensitivity to disgust (Disgust Scale⁴³) was revealed. Two participants were removed from the study because of possible clinical problems. The final sample included 28 healthy, heterosexual, right-handed women aged between 19 and 34 ($M = 23.70$, $SD = 4.19$), who were normosmic ($M = 13.42$, $SD = 1.46$, range= 11-16), and whose STAI state score before the task was within the normal range ($M = 33.70$, $SD = 4.31$, range= 24-42). Participants were instructed to not eat or drink anything but water one hour prior to testing, and to not wear any scented products on the day of testing. The SISSA Ethics Committee approved the study, which is in accordance with the Declaration of Helsinki and an informed written consent was obtained from each participant.

2.3 General procedure

At the beginning of the experiment, participants were seated in a quiet room and they were instructed about the experiment. Then participants performed the odor identification test⁴¹ and they completed the State–Trait Anxiety Inventory (STAI-T and STAI-S). Moreover, a rating odor task was proposed, followed by the moral decision-making task. Afterwards participants completed, inside the MRI scanner, an odor rating task, the moral decision-making task and again the odor rating task. Each image was presented to the participants at the center of a 17” monitor (15.16° visual angle), upon a uniform white background. A central black or green fixation cross (0.2° visual angle) was presented before each image. Odor and visual presentation, as well as response collection, was regulated by the stimulus presentation program E-Prime Professional 2.0 (Psychological Software Tools. Sharpsburg, PA).

2.4 Moral dilemmas

The 4CONFiDE moral set described in Cecchetto *et al.*²⁰ was reshaped for this study, to include congruent and incongruent dilemmas. A total of 64 dilemmas were presented, 32 congruent and 32 incongruent. Furthermore, half of the congruent and incongruent dilemmas were accidental and the remaining instrumental. Each dilemma type was presented in 16 alternative versions to allow for the presentation of the same factors’ combination in both odor conditions. The order of presentation of the dilemmas was randomized across subjects to exclude any presentation order effects on moral decision-making. Each dilemma was presented on two subsequent screens. The first screen described the scenario, in which a danger threatens to kill a group of persons, and a hypothetical action would save these people but cause the death of another person. The second screen presented the question *Do you...[action verb] so that...?* Participants had to choose between four options: “I certainly do it”, “I do it”, “I do not do it”, and “I certainly do not do it”. The first two were considered to be utilitarian, as they maximize overall utility (i.e., saving more lives), whereas the second two choices were considered to be non-utilitarian (deontological). Dilemmas

were presented using black font color (font: Calibri, size: 24) against a white background on a 19-in. computer screen at a viewing distance of 60 cm. Stimulus presentation was delivered with E-prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

2.5 Odor stimuli

Two odor conditions were presented within participants. One set of dilemma alternatives ($N = 32$) was presented following the exposure to an emotionally neutral, rather unfamiliar odor (aka, *masker odor*; 200uL of cedarwood oil, Sigma-Aldrich), as determined via pilot studies ($N = 53$ participants). Such odor was used also in the other odor condition (aka, *masked social odor*) to perceptually mask the body odor samples. The masker social odor consisted of the combination of one equally-sized quadrants of t-shirt collected from each of the four donors⁴⁴. Each participant smelled the samples of four of the ten donors, but in order to reduce the stimuli similarity⁴⁵, the combination varied in terms of the axilla the sample came from and the day at which it was collected.

2.6 Olfactometer

Odors were presented bi-rhinally in a temporally-precise, square-shaped manner using a computer-automated olfactometer⁴⁶. A low bi-rhinal flow rate of 1.0 L/m (a total of 0.5 L/m per nostril) was used to prevent irritation of the nasal mucosa over time^{47,46}. Odorous air was directed to the nose when the odor was delivered, and clean air was presented subsequently for approximately 1.6 (± 0.2) sec. After odor presentation, clean air was presented until participant's response (5 sec) to minimize odor residuals⁴⁸. Odor stimuli were delivered directly to both participants' nostrils from a nasal manifold, attached to the participant's chest by means of a chest strap, connected to the olfactometer via Teflon tubing.

2.7 Odor rating task

To test whether the masking procedure applied to cover the body odor had the expected perceptual impact and was equivalent across olfactory conditions, participants were asked to rate intensity, pleasantness and familiarity of the masker, masked social odor and clean air before and after the moral decision-making task. Each odor presentation was preceded by a green fixation cross on the screen for 0.5 seconds followed by a black screen while an odor was presented for 4 sec; a white screen followed for an average inter-stimulus interval of 6 sec (± 0.12 sec). Subsequently, three questions were asked in succession and in a random order, namely “How intense was the odor you just smelled?”, “How pleasant was the odor you just smelled?”, and “How familiar was the odor you just smelled?”. Perceptual ratings for odor intensity, pleasantness, and familiarity were collected on a 10-point computerized VAS, ranging from “not at all” to “very much”. Participants were instructed to answer even if they did not perceive odor. Odors rating task was performed inside the scanner to reduce the time of the experimental session but without collecting functional MRI data.

2.8 Moral decision-making task

Before starting the moral decision-making task, participants performed two practice trials. Participants were instructed using an Italian version of the instructions suggested by Christensen et al.,¹⁹ and previously used in Cecchetto et al.²⁰. Each trial began with a white screen presented for 10 sec followed by a black cross that was displayed for 5 sec (jittered randomly ± 0.294 sec). Then, a green cross was presented for 4 sec and the odor started to be delivered. Successively the scenario was presented for 25 sec. The scenario presentation was combined with the odor presentation. Afterwards, the question slide was presented together with the releasing of clean air. The four choices (“I certainly do it”, “I do it”, “I do not do it”, and “I certainly do not do it”) were displayed below the question.

Dilemmas were divided into four runs. During each run, 16 trials balanced for moral dilemmas types and odor conditions, were presented in randomized order. Each trial began with a

black cross that was displayed for 5 sec (jittered randomly ± 0.294 sec). Then, a green cross was presented for 1.2 sec (jittered randomly ± 0.159 sec) and the odor started to be delivered. The scenario presentation was 22 sec long and it was combined with the odor presentation. Afterwards, the question slide was presented together with the releasing of clean air as. Participants had maximum 5 sec to answer. After the answer a black cross was presented for 5 sec. Participants were allowed to take a short break at the end of each run.

2.9 Behavioral data analysis

Frequency analysis was performed on the four distinctive options to see whether the number of each option change on odor condition. Since no significant differences were found among the four response options in relation to odour condition, we collapse them for the following analyses.

Behavioral data were analyzed with linear mixed-effects models (LMMs) using R (version 2.10.1; <http://www.r-project.org/>) and in particular using *lme* function (*nlme* package; <https://cran.r-project.org/web/packages/nlme/nlme.pdf>) for continuous variables and the *glmer* function (*lme4* package; <http://cran.r-project.org/web/packages/lme4/index.html>). To account for individual differences (e.g., some people are more “deontological” than others), participants were included in the models as *random*. To avoid a warning of non-convergence, an optimizer (bobyqa) was applied⁴⁹. Results with and without the optimizer are not significantly different (https://github.com/lme4/lme4/blob/master/misc/notes/release_notes.md). Estimates on the choice between utilitarian and deontological responses were based on an adaptive Gaussian Hermite approximation of the likelihood with 10 integration points. For odor ratings, models with odor factor and session were tested. For moral choice analyses, two models were performed: the first included odor factor, as the main interest of our analysis, and congruency, as factors describing our items. The second model included odor factor and intentionality and it was performed considering only the incongruent dilemmas.

Outliers in reaction times were determined by means of the outliers-labelling rules. From a sample of 1792, 127 trials were removed for no response ($N = 127/1792$, 7.08%), and 43 trials were removed because of extremely long choice reaction times (>2.59 seconds; $N = 43/1665$, 2.58%). Conditions have equivalent final samples of trials (Masker odor = 810, Masked Social Odor = 812; $\chi^2_1 = 0.0025$, $p = 0.96$).

2.10 MRI data acquisition and pre-processing

A 3 Tesla Philips Achieva whole-body MR Scanner at the University Hospital of Udine (ASUI Udine, Italy), equipped with an 8-channel head coil, was used for MRI scanning. Head movement was minimized through cushioning within the coil. Functional volumes were obtained using a whole-head T2*-weighted echoplanar image (EPI) sequence (repetition time [TR] = 2.5s, echo time = 35ms, flip angle = 90, 28 transverse axial slices with interleaved acquisition, $3.5 \times 3.59 \times 4 \text{ mm}^3$ voxel resolution, field of view = $230 \times 230 \text{ mm}^2$, acquisition matrix = 68×62 , SENSE factors: 2 in the anterior–posterior direction). The number of volumes acquired varied for each participant and run given the task duration based on participants' reaction times (mean volumes per run = 260, SD = 4.60, range 153 – 270). Anatomical images were acquired during the final odor ratings task as 180 T1-weighted images (0.75mm slice thickness). Stimuli were viewed through VisuaStim Goggles system (Resonance Technology) mounted to the head coil, which were adjusted on each participant's vision. Responses were made and recorded through one MR-compatible response pads (Lumitouch, Lightwave Medical Industries, Coldswitch technologies, Richmond, CA) using the right hand. Due to technical problems, images from the first session of one participant and the second session of another participant were removed from the analysis.

Data were analyzed with SPM12 (Wellcome Trust Centre for Neuroimaging, London, UK). All functional volumes were realigned to the first volume, segmented in gray matter, white matter and cerebrospinal fluid tissues, spatially normalized to the standard EPI template, and smoothed using a Gaussian kernel with full width at half maximum (FWHM) of 8 mm^3 . Movement-related

variance was analyzed using the Art toolbox (www.nitrc.org/projects/artifact_detect). For each run, outlier scans were identified based on the TR-to-TR composite motion more than 2mm and/or considering whether the scan-to-scan global BOLD signal normalized to z-scores deviated from mean more than $z = 3$. The time-points identified as outliers were regressed out as separate nuisance covariates in the first-level design matrix. All participants display a percentage of outlier scan inferior to the cutoff (25%), therefore no one was excluded from the analyses and all trials were retained.

2.11 fMRI data analysis

Two separated fMRI data analyses were carried out: in the first analysis, odor conditions and congruency of dilemmas were considered to explore whether the effect of social odor was modulated by the dilemmatic nature of the presented scenario; in the second analysis, which was performed only on incongruent dilemmas, odor conditions and intentionality as the type of dilemmas were considered to investigate the effects of masker social odor on the processing of different types of harm.

Statistical analyses were performed using a general linear model (GLM) approach. In the first-level analysis data were analyzed separately for each participant. In each trial, four events were modelled: the presentation of clean air, of an odor, of the scenario combined with an odor and, of the slide including the question. The duration of each of these events was set to 0 except for the scenario presentation, which was set to a fixed time of 22s. The combination of these four event types with dilemma congruency (congruent vs incongruent) or dilemma intentionality (accidental vs instrumental) and the two odor conditions (masker or masked social odor) led to a total of 16 regressors for each run. The six motion parameters were also included as regressors of no interest in the design matrix. All regressors were convolved with a canonical hemodynamic response function. Low frequency signal drifts were filtered using a cutoff period of 128 sec. As a next step, at the individual level, contrast parameters were estimated for all the 16 regressors of interest, averaged

across the four runs. Subsequently, at the second-level analysis, 4 contrast images of the event scenario presentations from the combination odor conditions with congruency or intentionality of each participant were submitted to a flexible factorial design, with subject as random factor, odor conditions and congruency or intentionality as fixed factors, to assess neural activations of the dilemma processing during the exposure to the odor. Later, the 4 contrast images were entered to linear contrasts of the repeated measure ANOVA with two within-subject factors to investigate main effects and interactions. To identify the neuronal substrates of single odor condition or single dilemma type, simple main effects (i.e., [masker odor – masked social odor] for each odor condition and each dilemma type separately) were analyzed. To investigate whether odor conditions affect neural activity related to moral dilemma processing, we performed a dilemma types (i.e. congruent/incongruent or accidental/instrumental) by odor condition (masker odor/masked social odor) interaction at group level. Moreover, to clarify whether the neural underpinning involved in the masker social odor effects for one dilemma type (i.e. incongruent or accidental) are shared by the opposing dilemma type (i.e. congruent or instrumental), exclusive and inclusive conjunction analyses were performed between the neural areas recruited for the interactions [odor conditions X congruency or intentionality].

Finally, in order to investigate the relation between brain activations and moral choices, the mean beta values of the activated clusters were extracted using the REX toolbox (Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, MA) and simple correlation analyses were performed with percentage of utilitarian responses.

Whole-brain analyses were thresholded at $p < 0.05$, family-wise error (FWE) cluster-level corrected for multiple comparisons across the whole brain. The AAL2 toolbox^{50,51} was used to guide the labelling of the activated clusters.

3. Results

3.1 The two odor conditions are perceptually equivalent

We first tested whether the masking procedure applied to cover the masked social odor had the expected perceptual impact and rendered the olfactory conditions equivalent in their basic perceptual dimensions. The LMM on intensity ratings (clean air: $M = 2.45$, $SD = 0.13$; masker: $M = 5.83$, $SD = 0.18$; masked social odor: $M = 6.10$, $SD = 0.16$; see Figure 2A and Table 1) revealed that both the masker and the masked social odor were perceived as significantly more intense than clean air ($p < 0.001$; reference factor: clean air), but no significant difference was found between the masker and the masked social odor ($p = 0.48$; reference factor: masker). A difference emerged when looking at the effect of session (pre moral decision-making task: $M = 5.23$, $SD = 0.21$; post moral decision-making task: $M = 4.56$, $SD = 0.20$; $p = 0.024$): odors were rated as less intense during the second session compared to the first session suggesting that participants might have adapted during the task (Dalton, 2000).

The LMM on familiarity ratings (clean air: $M = 3.78$, $SD = 0.14$; masker: $M = 5.61$, $SD = 0.20$; masked social odor: $M = 5.91$, $SD = 0.17$; see Figure 2B and Table 1) showed that both the masker and the masked social odor were perceived as significantly more familiar than clean air ($p < 0.001$; reference factor: clean air), but no significant difference was found between the masker and the masked social odor ($p = 0.40$; reference factor: masker). No significant differences were found between the ratings performed before and after the task ($p = 0.32$; reference factor: pre).

The LMM on pleasantness ratings (clean air: $M = 4.48$, $SD = 0.12$; masker: $M = 4.89$, $SD = 0.16$; masked social odor: $M = 4.58$, $SD = 0.18$; Figure 2C) showed no significant differences across the three odor conditions. Moreover, no significant differences were found between sessions. Please, refer to Table 1 for descriptive data.

Figure 1. Distribution of participants' odor ratings. The black dots represent single data points, whereas the box-plot represents the interquartile range of each distribution, with the thick black horizontal bar corresponding to the median. Each box-plot is surrounded by a violin plot representing the smoothed distribution of data. Significant differences ($p < 0.05$) are indicated with a star.

Table 1. Summary of linear mixed effects model on intensity, familiarity and pleasantness odor ratings.

Intensity Ratings					95%CI	
<i>Fixed effects</i>	β	<i>SE</i>	<i>t value</i>	<i>p value</i>	<i>Lower</i>	<i>Upper</i>
<i>Intercept</i>	6.18	0.32	19.20	<0.001	5.546	6.807
Clean Air	-3.31	0.35	-9.28	<0.001	-4.016	-2.615
Masked social odor	0.24	0.34	0.70	0.484	-0.432	0.914
Session (Post)	-0.66	0.29	-2.28	0.024	-1.233	-0.093
Familiarity Ratings					95%CI	
<i>Fixed effects</i>	β	<i>SE</i>	<i>t value</i>	<i>p value</i>	<i>Lower</i>	<i>Upper</i>
<i>Intercept</i>	5.76	0.37	15.61	<0.001	5.035	6.480
Clean Air	-1.85	0.33	-5.61	<0.001	-2.502	-1.207
Masked social odor	0.27	0.33	0.83	0.410	-0.370	0.910
Session (Post)	-0.27	0.27	-0.99	0.323	-0.814	0.267
Pleasantness Ratings					95%CI	
<i>Fixed effects</i>	β	<i>SE</i>	<i>t value</i>	<i>p value</i>	<i>Lower</i>	<i>Upper</i>
<i>Intercept</i>	5.05	0.32	15.55	<0.001	4.416	5.689
Clean Air	-0.47	0.31	-1.51	0.132	-1.079	0.138
Masked social odor	-0.38	0.30	-1.26	0.210	-0.976	0.212
Session (Post)	-0.20	0.25	-0.78	0.436	-0.695	0.298

Note: β = estimate; SE = standard error; 95% CI = confidence interval. Significant p values are reported in bold. Table shows model with masker condition set as reference.

3.2 Anxiety is increased at the end of the task

A Wilcoxon test ($W = 148801$, $p < 0.0001$) determined that participants' state anxiety was increased at the end of the task ($M = 34.36$, $SD = 6.45$, range = 22 - 48) as compared to its beginning ($M = 33.67$, $SD = 4.33$, range = 24 - 42).

3.3 Irrespective of odor condition, incongruent dilemmas produce more utilitarian responses

First, the model including odor conditions, congruency and the interaction between them was performed (see Table 2 for descriptive data of single parameters). There was a significant effect of congruency on moral choice ($z = 10.08$, $p < 0.001$): the likelihood of choosing the utilitarian option increased when dilemmas were incongruent. In other words, when cognitive and emotional processes diverge (real dilemmas), more utilitarian answers are produced than when cognitive and emotional processes converge (fake dilemmas). No significant effects were found for the main effect of odor condition or for the interaction odor*congruency.

Table 2. Summary of the linear mixed effects model on moral choices with odor and congruency as fixed factors.

Moral choices	β	SE	z <i>value</i>	p <i>value</i>	β_{exp}	95%CI	
<i>Fixed effects</i>						Lower	Upper
<i>Intercept</i>	-1.19	0.18	-6.37	<0.001	0.302	0.209	0.436
Masked social odor	0.25	0.16	1.50	0.13	1.282	0.926	1.775
Incongruency (<i>Incongruent</i>)	1.65	0.16	10.08	<0.001	5.223	3.788	7.202
Masked social odor * Incongruency (<i>Incongruent</i>)	-0.32	0.22	-1.42	0.15	0.726	0.466	1.129

Note: β = estimate; SE = standard error; β_{exp} = exponential of β coefficient; 95% CI = confidence interval. Significant p values are reported in bold. Table shows model with deontological choice and masker odor condition set as references. The contrast condition from the reference for categorical factors is reported in italic in brackets.

3.4 Irrespective of odor condition, accidental dilemmas produce more utilitarian responses

Considering the results of the previous model, we tested the effect of odor conditions, intentionality and the interaction between these two factors on incongruent dilemmas only (see Table 3 for descriptive data of single parameters). A significant effect of intentionality emerged ($z = -0.43$, $p < 0.001$): in incongruent dilemmas, the likelihood of choosing the utilitarian option increased when dilemmas were accidental (vs. instrumental). The odor condition, alone or in interaction, did not affect the type of moral choice made.

Table 3. Summary of the linear mixed effects model on moral choices with odor and intentionality as fixed factors, performed on incongruent dilemmas.

Moral choices	β	SE	z value	p value	β_{exp}	95%CI	
<i>Fixed effects</i>						Lower	Upper
<i>Intercept</i>	0.004	0.17	0.02	0.98	1.003	0.717	1.405
Masked social odor	0.24	0.15	1.58	0.11	1.268	0.945	1.704
Intentionality (<i>Instrumental</i>)	-0.67	0.15	-0.43	<0.001	0.512	0.380	0.690
Masked social odor * Intentionality (<i>Instrumental</i>)	-0.34	0.22	-1.56	0.12	0.714	0.468	1.090

Note: β = estimate; SE = standard error; β_{exp} = exponential of β coefficient; 95% CI = confidence interval. Significant p values are reported in bold. Table shows model with utilitarian choice and mask only odor condition set as references. The contrast condition from the reference for categorical factors is reported in italic in brackets.

3.4 fMRI data

3.4.1 Areas involved in moral cognition are selectively activated by incongruent dilemmas

The processing of real dilemmas (contrast incongruent vs congruent dilemmas) revealed activations in the left middle frontal gyrus, left inferior parietal gyrus and bilateral precuneus (see Table 3 and Figure 2). The correlation analysis performed between beta values and percentage of utilitarian answers did not show significant results. No significant activations emerged when considering the processing of fake dilemmas (congruent vs incongruent dilemmas).

3.4.2 Activation in visual areas tracks the utilitarian responses to incongruent dilemmas when exposed to the masker odor only

The presence of the masked social odor (vs the masker odor) during the presentation of both incongruent and congruent dilemmas was accompanied by activations in the left supramarginal gyrus (see Table 4 and Figure 2). In contrast, the presence of the masker odor (vs. the masked social odor) activates the bilateral calcarine cortex, the left middle occipital gyrus, the right precuneus, the left lingual gyrus and the left posterior cingulum (see Table 4 and Figure 2). The beta values extracted from the cluster including the bilateral calcarine cortex and the left middle occipital gyrus significantly correlate with the number of utilitarian responses to incongruent dilemmas when exposed to the masker odor ($r = 0.48$, $p = .009$). No other significant correlation between behavioral responses and neural activations emerged.

3.4.3 Exposure to the masked social odor during incongruent dilemmas activates areas processing sensory-emotional information

To identify whether the brain regions that are active components in the masked social odor effect for the incongruent dilemmas are shared also for the masked social odor effect in congruent dilemmas, exclusion and inclusion conjunction analyses were performed between the areas recruited for the interaction “masked social odor and incongruent dilemmas” and for the interaction “masked social odor and congruent dilemmas”. The exclusion conjunction analysis for [incongruent (masked social odor > masker) > congruent dilemmas (masked social odor > masker)] showed that the left inferior parietal gyrus was significantly recruited only when the masked social odor was presented during the processing of incongruent dilemmas (see Table 4 and Figure 2). No significant correlations were found between the extracted beta values and percentage of utilitarian answers in this contrast. The inclusion conjunction analysis and the opposite exclusion conjunction analysis did not reveal any significant results.

Table 4. Brain regions exhibiting significant differential activity for the main effects, interactions and conjunction analysis of congruency and odor conditions.

Brain region	Side	Cluster size	peak MNI coordinates			<i>p</i> (FWE-corr)	T	Z score
			x	y	z			
Incongruent > Congruent								
Middle frontal gyrus	L	57	-27	11	56	0.037	4.98	4.64
Middle frontal gyrus	L		-31	21	39		3.41	3.29
Inferior parietal gyrus	L	177	-52	-42	39	< 0.001	4.41	4.16
Inferior parietal gyrus	L		-34	-46	39		4.17	3.96
Precuneus	L	78	-6	-67	49	0.012	4.21	4
Precuneus	L		-13	-49	53		3.81	3.65
Precuneus	R		5	-60	49		3.8	3.64
Masked social odor > Masker								
Supramarginal gyrus	L	72	-59	-35	42	0.017	5.39	4.97
Supramarginal gyrus	L		-62	-32	28		4.6	4.32
Masker > Masked social odor								
Calcarine cortex	L	259	-10	-91	-11	< 0.001	4.37	4.13
Middle occipital gyrus	L		-17	-91	7		4.08	3.88
Calcarine cortex	R		8	-88	7		4.08	3.88
Precuneus	R	164	1	-53	28	< 0.001	4.14	3.94
Lingual gyrus	L		-20	-53	4		3.97	3.79
Posterior cingulum	L		-6	-49	32		3.81	3.65
Incongruent (masker social odor) vs Congruent (masker)								
Inferior parietal gyrus	L	244	-59	-35	42	< 0.001	6.26	5.64
Inferior parietal gyrus	L		-45	-46	56		4.11	3.91
Inferior parietal gyrus	L		-27	-42	35		4.03	3.83
Congruent (masker) vs Incongruent (masked social odor)								
Calcarine cortex	L	109	-10	-95	-7	0.001	4.11	3.91
Calcarine cortex	R		5	-91	0		4.05	3.86
Calcarine cortex	L		-6	-95	7		3.91	3.73
Incongruent (masked social odor > masker)> Congruent (masked social odor > masker)								
Supramarginal gyrus	L	233	-59	-35	42	< 0.001	6.26	5.64
Supramarginal gyrus	L		-45	-46	56		4.11	3.91

Note: Anatomical labels follow the nomenclature of the Automated Anatomical Labelling (AAL2).

Peak locations are expressed in MNI coordinates. Voxelwise threshold, $p < 0.001$. FWE cluster level corrected $p < 0.05$.

Figure 2. Brain activation maps showing significant cluster of activations. Statistical maps are derived with a threshold of $p < .05$ FWE corrected and superimposed on a standard T1 template (Coronal and sagittal views are displayed). Image labels: L = left, R = right.

3.4.4 Emotional areas are involved in instrumental vs accidental incongruent dilemmas

To evaluate the effect of intentionality, only incongruent dilemmas were considered. Processing accidental (vs instrumental) dilemmas significantly activated the left lingual gyrus, left fusiform gyrus, the left inferior occipital gyrus and the left middle occipital gyrus, whereas processing instrumental (vs accidental dilemmas) was related to significant activation in the bilateral precuneus (see Table 5 and Figure 3). No significant correlations with behavioral responses were retrieved.

3.4.5 Exposure to the masked social odor during accidental dilemmas activates areas processing sensory-emotional information

To clarify whether the brain regions that are active components in the masked social odor effect for the accidental dilemmas are shared also for the masked social odor effect in instrumental dilemmas, conjunction analyses were performed between the neural areas recruited for the interaction “masked social odor and accidental dilemmas” and for the interaction “masked social odor and instrumental dilemmas”. The exclusive conjunction analysis for accidental (masked social odor > masker) > instrumental (masked social odor > masker) showed significant activations in left superior and inferior parietal gyrus and in the right angular gyrus. The inclusive conjunction analysis and the opposite exclusion conjunction analysis did not reveal any significant results suggesting that the masked social odor modulated only the processing of accidental dilemmas (see Table 5 and Figure 3). The correlation analysis between the beta values extracted and the percentage of utilitarian responses did not reveal any significant results.

Table 5. Brain regions exhibiting significant differential activity for the main effects, interactions and conjunction analysis of intentionality and odor conditions.

Brain region	Side	Cluster size	peak MNI coordinates			p (FWE-corr)	T	Z score
			x	y	z			
Accidental > Instrumental								
Lingual gyrus	L	165	-10	-81	-4	< 0.001	4.74	4.44
Fusiform gyrus	L		-24	-74	-7		3.95	3.77
Inferior occipital gyrus	L		-24	-95	-11		3.68	3.53
Middle occipital gyrus	L	163	-27	-70	32	< 0.001	4.57	4.3
Middle occipital gyrus	L		-34	-88	14		4.29	4.07
Middle occipital gyrus	L		-27	-88	25		4.27	4.05
Instrumental > Accidental								
Precuneus	L	88	-10	-53	32	0.006	5	4.66
Precuneus	R		5	-56	32		3.92	3.74
Accidental (masker odor) vs Instrumental (masked social odor)								
Calcarine	L	1252	-6	-88	7	< 0.001	5.43	5.01
Lingual gyrus	L		-6	-84	-7		5.36	4.94
Calcarine	L		-20	-63	7		5.16	4.79
Accidental (masker social odor) vs Instrumental (masker odor)								
superior parietal gyrus	L	141	-24	-63	46	< 0.001	4.52	4.25
Inferior parietal gyrus	L		-34	-53	46		4.03	3.84
Inferior parietal gyrus	L		-45	-42	42		3.81	3.65
Angular gyrus	R	56	33	-67	46	0.032	4.22	4
Instrumental (masker odor) > Accidental (masked social odor)								
Precuneus	L	257	-10	-53	32	< 0.001	7.1	6.25
Precuneus	R		1	-53	28		6.46	5.79
Angular gyrus	L	106	-48	-63	32	0.002	5.09	4.73
Accidental (masked social odor > masker) > Instrumental (masked social odor > masker)								
Superior parietal gyrus	L	140	-24	-63	46	0.001	4.52	4.25
Inferior parietal gyrus	L		-34	-53	46		4.03	3.84
Inferior parietal gyrus	L		-45	-42	42		3.81	3.65
Angular gyrus	R	56	33	-67	46	0.032	4.22	4

Note: Anatomical labels follow the nomenclature of the Automated Anatomical Labelling (AAL2).

Peak locations are expressed in MNI coordinates. Voxelwise threshold, $p < 0.001$. FWE cluster level corrected $p < 0.05$.

Figure 3. Brain activation maps showing significant cluster of activations. Statistical maps are derived with a threshold of $p < .05$ FWE corrected and superimposed on a standard T1 template (Coronal and sagittal views are displayed). Image labels: L = left, R = right.

Discussion

Previous research suggests that moral rules are developed within specific social-relational contexts that, in turn, play a critical role in shaping moral choices^{9,10}. As human body odors are powerful messengers for socially-relevant information⁵², able to modulate the behavior and neural processing of the receiver^{23,14,37,13,53–55}, we hypothesized that social odors might affect moral choices through the modulation of the perceived social context (i.e., by inducing the perception of the real presence of a person). With this in mind, we asked participants to decide their course of action to moral scenarios while exposed to a neutral fragrance (masker) or to a body odor hidden by the same masker odor. The analysis of the neural correlates revealed that the exposure to the masked social odor: a) modulates the activity in the brain areas involved in the processing of incongruent (real) dilemmas, but not in those involved in the processing of congruent (fake) dilemmas; and b) increases the activations in areas processing sensory and emotional information when incongruent accidental dilemmas are presented.

In our study, we investigated whether masked social odors influence any decision-making task or whether the influence is specific to moral dilemmas, as we had anticipated. The analysis we performed revealed that the masked social odors moderate the neural responses only related with incongruent (but not congruent) dilemmas, increasing the involvement of the supramarginal gyrus. While presented with a real (incongruent) moral dilemma, the participants immediately experience a negative emotional reaction at the thought of provoking harm: the final decision will be deontological providing that this emotional reaction is sufficiently influential, and that participants have limited time and cognitive resources to answer. On the other hand, if participants have enough time, motivation and cognitive resources, they will have the possibility to engage in cognitive deliberation about costs and benefits, in which case the emotional response may be overshadowed, resulting in an utilitarian response to the dilemma^{2,32}. The information of the masked social odor

might interfere with this conflict enhancing the neural pathways that promotes prosocial behavior⁵⁶, therefore emphasizing the emotional processing of the sensory information, and facilitate the emergence of deontological responses. Since in the fake (congruent) dilemmas there is no conflict between emotional and cognitive aspects (i.e., the benefits do not balance the costs), the social information about the presence of a person becomes irrelevant for the decision.

Moreover, in the present study, we clarified whether the masked social odor effect is modulated by the type of harm, being it deliberate (instrumental dilemmas) or an inadvertent effect (accidental dilemmas). Previous studies showed that the accidental harm is judged as being more morally acceptable, it receives higher percentage of utilitarian answers, and it engages lower emotional reaction compared to intentional harming^{4,56}. Our results are in line with this literature: instrumental dilemmas presented higher percentage of deontological answers and recruited neural areas involved in emotional processing (e.g., precuneus) when compared to accidental dilemmas. Interestingly, the masked social odor seems to moderate the processing of the accidental dilemmas by enhancing the activation of the angular gyrus, which is usually associated with social cognition, multisensory integration and “theory of mind”²⁷, and the inferior parietal gyrus, which is important for the self-other discrimination⁵⁷. This result seems to support our hypothesis that the presence of a social odor can induce the participant to perceive the social context of the dilemmas as more concrete, as if the odor signaled the presence of a real person, and not just of a hypothetical context. The reason why the social odor seems to selectively affect the processing of the accidental dilemmas may be due to the higher emotional involvement of the instrumental dilemmas, which prevents the participants to consider the additional emotional information provided by the odor.

The present fMRI data replicate and extend previous data on the neural networks recruited by the processing of social and common odors. Indeed, the moral dilemmas processed together with the masked social odor seem to involve the left supramarginal gyrus, which is located close to the angular gyrus²⁷, one of the neural areas previously found to be involved in the specialized neural network for social odors^{23,14}. The supramarginal gyrus has been often included in the temporo-

parietal junction (TPJ) - a neural area associated with self-awareness and body-related information processing^{34,58}, that is also involved in theory of mind^{34,59}, empathy for pain⁶⁰ and in the perception of anxiety social odors⁶¹, all aspects that become relevant when considering a social odor in the context of moral dilemmas.

In our study, the social odor was masked by a neutral odor. This masker was applied to simulate the hygiene products usually used to cover the natural body odors we produce and to make the paradigm more ecologically valid⁶². However, this paradigm has also other advantages: it allowed studying the effects of the social odor when they are unconsciously perceived. As seen in a previous study⁶³, odor effects can emerge irrespective of the perceiving the presence of an odor; moreover, masking the social odor limited the inter-individual differences in odor intensity and pleasantness that can significantly affect decisions, as it seemed in the previous cases when intensity and pleasantness differences across odor conditions were evident^{17,63}. Here we succeeded in making these conditions perceptually similar for intensity, familiarity and pleasantness, removing the possible confounding effect of these factors on the differences in the moral decisions.

The present study was designed around a moral decision-making paradigm based on the presentation of moral dilemmas. Many criticisms have been raised against such stimuli (e.g.⁶⁴⁻⁶⁶). First, such dilemmas are described in lengthy written texts, which increase the time needed by the participants to process each stimulus and, second, to make dilemmas credible they cannot be repeated and the conceptual factors have to be intermingled along the dilemmas. These aspects reduce the possibility to present paradigms with large numbers of trials, therefore limiting the power of the study. To account for these issues, we have used here a standardized, culturally-equivalent moral set which has been specifically designed for imaging experiments and which shows high consistency across the different dilemmas²⁰. Moreover, to increase the power of our observations, the selection of one out of four conceptual factors was based on a theoretical question.

Despite these efforts, the behavioral analysis did not reveal significant mean effects of the odor conditions or significant interactions with odor and dilemma congruency or intentionality. One

explanation could be that the dilemmas were designed to simultaneously assess also other conceptual factors, such as personal force, benefit recipient and evitability. It is for future studies to clarify whether the social odor present different effects on moral choices when different conceptual factors are considered.

To our knowledge, this is the first study that tests the effect of social odors on moral decision-making. The value of these results is highlighted by the consideration that most of the moral decisions, from everyday choices to choices that we are forced to make under unexpected circumstances, are made in the presence of other people. Starting from the theory proposed by Rai and Fiske⁹, which advanced the hypothesis that actions and outcomes should be considered in the context of specific social relationships, indeed any action - including violence and impure acts - can be perceived as morally acceptable depending on the social relationships it takes place in⁹, social odors were used as a means for triggering the social context and for making the social norms more salient. Our results indicate that social odors could effectively mediate moral decisions, possibly increasing the emotional experience during the decision process, and this effect is possible even when the perceiver cannot appreciate the presence of the social odors. Moreover, the current results suggest that, as Cikara et al.¹⁰ posited, the context in which the decisions are made is relevant for understanding which decision is made.

Acknowledgments

We would like to thank Luigi Alberto Gozzi for his help in the social odors collection, Carlotta Cogoni and Michele Furlan for their input regarding the neuroimaging analysis.

Data Availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Author Contributions

C.C, V.P. and R.I.R developed the study concept and the study design; C.C., V.P and E.L. collected the data; C.C., V.P. and D.B. conceptualized data analyses; C.C. performed data analyses under the supervision of D.B and V.P.; C.C and V.P interpreted the data and drafted the manuscript. E.L., D.B., R.I.R. provided critical revisions. All authors approved the final version of manuscript submission.

Competing financial interests

The authors declare that they have no competing interests.

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