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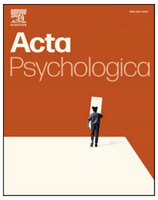

Competitive (but not cooperative) body odors bias the discrimination of action intentions towards cooperation

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ABSTRACT

Odors help us to interpret the environment, including the nature of social interactions. But, whether and how they influence the ability to discriminate the intentional states embedded in actions is unclear. In two experiments, we asked two independent groups of participants to discriminate motor intentions from videos showing one agent performing a reach-to-grasp movement with another agent with a cooperative or a competitive intent, and the same movement performed alone at either natural- or fast-speed, as controls. Task-irrelevant odor primes preceded each video presentation. Experiment 1 ($N = 19$) included masked cooperative and competitive body odors (human sweat collected while the donors were engaged in cooperative and competitive activities), whereas Experiment 2 ($N = 20$) included a common odor (cedarwood oil) and no odor (clean air) as primes. In an odor-primed, two-alternative forced choice task, participants discriminated the intention underlying the observed action. The results indicated that the odor exposure modulated the discrimination speed across different intentions, but only when the action intentions were hard to discriminate (cooperative vs. individual natural-speed, and competitive vs. individual fast-speed). Contrary to our hypothesis, a direct odor-action intention compatibility effect was not found. Instead, we propose a negative arousal compatibility-like effect to explain our results. Discrimination of high arousing action intentions (i.e., competitive) took longer when primed by high arousing odors (common odor and competitive body odor) than by low arousing odors (cooperative body odor and no odor). Discrimination of low arousing action intentions (i.e., cooperative) took longer when primed by low arousing odors than by high arousing odors. All in all, competitive (but not cooperative) body odors bias the discrimination of action intentions towards cooperation.

1. Introduction

Theories of embodied cognition and simulation suggest that reading the intention of others occurs through a direct and automatic matching process between observed and performed actions (Aglioti et al., 2008). The process occurs through the re-activation of the bodily states that were originally active during past, self-related sensorimotor experiences (Grafton, 2009). Evidence is accumulating that olfaction plays a role in this re-activation process (Aglioti & Pazzaglia, 2011; Partan & Marler, 2005). In particular, smelling human sweat activates in the receiver the simulation of the emotional experience of the donor (e.g., fear, disgust, and happiness; de Groot et al., 2012, 2015; Mujica-Parodi et al., 2009), and the ability to track the intensity of their stress response (de Groot et al., 2020). Additionally, smelling human sweat can prepare the receiver for complementary emotional responses (Mutic et al., 2016) which help establish social bonds (Parma et al., 2013b) as well as enhance competitiveness (Adolph et al., 2010; Mutic et al., 2019).

Whether sweat-based information can influence the ability to decode the intention coupled with a certain action is to date unclear. Previous evidence suggests that odor-motor interactions occur during not only action execution (Castiello et al., 2006; Parma et al., 2012, 2013a) and inhibition (Albayay et al., 2019, 2022), but also during action observation (Tubaldi et al., 2011). Indeed, olfactory representations are efficiently included in motor plans, and the action observation system

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(AOS; Keysers & Perrett, 2004) is engaged when one smells objects and observes goal-directed actions (Tubaldi et al., 2011). It is also known that olfactory stimuli congruent with to-be-grasped food items increase the corticospinal excitability of the muscles of the hand, thus strengthening the idea that olfactory stimuli influence the activation of the AOS (Rossi et al., 2008). Altogether, these findings suggest that odor stimuli impact both the observation and execution of motor patterns.

Furthermore, exposure to familiar human sweat can selectively modulate the processing of observed actions. For instance, smelling the sweat of a family member (e.g., their mother) allows children with autism spectrum disorder to execute actions that reflect the processing of the visual cues embedded in the actions of a model-person (Parma et al., 2013a, 2014). Yet, the same effect is not manifest in children with typical development, who do not need help to disambiguate the visual information associated with an action. All in all, at least in some specific cases, the socio-emotional content of human sweat can influence the unfolding of one's own actions and the understanding of the intentions behind the actions of others.

To test whether motor intentions can be decoded based on the socio-emotional content conveyed by human sweat, we capitalized on the evidence that humans are able to discriminate between social and non-social motor intentions via action observation (Sartori et al., 2011). Based on the evidence of predictive coding (Wolpert et al., 2003), Sartori et al. (2011) devised a task in which participants were shown temporally-occluded video clips of agents performing the same action with different intentions (i.e., the initial frames of individual, competitive and cooperative actions were shown, but not the actual interaction). The participants judged the model's motor intention by choosing between two options at a time in a series of two-alternative forced choice tasks. Based on the kinematic cues of the model's arm, participants were able to judge whether the presented video showed an intent to cooperate, compete, or perform an individual (fast or slow) action. Importantly, the authors report longer response latencies and lower accuracy when the participants had to judge action intentions in the presence of higher ambiguity, particularly when choosing between cooperative and natural speed actions (Sartori et al., 2011).

With this aim in mind, we sought to investigate whether and how body odor (BO) stimuli modulate the ability to discriminate different action intentions. BO stimuli were obtained from human sweat collected while the donors (i.e., individuals who produced the BO stimuli) were engaged in cooperative and competitive activities and then masked with cedarwood oil (successfully used to mask human sweat; Cecchetto et al., 2017b, 2020).

2. Experiment 1

In this experiment, participants performed the two-alternative forced choice task developed by Sartori et al. (2011; i.e., discrimination of action intentions) and adapted for this study, after being presented with either a masked cooperative or competitive BO. Considering that being exposed to a masked BO implicitly indicates the presence of a person (Lundström et al., 2008), the BO stimuli would be considered as a social proxy. Cooperative BOs could be interpreted as the sign of the presence of a cooperative person, and thus evoke intrinsic reinforcements (Schuster & Perelberg, 2004). In line with these findings, we anticipated a compatibility effect in that the cooperative BOs will facilitate the discrimination of action intentions in the two-alternative forced choice task (i.e., faster response times and higher accuracy) when the conditions include a cooperative action intention as one of the alternatives (see *Procedure* below for details on the experimental task). Conversely, the competitive BOs could be interpreted as a sign of the presence of a competitive person. If so, we may expect it to evoke signs of an intrinsic, arousing threat. Indeed, we anticipated the competitive BOs to be more arousing than the cooperative BOs, as previous studies have revealed that competitiveness (vs. cooperation) elicits greater cardiovascular activity (Harrison et al., 2001; Kivikangas et al., 2014) and self-reported arousal (Schmierbach, 2010). In this case, we expected the competitive BO to interfere with the discrimination of action intentions when judging conditions involving a social action (cooperation and competition) as an alternative.

2.1. *Method*

2.1.1. *Participants*

Nineteen healthy participants (ten women; mean age: 25.7 ± 4.1 years old; age range: 20–36 years old) were recruited in this experiment. An a priori power analysis (G*Power version 3.1; Faul et al., 2009) suggested a sample size of sixteen participants for a medium effect size ($f^2 = 0.25$) at power = 0.8 and $\alpha = 0.05$ (*F* test family, ANOVA: repeated measures, within factors). Additionally, twenty individuals (ten women; mean age: 22.9 ± 2.3 years old; age range: 19–28 years old) were recruited to donate their sweat (henceforth referred to as donors). All participants and donors were non-smokers, right-handed (score > 60 on the Edinburgh Handedness Inventory; Oldfield, 1971), normosmic (score ≥ 10 on the Sniffin' Sticks identification test; Burghart®, Wedel, Germany; Hummel et al., 2007; Oleszkiewicz et al., 2019), and self-reported normal or correct-to-normal vision. To ensure accurate olfactory perception, participants were screened for medication intake, history of neurological disorders (including head trauma), as well as endocrinological, respiratory, psychiatric, and autoimmune diseases, and exposure to toxins. To minimize the risks of extreme anxious, depressive, and competitiveness traits and states affecting performance, we only included participants and donors with average scores on the State-Trait Inventory for Cognitive and Somatic Anxiety (below the cut-off score of 43, considered optimal to detect probable cases of clinical anxiety; Grös et al., 2007), and the Beck Depression Inventory (below the cut-off score of 17; Beck et al., 1996). Furthermore, we ensured that participants and donors exhibited mean scores on the Cooperative/Competitive Strategy Scale (Simmons et al., 1988), indicating a moderate level of competitiveness and cooperativeness. Only female participants and donors not undergoing hormonal contraception or undergoing hormonal contraception for less than six months, and reporting to be in the early follicular phase of their cycle (day 2–7 after menses onset; Chung et al., 2016), were recruited for this study. This was done to control for changes in olfactory perception during the menstrual cycle; calculations were based on the starting date of their menstrual cycle and the length of it based on the past six months (Mutic et al., 2019). Participants were asked to refrain from using scented personal care products on the day of testing, as well as two days prior to it, and not to eat or drink anything (except water) for one hour prior to the beginning of the experimental sessions to minimize any distortion of olfactory perception. All participants and donors provided written informed consent before participating. Donors received 15 euros, while participants received 10 euros after completing the experiment. All procedures in this study were approved by the local Institutional Review Board (International School for Advanced Studies, Trieste, Italy) and were in compliance with the Declaration of Helsinki (World Medical Association, 2013). The descriptive statistics of the sample are reported in Table S1 in the *Supplementary material*.

2.1.2. *Apparatus and stimuli*

2.1.2.1. Visual stimuli. During the two-alternative forced choice task (see Section *2.1.3* below for details on the experimental task) we employed the video clips used in Sartori et al. (2011). The video clips were in .avi format and had disabled audio. They were recorded at 25 frames/s with a resolution of 720 × 576 pixels, bit rate of 1200, aspect ratio of 16:9, duration of 3 s, and subtended region of 22.62° × 33.40°. The clips featured a right-handed model performing four types of action sequences with wooden blocks in isolated and dual contexts (single-agent vs. two agents). The action sequences were as follows:

i) *Single-agent, natural-speed*: the agent reaches and grasps the wooden block positioned in front of his/her right hand and moves it to the middle of the working surface at a natural speed.
ii) *Single-agent, fast-speed*: the action sequence is similar to the previous one, except that the agent performs the action as fast as possible.
iii) *Two agents in cooperation*: two agents sit opposite to each other and cooperate to build a tower in the middle of the working surface. One agent positions the wooden block at the bottom, and the other at the top of the tower.
iv) *Two agents in competition*: the action sequence is similar to the previous one, but the agents compete to place their wooden block at the bottom of the tower as fast as possible.

To ensure that only the initial part of the action sequence (i.e., the reach to grasp of the wooden block) was used by the participants to infer the kind of intention driving the action, the video clips were temporally occluded. They started with an agent resting their right hand on a starting button and ended at the time they grasped the wooden block. The interacting agent was not shown in the video clip (see Fig. 1). For a more detailed description of the video stimuli (e.g., recording and analysis of kinematics), please refer to Sartori et al. (2011).

2.1.2.2. Body odor stimuli. For the collection of human sweat, donors were instructed to follow a strict protocol to avoid sweat contamination (Mitro et al., 2012; Parma et al., 2017). For two days prior to each donation session, donors were asked to refrain from eating odorous food (e.g., garlic, onion, asparagus), drink alcohol, smoke, perform excessive sport or schedule stressful experiences (e.g., academic exams, doctor appointments). Furthermore, donors were asked to solely use the scent-free personal-care products and detergents provided by the experimenter during the two days prior to each collection and during collection day. All donation sessions were performed between 8 a.m. and 12 p.m.; only a male experimenter took part in the donation sessions in order to minimize possible experimenter effects (Lundström & Olsson, 2005). The order of the donation sessions was counterbalanced across donors and separated by at least 24 ± 8 h.

At the beginning of each donation session, donors were asked to wash their armpits and torso with the scent-free personal-care product, and they wore a t-shirt in which the absorbent pads were sewn into the armpits. The cooperative and competitive conditions were similarly constructed and based on three tasks. First, donors rated how cooperative and competitive they felt at the moment in VAS ranging from 0 (*not at all*) to 100 (*very much*). Subsequently, they read a story whose central theme was either cooperation or competition, as judged by a pilot study on six participants. This induction method, in line with other types of state-induction manipulations (e.g., DeSteno et al., 2004), has proven successful in generating accurate mental images related to cooperation and competition and evoke the designated states in the donors. Second, the donors were presented with several short videos showing cooperative (e.g., human chains helping people) and competitive situations (e.g., boxing matches) for 18 min. This technique has been successfully used to elicit emotional sweat in humans, such as those of disgust, fear and happiness (e.g., de Groot et al., 2015). Third, donors were asked to rate their experience of cooperation and competition on a VAS and then to perform the same task that the participants of the experiment seen in the videos, namely, to build a tower cooperatively or competitively with a confederate (30 trials each). A final VAS to measure cooperation and competition was then administered.

At the end of each donation session, the samples were handled with disposable, odorless surgical gloves and the usability of the donated sample was assessed by a pool of minimum one and maximum three experimenters (if the case was questionable). The experimenters evaluated whether traces of exogenous odorants were retrieved (which would grant the exclusion of the sample from the donor pool) and the clear presence of human sweat (e.g., Mitro et al., 2012). Once deemed usable, each t-shirt was collected, the pads removed and frozen at −80 °C. To favor data comparison, clean pads on which the masker odor was applied were also frozen to serve in the comparisons that do not include BOs. Freezing sweat does not affect subjective ratings of pleasantness, intensity, attractiveness, and masculinity of the samples (Lenochová et al., 2009). The BO stimuli were subsequently created by cutting each pad into four, equally sized quadrants. To remove potential individual odor-donor effects on the participants of the experiments (Mitro et al., 2012), supra-donors were created. A supra-donor BO consists of four quadrants, each obtained from four same-sex and same approximate age donors (Martins et al., 2005).

Overall, each donation session took about 60 min. Based on the donors' subjective experience, the cooperative condition induced the donors to feel significantly more cooperative (75.4 ± 22.0) than competitive (36.9 ± 26.6), $\chi^2(1) = 345.69$, $p < 0.001$, $\text{AIC}_{\text{RL}} > 100$, $R^2_{\text{m}} = 0.380$, $R^2_{\text{c}} = 0.650$ (see Section *2.1.4* below for details on the statistical analyses). Further, the donors reported to feel more competitive (70.1 ± 24.8) than cooperative (30.5 ± 31.0) following the induction of competition, $\chi^2(1) = 286.25$, $p < 0.001$, $\text{AIC}_{\text{RL}} > 100$, $R^2_{\text{m}} = 0.308$, $R^2_{\text{c}} = 0.630$. Thus, we concluded that the induction procedure was successful.

During the main experiment, the Participants (receivers) were exposed to BO cues placed on absorbent pad quadrants (MAM, Neckarsulm, Germany) and positioned within straight-sided glass 4 oz. jars (Uline, Pleasant Prairie, WI, USA). Four pad quadrants were arranged along the walls of the jar, as well as on the bottom of the jar, to maximize exposure of the odorous surface. We presented the participants with

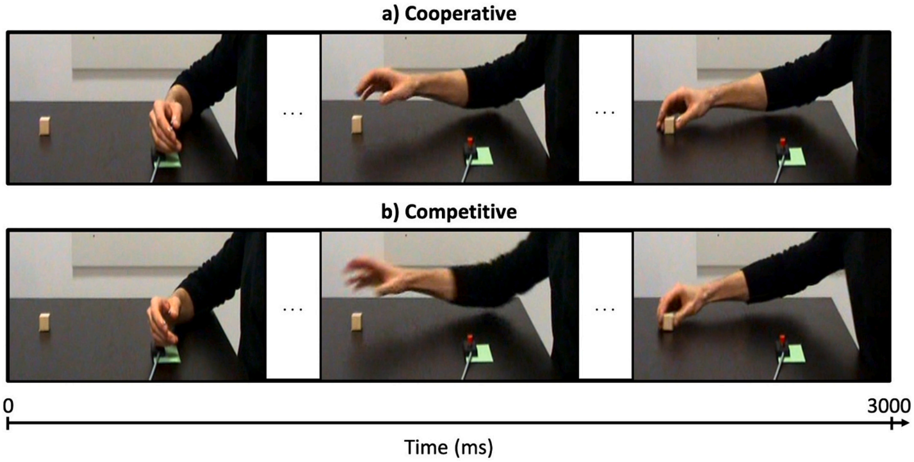

Fig. 1. Frames extracted from the video stimuli presented during the experimental task showing a cooperative action (panel a) and a competitive action (panel b).

cooperative and competitive BOs (i.e., human sweat collected in cooperative and competitive situations, respectively) that were masked with cedarwood oil (200 μL, Sigma-Aldrich, Italy; Cecchetto et al., 2017b); please see below for a detailed explanation of the collection procedures. This was done to reduce the possibility of conscious detection of the BOs (Cecchetto et al., 2019; Lundström & Olsson, 2010; Parma et al., 2017). Olfactory stimulation was provided by a computer-controlled olfactometer (Sniff-0, CyNexo, Udine, Italy, https://www.cynexo.com). A constant flowing air stream (0.5 L/min) was maintained throughout the experiment, while the odor stimuli were presented at a flow of 3 L/min (Albayay et al., 2019, 2022). The odor stimuli and clean air were delivered through two cannulas covered with custom-made nosepieces that were placed in the participants' nostrils.

2.1.3. *Procedures*

2.1.3.1. Two-alternative forced choice task. The main experimental task was the same as in Sartori et al. (2011), except for two aspects: the addition of the olfactory stimulation and a longer time window between primes and targets (see below). The participants seated in front of a 19″ computer monitor (background luminance of 250 cd/m^2), with the head positioned on a chinrest to ensure that the eye-screen distance was of 50 cm. Participants placed the right and left index fingers upon two keyboard keys (i.e., Z and M, respectively). Participants familiarized themselves with the video clips by watching one clip for each condition (natural-speed, fast-speed, cooperative, and competitive) before starting the experiment.

Each trial for the main experimental task (see Fig. 2) began with the presentation of a white fixation cross against a black background which set the start of the flow of clean air; participants were instructed to breathe normally upon seeing the cross. After 1000 ms, the odor stimulus was delivered for 3000 ms; this duration ensured that the participant could smell the odor stimuli while breathing naturally. Then, a green fixation cross was displayed at the center of the screen serving as a preparation cue for the video stimulus; the duration of the cue ranged from 500 to 1500 ms in order to avoid early responses. Subsequently, the target video clip showing the reach-to-grasp phase of the movement in one of the four conditions was presented. By means of a two-alternative forced choice task, participants had to discriminate (by pressing one of the two keyboard keys: Z or M) as fast and accurately as possible whether the video clip represented: (i) a natural-speed vs. a fast-speed action (Nat–Fast), (ii) a cooperative vs. a competitive action (Coop–Comp), (iii) a competitive vs. a fast-speed action (Comp–Fast), (iv) a cooperative vs. a natural-speed action (Coop–Nat).

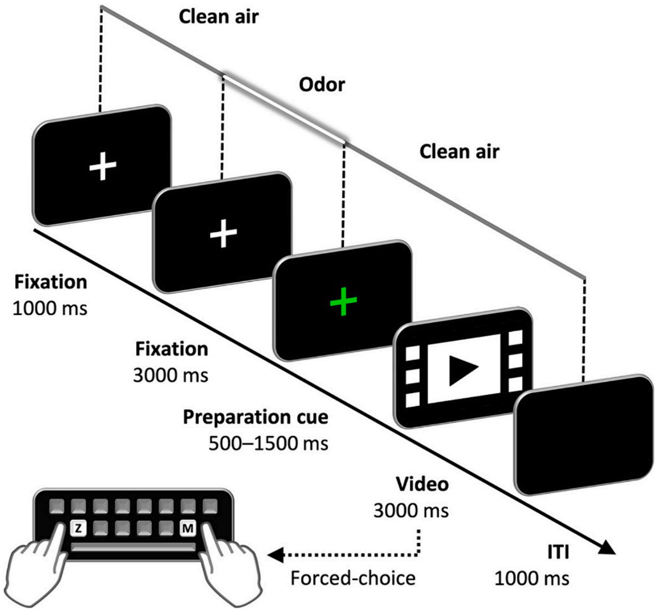

Fig. 2. Graphical description of the two-alternative forced choice task (discrimination of action intentions).

The mapping rule between action intentions and keyboard keys was counterbalanced across participants (e.g., in the Coop–Comp condition half of the participants had to press the Z key if they judged the observed action as cooperative and the M key if they judged it as competitive). In case of a missed response (i.e., > 6000 ms response deadline), feedback was provided in the center of the screen (*missed response*). Clean air was delivered during the presentation of the video and during a fixed inter-trial interval (ITI) of 1000 ms. A total of 240 trials were presented in four blocks of 60 trials each; the odor stimuli were presented equiprobably. Each block contained one of the possible conditions (Nat–Fast, Coop–Comp, Comp–Fast, Coop–Nat). The order of the blocks was counterbalanced across participants.

2.1.3.2. Rating procedure. Before and after completing the main experimental task, participants rated each odor stimulus regarding its perceived intensity, familiarity and pleasantness in visual analog scales (VAS) ranging from 0 (*not at all*) to 100 (*very much*). The experiment took place in a room apt for human chemosensory testing, provided with air replacement by a ventilation system. The experiment was carried out using the *E*-Prime 2.0 software (Psychology Software Tools, Inc, 2012) and lasted about 60 min.

2.1.4. *Statistical analyses*

We used RStudio (version 1.4.1103; RStudio Team, 2016) for all our analyses. We considered the following dependent variables: odor ratings (intensity, familiarity and pleasantness), response time (RT, i.e., time elapsed from the moment at which the agent on the video started the movement until the participant pressed one of the two keyboard keys), and accuracy at discriminating action intentions. We also compute the *d*’ parameter from the Signal Detection Theory (Macmillan & Creelman, 2004), which represents a participant's sensitivity to a given stimulus independent of their bias to respond *yes* or *no* at the forced-choice discrimination task. Greater values indicate a greater ability to discriminate signal from noise while a value of 0 indicates chance performance. The *d*’ parameter was computed as the difference of the normalized *z* values of the rates of hits (H, correctly detected stimuli) and false alarms (FA, stimuli reported when not present): $d' = z(\mathrm{H}) - z(\mathrm{FA})$. Given that Sartori et al. (2011) found that the participants tend to classify natural-speed and competitive action as cooperative ones, we computed the *c* (criterion) parameter from the Signal Detection Theory to account for the possible presence of such bias after being exposed to the different odor conditions. The *c* parameter represents a general tendency to respond *yes* or *no*, with a value of 0 indicating no bias towards either choice. The *c* parameter was computed as: $c = -[\mathrm{z(H)} + \mathrm{z(F)}]/2$. In order to avoid indeterminate values [i.e., perfect H (1) or FA (0)] for the computation of both *d*’ and *c*, we added 0.5 to both the number of H and FA and 1 to the number of trials (Hautus, 1995; Snodgrass & Corwin, 1988). To determine if the participants' performance was above or below the chance level, the *d*’ parameter was contrasted against 0 (i.e., chance level performance) by means of one-sample *t*-tests for each condition. Furthermore, to account for the presence of the bias towards classifying cooperative action intentions (Sartori et al., 2011), we planned to contrast the *c* parameter against 0 (i.e., neutral bias) by means of one-sample *t*-tests for the Coop–Comp and Coop–Nat conditions.

We computed linear mixed-effects models (LME) for the perceived intensity, familiarity and pleasantness of the odor stimuli, as well as for RT and *d*’, and generalized linear mixed-effects models (GLME) with binomial link function for accuracy. For details on the advantages of mixed-effects modeling as compared to more traditional approaches (e.g., analysis of variance), we refer the interested reader to Baayen et al.

Table 1
Descriptive statistics and multiple comparisons for the response time and accuracy at discriminating action intentions per odor condition in Experiment 1.

Measure	Odor	Intention	Mean ± *SD* / %	Comparison	*p* value
Response time	Masked competitive BO	Nat–Fast	2678 ± 666 ms	Coop–Comp	**< 0.001*****
				Comp–Fast	**< 0.001*****
				Coop–Nat	**< 0.001*****
		Coop–Comp	2904 ± 569 ms	Comp–Fast	**< 0.001*****
				Coop–Nat	**0.005****
		Comp–Fast	3353 ± 454 ms	Coop–Nat	**< 0.001*****
		Coop–Nat	3033 ± 591 ms	–	–
	Masked cooperative BO	Nat–Fast	2717 ± 583 ms	Coop–Comp	**< 0.001*****
				Comp–Fast	**< 0.001*****
				Coop–Nat	**< 0.001*****
		Coop–Comp	2951 ± 492 ms	Comp–Fast	**< 0.001*****
				Coop–Nat	**< 0.001*****
		Comp–Fast	3245 ± 413 ms	Coop–Nat	0.999
		Coop–Nat	3258 ± 657 ms	–	–
Accuracy	Masked competitive BO	Nat–Fast	91.9 %	Coop–Comp	**< 0.001*****
				Comp–Fast	**< 0.001*****
				Coop–Nat	**< 0.001*****
		Coop–Comp	74.5 %	Comp–Fast	**< 0.001*****
				Coop–Nat	**< 0.001*****
		Comp–Fast	54.7 %	Coop–Nat	0.097
		Coop–Nat	46.6 %	–	–
	Masked cooperative BO	Nat–Fast	94.0 %	Coop–Comp	**< 0.001*****
				Comp–Fast	**< 0.001*****
				Coop–Nat	**< 0.001*****
		Coop–Comp	78.9 %	Comp–Fast	**< 0.001*****
				Coop–Nat	**< 0.001*****
		Comp–Fast	62.8 %	Coop–Nat	**< 0.001*****
		Coop–Nat	38.9 %	–	–

Bold values denote statistical significance ($p < 0.05^{*}$, $p < 0.01^{**}$, $p < 0.001^{***}$).

(2008). Trials in which participants did not respond (0.7 %), as well as trials exceeding 2.5 standard deviations the average RT (2.4 %) were considered outliers and excluded from the analyses. The LME models for the perceived intensity, familiarity and pleasantness included the factors *odor* (masked cooperative BO vs. masked competitive BO) and *session* (pre vs. post; odor ratings before starting the experimental task and after its completion, respectively) as fixed effects. LME models for RT and *d*' and GLME models for accuracy included the factors *odor* and *intention* (Nat–Fast vs. Coop–Comp vs. Comp–Fast vs. Coop–Nat) as fixed effects. All models included *sex* (female vs. male) as a covariate and *participants* as a random effect in order to account for the stochastic variability in the data and reflect a more general estimate of the fixed effects (Singmann & Kellen, 2017).

By following a model comparison approach (McElreath, 2016), we compared nested models by means of likelihood ratio tests to determine the best fitting model using the Akaike information criterion (AIC). Lower AIC indicates the best fitting model. We estimated the exponential of the difference between the AIC of the models to establish the relative likelihood of a given model [$\text{AIC}_{\text{RL}} = \exp.(\Delta\text{AIC}/2)$, e.g., Albayay et al., 2019, 2022]. All models were fitted with maximum likelihood estimation. We performed multiple comparisons for significant main effects with more than two levels and first order interactions. We selected the Tukey method for the adjustment of *p* values to reduce the probability of type 1 error with $\alpha = 0.05$. Further, we computed marginal and conditional R^2 to account for the proportion of variance explained by the fixed effects only (R^2_{m}) and by both the fixed and random effects (R^2_{c}), respectively. We reported the mean and standard deviation of the experimental conditions for LME models, and the accuracy in percentage per condition for GLME models.

2.2. *Results*

For brevity, we report the highest order significant effects and the effects relevant to the argument at stake. For completeness, the main effects of odor, intention and sex and all the effects related to the ratings (intensity, familiarity and pleasantness) of the odor stimuli are reported in the *Supplementary material*. In short, the odor stimuli were equivalent in intensity, familiarity and pleasantness. The main effect of sex was not significant for any of the dependent variables (see Table S2 in the *Supplementary material*).

2.2.1. *Masked competitive body odors slows down action discrimination of Comp – Fast condition and speeds up action discrimination of Coop-Nat condition*

The interaction odor × intention on the response time was significant, $\chi^2(3) = 27.966$, $p < 0.001$, $\text{AIC}_{\text{RL}} > 100$, $R^2_{\text{m}} = 0.140$, $R^2_{\text{c}} = 0.311$; the descriptive statistics per condition are presented in Table 1. As shown in Fig. 3, the masked competitive BOs exhibit a dual effect. When paired with the Comp-Fast condition, it decelerates the discrimination of the action intention ($p = 0.025$). Conversely, it accelerates the discrimination in the Coop-Nat condition ($p = 0.001$). There were no significant differences observed in the other comparisons (refer to Table 1). Furthermore, no significant difference was found in the impact of cooperative BOs on the discrimination of action intention (Fig. 3).

2.2.2. *Smelling masked competitive (vs. cooperative) body odors does not modulate the discrimination accuracy between action intentions*

Overall accuracy, collapsed across conditions, was 67.9 %. The interaction odor × intention on accuracy was significant, $\chi^2(3) = 18.269$, $p < 0.001$, $\text{AIC}_{\text{RL}} > 100$, $R^2_{\text{m}} = 0.211$, $R^2_{\text{c}} = 0.236$; the descriptive statistics per condition are presented in Table 1. Discrimination accuracy did not differ when masked competitive BOs were presented (vs. masked cooperative BOs) for any of the experimental conditions: Nat–Fast ($p = 0.848$), Coop–Comp ($p = 0.652$), Comp–Fast ($p = 0.107$), Coop–Nat ($p = 0.124$). As expected, accuracy was lower in the Coop–Nat condition as compared to the other conditions when exposed to both BOs. In short, when directly contrasted, the accuracy at discriminating the intentions of others is not affected by the level of cooperativeness/competitiveness elicited via BOs.

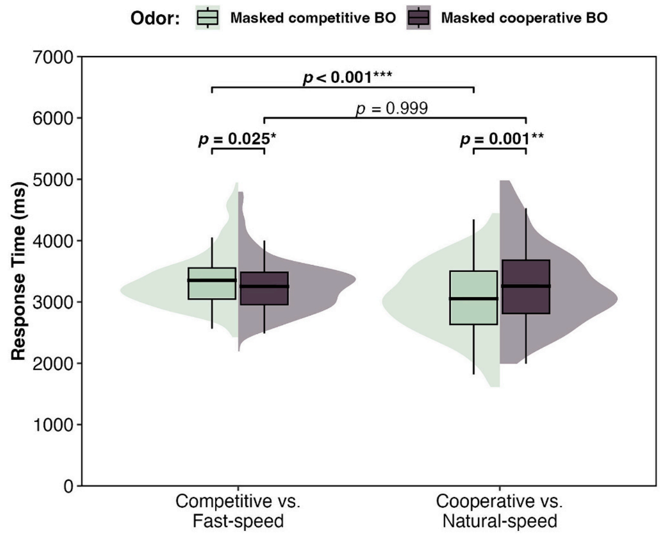

Fig. 3. Split violin plots for the response time at discriminating action intentions per odor condition in Experiment 1. The horizontal thick line within the boxes represents the mean. The lower and upper horizontal lines indicate the 25th and 75th percentiles of the distribution, respectively (interquartile range). The whiskers indicate the minimum and maximum values located 1.5 times the interquartile range. The shaded area surrounding each box depicts a rotated kernel density plot. Bold values denote statistical significance ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$).

2.2.3. *Participants discriminate cooperative vs. natural-speed action intentions more poorly than expected by chance*

The main effect of intention on the *d*' parameter was significant, $\chi^2(3) = 142.81$, $p < 0.001$, $\text{AIC}_{\text{RL}} > 100$, $R^2_{\text{m}} = 0.597$, $R^2_{\text{c}} = 0.644$, whereas the main effect of odor, $\chi^2(1) = 0.228$, $p = 0.412$, $\text{AIC}_{\text{RL}} = 0.638$, $R^2_{\text{m}} < 0.001$, $R^2_{\text{c}} < 0.001$ [masked competitive BO (1.1 ± 1.5), masked cooperative BO (1.2 ± 1.8)], and the interaction odor × intention, $\chi^2(3) = 3.139$, $p = 0.301$, $\text{AIC}_{\text{RL}} = 0.139$, $R^2_{\text{m}} = 0.605$, $R^2_{\text{c}} = 0.653$, were not. The value of the sensitivity index was lower for the Coop–Nat condition (−0.4 ± 0.7) than for the Nat–Fast (2.9 ± 0.5), the Coop–Comp (1.8 ± 1.7), and the Comp–Fast (0.5 ± 0.8) conditions (all *ps* < 0.001). The *d*' index was also lower for the Comp–Fast condition as compared to both the Nat–Fast and the Coop–Comp conditions (*ps* < 0.001). *d*' was lower for the Coop–Comp than for the Nat–Fast condition as well ($p < 0.001$). One-sample *t*-tests revealed that the *d*' parameter was significantly >0 for the Nat–Fast, $t(37) = 34.178$, $p < 0.001$, the Coop–Comp, $t(37) = 6.367$, $p < 0.001$, and the Comp–Fast conditions, $t(37) = 3.595$, $p = 0.002$, but significantly lower than 0 for the Coop–Nat condition, $t(37) = -3.737$, $p < 0.001$. To sum up, discriminating Coop–Nat action intentions was more challenging as compared to all other conditions, regardless of the odor prime.

2.2.4. *Smelling competitive (but not cooperative) body odors biases the discrimination towards cooperation*

Concerning the presence of a bias towards reporting cooperation, one-sample *t*-tests for the Coop–Comp condition showed that the *c* parameter was significantly lower than 0 when competitive BOs were presented, $t(18) = -3.340$, $p = 0.004$, but not for cooperative BOs, $t(18) = -0.901$, $p = 0.379$, suggesting a bias towards judging competitive actions as cooperative ones, when competitive BOs are smelled. As for the Coop–Nat condition, the *c* parameter was lower than 0 when competitive BOs were presented, $t(18) = -4.473$, $p < 0.001$, but not for cooperative BOs, $t(18) = 0.015$, $p = 0.988$, indicating a bias towards judging natural-speed actions as cooperative ones when competitive BOs are smelled. In short, unexpectedly, we found that smelling competitive (but not cooperative) BOs biases the classification of action intentions towards judging natural-speed and competitive action intentions as cooperative ones.

2.3. *Discussion*

Our results showed that masked cooperative and competitive BOs preceding the presentation of the video can modulate the ability to discriminate action intentions. The effect of the olfactory manipulation was revealed only in certain conditions, namely, at judging between a cooperative action vs. an individual action at natural-speed, and between a competitive action vs. an individual action at fast-speed. These conditions were reported as the hardest to discriminate by Sartori et al. (2011). These results are in accordance with the Bayesian perspective that prior information would have a greater influence on decision making when sensory evidence is more ambiguous (Koul et al., 2019; Summerfield & De Lange, 2014). Thus, it is expected that the effect of the olfactory manipulation is stronger for the conditions that are harder to discriminate (i.e., higher ambiguity in the visual domain). However, contrary to our hypotheses, we did not reveal an identity compatibility effect, for instance a facilitation effect when a cooperative BO preceded a cooperative action.

Instead, results reveal that the masked BOs accelerates action discrimination in the Coop- Nat condition and slows the action discrimination down in the Comp-Fast condition, while not affecting the accuracy at which each action intention is discriminated. When considering the criterion or bias, masked BOs bias action discrimination towards cooperative actions in the Comp- Coop and in the Coop-Nat conditions.

Altogether, our results suggest that the effect of masked BOs at discriminating action intentions might be related to the compatibility between the odor primes and the visual targets in terms of arousal, rather than action intention. It might be argued that the condition in which participants had to discriminate between competitive vs. fast-speed intentions is more arousing than the condition in which they had to discriminate cooperative vs. individual natural-speed action intentions. This idea is supported by previous research showing that competition (vs. cooperation) elicits higher arousal, both self-reported (Schmierbach, 2010) and indexed by higher heart rate (Kivikangas et al., 2014), and so does fast-speed (vs. slow-speed) stimuli. For instance, Sundar and Kalyanaraman (2004) found that fast-animation speeds trigger greater physiological arousal. Further, Robitaille and McGuffin (2019) showed that the maximum speed reached by arm movements in virtual reality provides a reliable signal of increased arousal. We argue that the cooperative BO is less arousing in line with previous studies linking cooperative activity to lower self-reported arousal (Schmierbach, 2010). Following this reasoning, in line with the hypothesis of high arousing interference (Nishisato, 1966; Sohn et al., 2015), slower discrimination is triggered when a high arousing odor stimulus (e.g., competitive BOs) is smelled prior the presentation of high arousing visual information (e.g., competitive and fast-speed video clips).

Any given BO contains different types of information about the sender, such as familiarity (kin vs. stranger; Parma et al., 2017), gender, health status, and the socio-emotional state in which the odor was donated (de Groot et al., 2012, 2015; Mujica-Parodi et al., 2009; Mutic et al., 2016). However, it appears that some sort of hierarchy between these different kinds of information exists. From a behavioral immune system perspective, it is plausible that information relative to harm avoidance is prioritized. This form of communication seems to be sustained by the peculiarity of the olfactory system in that it is the only sensory system without the need for a thalamic relay, as its receptors directly project to the olfactory bulb and to the primary olfactory cortical areas (Carmichael et al., 1994). This allows for the fast and subliminal detection of harmful stimuli. In a social context, smelling the competitive BO of a stranger might prime a reaction of harm avoidance, with an increase in stress and anxiety. We deem this being the case when participants are classifying action intentions that are more compatible (i.e., competitive and fast-speed) under the exposure of masked competitive (vs. cooperative) BOs. Under the assumption that masked cooperative BOs would evoke an intrinsic reinforcement associated with cooperative activities (Schuster & Perelberg, 2004), we argue that the participants would feel less aroused following the presentation of cooperative BOs as compared to competitive BOs. Following the arousal compatibility-like effect outlined above, we found that response times were significantly slower following the presentation of cooperative BOs as compared to competitive BOs in the Coop-Nat condition (i.e., the less arousing condition). This seems to reinforce the idea that participants felt more relaxed after being exposed to a cooperative BO, following the notion that decision-making is impaired with low levels of arousal (Jackson et al., 2014).

To further explore the arousal compatibility-like effects proposed in Experiment 1 and detach them from the presentation of socially-relevant information, namely the BOs, we carried out a second experiment where odor stimuli of different intensity (i.e., a common odor vs. clean air) were presented while participants performed the same task as in Experiment 1. In Experiment 2, we examined the exposure to a hedonically neutral common odor, specifically an odor stemming from a common odor source, such as cedarwood oil in this specific case (used to mask the BOs in Experiment 1), to determine if it modulates the ability to discriminate an agent's action intention compared to when no odor (i.e., clean air) is smelled. Unlike Experiment 1, where the BO stimuli were isointense, we anticipated the common odor to be perceived as more intense (a proxy for arousal; Bensafi et al., 2002; Cecchetto et al., 2017a) compared to the no odor stimulus. We expected to find the arousal compatibility-like effect described in Experiment 1. Furthermore, in accordance with Sartori et al. (2011) and the results of Experiment 1, we hypothesized that these effects would be observed in the conditions in which the discrimination of action intention entailed more ambiguity (i.e., when discriminating competitive vs. fast-speed action, and cooperative vs. natural-speed action intentions).

3. Experiment 2

3.1. Method

3.1.1. Participants

Twenty healthy participants (ten women, mean age: 24.4 ± 2.9 years old, age range: 20–31 years old) were recruited in this experiment. Inclusion criteria were the same as in Experiments 1. All participants signed a written informed consent and were rewarded as reported in Experiment 1. The descriptive statistics of the sample are presented in Table S1 in the *Supplementary material*.

3.1.2. Apparatus and stimuli

Visual stimuli were the same as in Experiment 1. As for the odor stimuli, we included two odor conditions with neutral valence, namely a common odor (100 μL of cedarwood oil, Sigma-Aldrich, Italy) and no odor (i.e., clean air over 2 mL propylene glycol, Sigma-Aldrich, Burlington, MA, United States).

3.1.3. Procedure

Participants performed the same task described in Experiment 1 except for the fact that the odor stimuli corresponded to the common odor (cedarwood oil) and a no odor. All other procedures were the same as in Experiment 1.

3.1.4. Statistical analyses

Data analyses were in line with those reported in Experiment 1, except that the levels of the fixed factor *odor* were common odor vs. no odor (clean air). Trials in which participants did not respond corresponded to 0.8 % of the total amount of trials. RTs exceeding 2.5 standard deviations corresponded to 2.2 % of the remaining trials, which were considered as outliers and excluded from analyses.

3.2. Results

For brevity, the main effects of odor, intention and sex, as well as the

Table 2
Descriptive statistics and multiple comparisons for the response time and accuracy at discriminating action intentions per odor condition in Experiment 2.

Measure	Odor	Intention	Mean ± *SD* / %	Comparison	*p* value
Response time	Common odor	Nat–Fast	2811 ± 745 ms	Coop–Comp	0.287
				Comp–Fast	**< 0.001*** **
				Coop–Nat	**0.024***
		Coop–Comp	2927 ± 644 ms	Comp–Fast	**< 0.001*** **
				Coop–Nat	0.933
		Comp–Fast	3398 ± 644 ms	Coop–Nat	**< 0.001*** **
		Coop–Nat	2947 ± 844 ms	–	–
	No odor	Nat–Fast	2915 ± 658 ms	Coop–Comp	0.986
				Comp–Fast	**< 0.001*** **
				Coop–Nat	**< 0.001*** **
		Coop–Comp	2973 ± 600 ms	Comp–Fast	**< 0.001*** **
				Coop–Nat	**< 0.001*** **
		Comp–Fast	3213 ± 711 ms	Coop–Nat	0.947
		Coop–Nat	3156 ± 819 ms	–	–
Accuracy	Common odor	Nat–Fast	80.1 %	Coop–Comp	0.277
				Comp–Fast	**< 0.001*** **
				Coop–Nat	**< 0.001*** **
		Coop–Comp	74.5 %	Comp–Fast	**< 0.001*** **
				Coop–Nat	**< 0.001*** **
		Comp–Fast	57.5 %	Coop–Nat	**< 0.001*** **
		Coop–Nat	45.7 %	–	–
	No odor	Nat–Fast	84.5 %	Coop–Comp	**< 0.001*** **
				Comp–Fast	**< 0.001*** **
				Coop–Nat	**< 0.001*** **
		Coop–Comp	72.5 %	Comp–Fast	**= 0.001** **
				Coop–Nat	**< 0.001*** **
		Comp–Fast	61.8 %	Coop–Nat	**< 0.001*** **
		Coop–Nat	38.8 %	–	–

Bold values denote statistical significance ($p < 0.05$*, $p < 0.01$**, $p < 0.001$***).

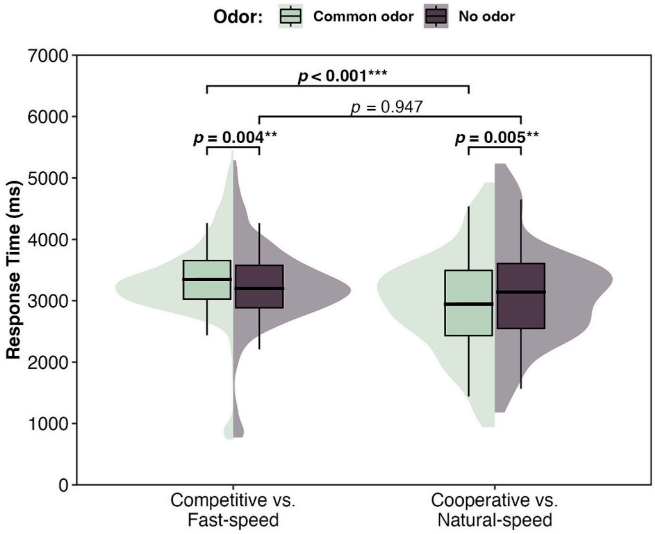

Fig. 4. Split violin plots for the response time at discriminating action intentions per odor condition in Experiment 1. The horizontal thick line within the boxes represents the mean. The lower and upper horizontal lines indicate the 25th and 75th percentiles of the distribution, respectively (interquartile range). The whiskers indicate the minimum and maximum values located 1.5 times the interquartile range. The shaded area surrounding each box depicts a rotated kernel density plot. Bold values denote statistical significance ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$).

ratings of familiarity and pleasantness are presented in the *Supplementary material*. There was no significant main effect of sex on any of the dependent variables (see Table S2 in the *Supplementary material*).

3.2.1. The common odor is more intense than no odor

As expected, the common odor (68.0 ± 21.5) was perceived as more intense than no odor (49.3 ± 28.3); the main effect of odor on the perceived intensity was significant, $\chi^2(1) = 12.429$, $p < 0.001$, $\mathrm{AIC_{RL}} > 100$, $R^2_\mathrm{m} = 0.129$, $R^2_\mathrm{c} = 0.285$, whereas neither the main effect of session, $\chi^2(1) = 0.276$, $p = 0.599$, $\mathrm{AIC_{RL}} = 0.422$, $R^2_\mathrm{m} = 0.002$, $R^2_\mathrm{c} = 0.114$ (pre = 59.9 ± 25.9, post = 57.5 ± 27.7), nor the interaction odor × session, $\chi^2(1) = 1.083$, $p = 0.298$, $\mathrm{AIC_{RL}} = 0.632$, $R^2_\mathrm{m} = 0.141$, $R^2_\mathrm{c} = 0.301$, reached significance. Furthermore, the two odor stimuli were equivalent in terms of pleasantness and familiarity (see *Supplementary material*).

3.2.2. Smelling a common odor modulates the discrimination speed of action intentions

The interaction odor × intention on the response time was significant, $\chi^2(3) = 33.271$, $p < 0.001$, $\mathrm{AIC_{RL}} > 100$, $R^2_\mathrm{m} = 0.059$, $R^2_\mathrm{c} = 0.372$; the descriptive statistics per condition are presented in Table 2. As evident from Fig. 4, the common odor, the high arousal odor in this pair, exhibits a dual effect. When paired with the Comp-Fast condition, it decelerates the discrimination of the action intention ($p = 0.004$). Conversely, it accelerates the discrimination in the Coop-Nat condition ($p = 0.005$). There were no significant differences observed in the other comparisons (refer to Table 2). Furthermore, slower responses were elicited when discriminating Comp–Fast and Coop–Nat intentions as compared to the other conditions, especially in the former, when exposed to both the common odor and no odor. To sum up, smelling the common odor modulated the speed at which participants discriminate between Comp–Fast and Coop–Nat action intentions.

3.2.3. Smelling a common odor does not modulate the discrimination accuracy of action intentions

Overall accuracy, collapsed across conditions, was 64.4 %. The interaction odor × intention on the accuracy at discriminating action intentions was significant, $\chi^2(3) = 13.321$, $p = 0.004$, $\mathrm{AIC_{RL}} = 38.886$, $R^2_\mathrm{m} = 0.106$, $R^2_\mathrm{c} = 0.149$; the descriptive statistics per condition are presented in Table 2. The accuracy level did not differ when the common odor was presented as compared to when no odor was delivered for any of the action intentions (Nat–Fast, $p = 0.463$; Coop–Comp, $p = 0.994$; Comp–Fast, $p = 0.787$, Coop–Nat, $p = 0.200$). Lower accuracy values were found for the Coop–Nat condition as compared to the other conditions when exposed to both the common odor and no odor. In brief, the presentation of the common odor did not modulate the discrimination accuracy of action intentions.

3.2.4. Participants discriminate cooperative vs. natural-speed action intentions more poorly than expected by chance

The main effect of intention on *d*' was significant, $\chi^2(3) = 61.619$, $p < 0.001$, $\mathrm{AIC_{RL}} > 100$, $R^2_\mathrm{m} = 0.308$, $R^2_\mathrm{c} = 0.367$, whereas the main effect of odor, $\chi^2(1) = 0.005$, $p = 0.944$, $\mathrm{AIC_{RL}} = 0.369$, $R^2_\mathrm{m} < 0.001$, $R^2_\mathrm{c} = 0.016$ (masker odor = 0.9 ± 1.8, no odor = 0.9 ± 1.7), and the interaction odor × intention, $\chi^2(3) = 1.614$, $p = 0.656$, $\mathrm{AIC_{RL}} = 0.112$, $R^2_\mathrm{m} = 0.314$, $R^2_\mathrm{c} = 0.375$, were not. The sensitivity index was lower for the Coop–Nat condition (−0.4 ± 0.7) than for the Nat–Fast (2.1 ± 1.9, $p < 0.001$), the Coop–Comp (1.5 ± 2.0, $p < 0.001$), and the Comp–Fast (0.5 ± 0.8, $p = 0.014$) conditions. *d*' was also lower for the Comp–Fast condition as compared to both the Nat–Fast ($p < 0.001$) and the Coop–Comp ($p = 0.015$) conditions. Instead, the Nat–Fast and the Coop–Comp conditions did not differ ($p = 0.175$). Furthermore, one-sample *t*-tests revealed that *d*' values were significantly >0 for the Nat–Fast, $t(39) = 7.000$, $p < 0.001$, the Coop–Comp, $t(39) = 4.740$, $p < 0.001$, and the Comp–Fast conditions, $t(39) = 3.966$, $p < 0.001$, but significantly lower than 0 for the Coop–Nat condition, $t(39) = -3.988$, $p < 0.001$. This indicates that discrimination performance was below chance level in this condition. In short, discrimination performance was more challenging in the Coop–Nat and the Coop–Comp conditions (particularly in the former), regardless of the odor prime.

3.2.5. Smelling a common odor (as opposed to no odor) biases the discrimination intentions towards cooperation

When testing the presence of a bias towards reporting cooperative action intentions, one-sample *t*-tests showed that for the Coop–Comp condition, the *c* parameter was lower than 0 when presented with the common odor, $t(19) = -3.125$, $p = 0.006$, but not when no odor was displayed, $t(19) = 0.296$, $p = 0.770$. This suggests a bias towards judging competitive actions as cooperative actions when a common odor is smelled. Moreover, *c* was lower than 0 within the Coop–Nat condition when the common odor was presented, $t(19) = -5.618$, $p < 0.001$, but not when no odor was displayed, $t(19) = 1.177$, $p = 0.243$, suggesting a bias towards judging natural-speed actions as cooperative actions when a common odor is smelled. In short, smelling a common odor biases the discrimination of action intentions towards classifying natural-speed and competitive actions as cooperative actions.

4. General discussion

In two experiments we aimed to determine whether odor stimuli can influence the discrimination of action intentions. Prior to the discrimination of the action intention of external agents based on the kinematics of their movements, the participants were exposed to cooperative vs. competitive BOs (Experiment 1), and a common odor vs. no odor (Experiment 2). The results of Experiment 2 aligned with those of Experiment 1, suggesting the presence of an arousal compatibility-like mechanism.

4.1. Odor stimuli interfere with the discrimination of action intentions in the presence of high ambiguity

Overall, both in Experiment 1 and 2, the discrimination speed was slower when the participants had to discriminate competitive vs. fast-speed and cooperative vs. natural-speed action intentions (particularly in the former condition) as compared to when they had to discriminate natural- vs fast-speed and cooperative vs. competitive action intentions. Additionally, both the accuracy level and the *d'* sensitivity index showed that discrimination was harder in the competitive vs. fast-speed and the cooperative vs. natural-speed conditions, with performance below the chance level in the latter across the two experiments. This pattern of results is in line with the idea that response times increase with the difficulty of the perceptual task (Schneider et al., 2011). Further, our results mirror those of Sartori et al. (2011), who found that these conditions are harder to discriminate, identifying cooperative vs. natural-speed as the most challenging one. They argued that a bias towards reporting cooperative action intentions responds to a natural human inclination to perceive cooperation even when this is not present (Sartori et al., 2011). Although in our experiments the participants were less accurate at discriminating cooperative vs. natural-speed than competitive vs. fast-speed action intentions, and responses were faster in the former condition. This might be interpreted as a trade-off between response speed and accuracy, as the performance in the cooperative vs. natural-speed condition was below the chance level, meaning that the participants systematically (and rapidly) misclassified as cooperative the individual natural-speed action intentions.

When comparing discrimination performance between the odor conditions, we found that smelling the masked BOs and the common odor differentially affected the discrimination speed of different action intentions, while the discrimination accuracy remained mostly unaffected. Both the common odor and the BO stimuli affected the response latencies, but only when more ambiguity was present at discriminating action intentions. This indicates that the kinematic features provide the information on which the olfactory stimuli rely to bias the categorization speed. We anticipated this to occur based on previous evidence showing that kinematic information is able to drive decision-making (Koul et al., 2019), and the idea that previously presented information has a greater influence on decision-making when the sensory evidence is more ambiguous (Summerfield & De Lange, 2014).

4.2. Arousal compatibility between olfactory and visual information

The effect of our olfactory manipulation was evident in those conditions where the arousal level of the action intentions was comparable. An interference effect in the speed at discriminating emerged in the more arousing conditions, namely, during the presentation of video clips showing competitive or fast-speed actions following the delivery of high arousing odor information such as a common odor (vs. no odor) and competitive (vs. cooperative) BOs. In other words, response times increase with high arousing interferences (Nishisato, 1966; Sohn et al., 2015). Following Jackson et al. (2014), optimal performance occurs with moderate (vs. low) levels of cognitive load and arousal. Low levels might lead to a poor performance due to distraction and lack of stimulation, resulting in decision-making errors. This seems to be the case for the discrimination of Coop-Nat action intentions, as reflected a low overall accuracy and a systematic misclassification, particularly when no odor and the cooperative BO were smelled. Less engagement with the task in this condition might have caused less inhibition of inappropriate response and fast impulsive errors, in line with recent evidence showing that odor stimuli can interfere with inhibitory control (Albayay et al., 2019, 2022).

The present findings seem to reflect a negative compatibility effect (NCE; Klapp & Hinkley, 2002; Ocampo & Finkbeiner, 2013; Schlaghecken et al., 2007). In masked priming, the NCE is reflected in slower response latencies when primes and targets features are compatible, for instance, when a masked arrow prime and a visible arrow target point in the same direction (Klapp & Hinkley, 2002); this phenomenon has also been revealed in a larger set of conditions (see Schlaghecken et al., 2007). The prime triggers a given assigned response and simultaneously inhibits the alternative response. If the target is presented immediately after the prime, what emerges is a positive compatibility effect (i.e., faster responses when primes and targets match). However, the NCE is manifested when the time between the prime and the target is prolonged, which suppresses the association between them. This has been referred as a low-level motor self-inhibition account and it is supposed to reflect unconsciously triggered inhibitory control (Ocampo & Finkbeiner, 2013). In brief, this mechanism stops early motor activation that is no longer supported by the sensory evidence, and at the same time disinhibits the alternative avenue, resulting in faster responses for incompatible trials (Schlaghecken et al., 2007).

To the best of our knowledge, this is the first study reporting a negative compatibility effect using olfactory primes as most of the previous literature has been conducted using visual material. However, it is noteworthy that congruency effects have been documented in previous studies, even with larger intervals between odor and visual stimuli. For instance, Castiello et al. (2006) utilized intervals up to 2000 ms and found significant congruency effects. In their study, participants were tasked with smelling an odorant before grasping an object presented in central vision. The results indicated that, when the odor evoked an object larger or smaller than the target, it influenced the timing and amplitude of maximum hand aperture. This suggests that cross-modal links between olfaction and vision can exert a discernible impact on goal-directed actions, even with extended intervals. This discrepancy in findings highlights the intricate nature of cross-modal interactions and underscores the need for further research to explore how different intervals may lead to either congruency effects or NCE in forced-choice tasks involving odor primes and visual targets.

5. Conclusions

In summary, we revealed that both common odors and body odors can modulate the discrimination of the action intentions of external agents. The effect of odor stimuli is revealed only when the discrimination involves more ambiguity. We propose a negative arousal compatibility-like effect to explain our experimental results, where compatible olfactory and visual evidence yields to interference effects through two different mechanisms, reflected in slower response latencies at discriminating action intentions. Our results also seem to align with the predictions of the self-inhibition account that explains negative compatibility effects. More research is needed to further disentangle this phenomenon, for instance, by controlling parametrically the time between primes and targets to account for both positive and negative compatibility effects. Furthermore, future research might include objective and real-time arousal assessment, such as skin conductance response or EEG activation to account for the compatibility of the participants' arousal level at the moment of smelling the odors and observing the visual stimuli.

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CRediT authorship contribution statement

Javier Albayay: Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Matteo Zampieri:** Writing – original draft, Investigation, Data curation, Conceptualization. **Luisa Sartori:** Writing – original draft, Resources, Methodology, Conceptualization. **Umberto Castiello:** Writing – original draft, Resources, Methodology, Funding acquisition, Conceptualization. **Valentina Parma:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

Valentina Parma is a scientific consultant for CyNexo. All other authors do not declare any conflict of interest.

Data availability

For the sake of openness, transparency and reproducibility of research, all the data reported in this study and the RStudio analysis scripts are available in the Open Science Framework repository accessible at https://osf.io/xqtgj/?view_only=adfc0f863f3f4aff9ab3bc34f57b98af.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actpsy.2024.104392.

References

Adolph, D., Schlösser, S., Hawighorst, M., & Pause, B. M. (2010). Chemosensory signals of competition increase the skin conductance response in humans. *Physiology & Behavior, 101*(5), 666–671. https://doi.org/10.1016/j.physbeh.2010.08.004

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience, 11*(9), 1109. https://doi.org/10.1038/nn.2182

Aglioti, S. M., & Pazzaglia, M. (2011). Sounds and scents in (social) action. *Trends in Cognitive Sciences, 15*(2), 47–55. https://doi.org/10.1016/j.tics.2010.12.003

Albayay, J., Castiello, U., & Parma, V. (2019). Task-irrelevant odours affect both response inhibition and response readiness in fast-paced go/no-go task: The case of valence. *Scientific Reports, 9*(1), 19329. https://doi.org/10.1038/s41598-019-55977-z

Albayay, J., Castiello, U., & Parma, V. (2022). The effect of odour valence and odour detection threshold on the withholding and cancellation of reach-to-press responses. *Chemosensory Perception.* https://doi.org/10.1007/s12078-021-09292-5

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language, 59* (4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Beck, A. T., Steer, R. A., & Brown, G. K. (1996). *Manual for the Beck Depression Inventory-II.* San Antonio, TX: Psychological Corporation.

Bensafi, M., Rouby, C., Farget, V., Bertrand, B., Vigouroux, M., & Holley, A. (2002). Autonomic nervous system responses to odours: The role of pleasantness and arousal. *Chemical Senses, 27*(8), 703–709. https://doi.org/10.1093/chemse/27.8.703

Carmichael, S. T., Clugnet, M.-C., & Price, J. L. (1994). Central olfactory connections in the macaque monkey. *Journal of Comparative Neurology, 346*(3), 403–434. https://doi.org/10.1002/cne.903460306

Castiello, U., Zucco, G. M., Parma, V., Ansuini, C., & Tirindelli, R. (2006). Cross-modal interactions between olfaction and vision when grasping. *Chemical Senses, 31*(7), 665–671. https://doi.org/10.1093/chemse/bjl007

Cecchetto, C., Fischmeister, F. P. S., Gorkiewicz, S., Schuehly, W., Bagga, D., Parma, V., & Schöpf, V. (2020). Human body odor increases familiarity for faces during encoding-retrieval task. *Human Brain Mapping, 41*(7), 1904–1919. https://doi.org/10.1002/hbm.24920

Cecchetto, C., Lancini, E., Bueti, D., Rumiati, R. I., & Parma, V. (2019). Body odors (even when masked) make you more emotional: Behavioral and neural insights. *Scientific Reports, 9*(1), 5489. https://doi.org/10.1038/s41598-019-41937-0

Cecchetto, C., Rumiati, R. I., & Aiello, M. (2017a). Alexithymia and emotional reactions to odors. *Scientific Reports, 7*, 14097. https://doi.org/10.1038/s41598-017-14404-x

Cecchetto, C., Rumiati, R. I., & Parma, V. (2017b). Relative contribution of odour intensity and valence to moral decisions. *Perception, 46*(3–4), 447–474. https://doi.org/10.1177/030100661668927

Chung, K. C., Peisen, F., Kogler, L., Radke, S., Turetsky, B., Freiherr, J., & Derntl, B. (2016). The influence of menstrual cycle and androstadienone on female stress reactions: An fMRI study. *Frontiers in Human Neuroscience, 10*, 44. https://doi.org/10.3389/fnhum.2016.00044

DeSteno, D., Petty, R. E., Rucker, D. D., Wegener, D. T., & Braverman, J. (2004). Discrete emotions and persuasion: The role of emotion-induced expectancies. *Journal of Personality and Social Psychology, 86*(1), 43–56. https://doi.org/10.1037/0022-3514.86.1.43

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods, 41*, 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Grafton, S. T. (2009). Embodied cognition and the simulation of action to understand others. *Annals of the New York Academy of Sciences, 1156*(1), 97–117. https://doi.org/10.1111/j.1749-6632.2009.04425.x

de Groot, J. H., Kirk, P. A., & Gottfried, J. A. (2020). Encoding fear intensity in human sweat. *Philosophical Transactions of the Royal Society B, 375*(1800), 20190271. https://doi.org/10.1098/rstb.2019.0271

de Groot, J. H., Smeets, M. A., Kaldewaij, A., Duijndam, M. J., & Semin, G. R. (2012). Chemosignals communicate human emotions. *Psychological Science, 23*(11), 1417–1424. https://doi.org/10.1177/0956797612445317

de Groot, J. H., Smeets, M. A., Rowson, M. J., Bulsing, P. J., Blonk, C. G., Wilkinson, J. E., & Semin, G. R. (2015). A sniff of happiness. *Psychological Science, 26*(6), 684–700. https://doi.org/10.1177/0956797614566318

Grös, D. F., Antony, M. M., Simms, L. J., & McCabe, R. E. (2007). Psychometric properties of the state-trait inventory for cognitive and somatic anxiety (STICSA): Comparison to the state- trait anxiety inventory (STAI). *Psychological Assessment, 19*(4), 369–381. https://doi.org/10.1037/1040-3590.19.4.369

Harrison, L. K., Denning, S., Easton, H. L., Hall, J. C., Burns, V. E., Ring, C., & Carroll, D. (2001). The effects of competition and competitiveness on cardiovascular activity. *Psychophysiology, 38*(4), 601–606. https://doi.org/10.1111/1469-8986.3840601

Hautus, M. J. (1995). Corrections for extreme proportions and their biasing effects on estimated values ofd. *Behavior Research Methods, Instruments, & Computers, 27*(1), 46–51. https://doi.org/10.3758/BF03203619

Hummel, T., Kobal, G., Gudziol, H., & Mackay-Sim, A. (2007). Normative data for the "Sniffin' sticks" including tests of odor identification, odor discrimination, and olfactory thresholds: An upgrade based on a group of more than 3,000 subjects. *European Archives of Oto-Rhino-Laryngology, 264*(3), 237–243. https://doi.org/10.1007/s00405-006-0173-0

Jackson, S. A., Kleitman, S., & Aidman, E. (2014). Low cognitive load and reduced arousal impede practice effects on executive functioning, metacognitive confidence and decision making. *PLoS One, 9*(12), Article e115689. https://doi.org/10.1371/journal.pone.0115689

Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: A Hebbian perspective. *Trends in Cognitive Sciences, 8*(11), 501–507. https://doi.org/10.1016/j.tics.2004.09.005

Kivikangas, J. M., Kätsyri, J., Järvelä, S., & Ravaja, N. (2014). Gender differences in emotional responses to cooperative and competitive game play. *PLoS One, 9*(7), Article e100318. https://doi.org/10.1371/journal.pone.0100318

Klapp, S. T., & Hinkley, L. B. (2002). The negative compatibility effect: Unconscious inhibition influences reaction time and response selection. *Journal of Experimental Psychology: General, 131*(2), 255–269. https://doi.org/10.1037/0096-3445.131.2.255

Koul, A., Soriano, M., Tversky, B., Becchio, C., & Cavallo, A. (2019). The kinematics that you do not expect: Integrating prior information and kinematics to understand intentions. *Cognition, 182*, 213–219. https://doi.org/10.1016/j.cognition.2018.10.006

Lenochová, P., Roberts, S., & Havlicek, J. (2009). Methods in body odour sampling: The effect of sampling length. *Chemical Senses, 34*, 127–138. https://doi.org/10.1093/chemse/bjn067

Lundström, J. N., Boyle, J. A., Zatorre, R. J., & Jones-Gotman, M. (2008). Functional neuronal processing of body odors differs from that of similar common odors. *Cerebral Cortex, 18*(6), 1466–1474. https://doi.org/10.1093/cercor/bhm178

Lundström, J. N., & Olsson, M. J. (2005). Subthreshold amounts of social odorant affect mood, but not behavior, in heterosexual women when tested by a male, but not a female, experimenter. *Biological Psychology, 70*(3), 197–204. https://doi.org/10.1016/j.biopsycho.2005.01.008

Lundström, J. N., & Olsson, M. J. (2010). Functional neuronal processing of human body odors. *Vitamins and Hormones, 83*, 1–23. https://doi.org/10.1016/S0083-6729(10)83001-8

Macmillan, N. A., & Creelman, C. D. (2004). *Detection theory: A user's guide.* Psychology press.

Martins, Y., Preti, G., Crabtree, C. R., Runyan, T., Vainius, A. A., & Wysocki, C. J. (2005). Preference for human body odors is influenced by gender and sexual orientation. *Psychological Science, 16*(9), 694–701. https://doi.org/10.1111/j.1467-9280.2005.01598.x

McElreath, R. (2016). *Statistical rethinking: A bayesian course with examples in r and stan* (Vol. 122). CRC press.

Mitro, S., Gordon, A. R., Olsson, M. J., & Lundström, J. N. (2012). The smell of age: Perception and discrimination of body odors of different ages. *PLoS One, 7*(5), Article e38110. https://doi.org/10.1371/journal.pone.0038110

Mujica-Parodi, L. R., Strey, H. H., Frederick, B. D., Savoy, R. L., Cox, D. G., Botanov, Y., … Weber, J. (2009). Chemosensory cues to conspecific emotional stress activate amygdala in humans. *PLoS One, 4*(7). https://doi.org/10.1371/journal.pone.0006415

Mutic, S., Freiherr, J., Cavazzana, A., Rocha, M., Soares, S. C., & Parma, V. (2019). The scent of the other women: Body odor-induced behavioral and physiological effects on face categorization. *Physiology & Behavior, 210*, Article 112562. https://doi.org/10.1016/j.physbeh.2019.112562

Mutic, S., Parma, V., Brünner, Y. F., & Freiherr, J. (2016). You smell dangerous: Communicating fight responses through human chemosignals of aggression. *Chemical Senses, 41*(1), 35–43. https://doi.org/10.1093/chemse/bjv058

Nishisato, S. (1966). Reaction time as a function of arousal and anxiety. *Psychonomic Science, 6*(4), 157–158. https://doi.org/10.3758/BF03328005

Ocampo, B., & Finkbeiner, M. (2013). The negative compatibility effect with relevant masks: A case for automatic motor inhibition. *Frontiers in Psychology, 4*, 822. https://doi.org/10.3389/fpsyg.2013.00822

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Oleszkiewicz, A., Schriever, V. A., Croy, I., Hähner, A., & Hummel, T. (2019). Updated Sniffin' sticks normative data based on an extended sample of 9139 subjects. *European Archives of Oto-Rhino-Laryngology, 276*(3), 719–728. https://doi.org/10.1007/s00405-018-5248-1

Parma, V., Bulgheroni, M., Scaravilli, T., Tirindelli, R., & Castiello, U. (2013). Implicit olfactory processing attenuates motor disturbances in idiopathic Parkinson's disease. *Cortex, 49*(5), 1241–1251. https://doi.org/10.1016/j.cortex.2012.05.017

Parma, V., Bulgheroni, M., Tirindelli, R., & Castiello, U. (2013b). Body odors promote automatic imitation in autism. *Biological Psychiatry, 74*(3), 220–226. https://doi.org/10.1016/j.biopsych.2013.01.010

Parma, V., Bulgheroni, M., Tirindelli, R., & Castiello, U. (2014). Facilitation of action planning in children with autism: The contribution of the maternal body odor. *Brain and Cognition, 88*, 73–82. https://doi.org/10.1016/j.bandc.2014.05.002

Parma, V., Gordon, A. R., Cecchetto, C., Cavazzana, A., Lundström, J. N., & Olsson, M. J. (2017). Processing of human body odors. In *Springer handbook of odor* (pp. 127–128). Springer.

Parma, V., Straulino, E., Zanatto, D., Cantagallo, A., Tirindelli, R., & Castiello, U. (2012). Implicit olfactory abilities in traumatic brain injured patients. *Journal of Clinical and Experimental Neuropsychology, 34*(9), 977–988. https://doi.org/10.1080/13803395.2012.711811

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist, 166*(2), 231–245. https://doi.org/10.1086/431246

Psychology Software Tools, Inc. (2012). E-Prime 2.0. Available at http://www.pstnet.com.

Robitaille, P., & McGuffin, M. J. (2019). Increased affect-arousal in VR can be detected from faster body motion with increased heart rate. In *Proceedings of the ACM SIGGRAPH symposium on interactive 3D graphics and games* (pp. 1–6). https://doi.org/10.1145/3306131.3317022

Rossi, S., De Capua, A., Pasqualetti, P., Ulivelli, M., Fadiga, L., Falzarano, V., … Rossini, P. M. (2008). Distinct olfactory cross-modal effects on the human motor system. *PLoS One, 3*(2), Article e1702. https://doi.org/10.1371/journal.pone.0001702

RStudio Team. (2016). *RStudio: Integrated development for R*. Boston, MA: RStudio, Inc.. Retrieved from http://www.rstudio.com/.

Sartori, L., Becchio, C., & Castiello, U. (2011). Cues to intention: The role of movement information. *Cognition, 119*(2), 242–252. https://doi.org/10.1016/j.cognition.2011.01.014

Schlaghecken, F., Rowley, L., Sembi, S., Simmons, R., & Whitcomb, D. (2007). The negative compatibility effect: A case for self-inhibition. *Advances in Cognitive Psychology, 3*(1–2), 227–240. https://doi.org/10.2478/v10053-008-0027-y

Schmierbach, M. (2010). "Killing spree": Exploring the connection between competitive game play and aggressive cognition. *Communication Research, 37*(2), 256–274. https://doi.org/10.1177/0093650209356394

Schneider, K., Dogil, G., & Möbius, B. (2011). Reaction time and decision difficulty in the perception of intonation. In *Twelfth annual conference of the international speech communication association*. https://doi.org/10.21437/interspeech.2011-581

Schuster, R., & Perelberg, A. (2004). Why cooperate?: An economic perspective is not enough. *Behavioural Processes, 66*(3), 261–277. https://doi.org/10.1016/j.beproc.2004.03.008

Simmons, C. H., Wehner, E. A., Tucker, S. S., & King, C. S. (1988). The cooperative/competitive strategy scale: A measure of motivation to use cooperative or competitive strategies for success. *The Journal of Social Psychology, 128*(2), 199–205. https://doi.org/10.1080/00224545.1988.9711363

Singmann, H., & Kellen, D. (2017). An introduction to mixed models for experimental psychology. In D. H. Spieler, & E. Schumacher (Eds.), *New methods in cognitive psychology*. Psychology Press.

Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology: General, 117*(1), 34–50. https://doi.org/10.1037/0096-3445.117.1.34

Sohn, J.-H., Kim, H.-E., Sohn, S., Seok, J.-W., Choi, D., & Watanuki, S. (2015). Effect of emotional arousal on inter-temporal decision-making: An fMRI study. *Journal of Physiological Anthropology, 34*(1), 8. https://doi.org/10.1186/s40101-015-0047-5

Summerfield, C., & De Lange, F. P. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience, 15*(11), 745–756. https://doi.org/10.1038/nrn3838

Sundar, S. S., & Kalyanaraman, S. (2004). Arousal, memory, and impression-formation effects of animation speed in web advertising. *Journal of Advertising, 33*(1), 7–17.

Tubaldi, F., Turella, L., Pierno, A. C., Grodd, W., Tirindelli, R., & Castiello, U. (2011). Smelling odors, understanding actions. *Social Neuroscience, 6*(1), 31–47. https://doi.org/10.1080/17470911003691089

Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 358*(1431), 593–602. https://doi.org/10.1098/rstb.2002.1238

World Medical Association. (2013). WMA declaration of Helsinki: Ethical principles for medical research involving human subjects. *Journal of the American Medical Association, 310*(20), 2191–2194. https://doi.org/10.1001/jama.2013.281053