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► **To cite this version:**

Cédric Manesse, Arnaud Fournel, Moustafa Bensafi, Camille Ferdenzi. Visual Priming Influences Olfactomotor Response and Perceptual Experience of Smells. *Chemical Senses*, 2020, 45 (3), pp.211-218. 10.1093/chemse/bjaa008 . hal-03060296

HAL Id: hal-03060296

<https://hal.science/hal-03060296>

Submitted on 13 Dec 2020

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**Visual priming influences olfactomotor response
and perceptual experience of smells**

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[§]Equal contribution

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16 **Abstract**

17 Whereas contextual influences in the visual and auditory domains have been largely documented, little is known
18 about how chemical senses might be affected by our multi-sensory environment. In the present study, we aimed
19 to better understand how a visual context can affect the perception of a rather pleasant (floral) and a rather
20 unpleasant (damp) odor. To this end, 19 healthy participants performed a series of tasks including odor detection
21 followed by perceptual evaluations of odor intensity, pleasantness, flowery and damp characters of both odors
22 presented at two different concentrations. A visual context (either congruent or incongruent with the odor; or a
23 neutral control context) preceded odor stimulations. Olfactomotor responses as well as response times were
24 recorded during the detection task. Results showed an influence of the visual context on semantic and motor
25 responses to the target odors. First, congruency between context and odor increased the saliency of the olfactory
26 feature of the memory trace, for the pleasant floral odor only (higher perceived flowery note). Clinical
27 applications of this finding for olfactory remediation in dysosmic patients are proposed. Second, the unpleasant
28 odor remained unaffected by visual primes, whatever the condition. In addition, incongruency between context
29 and odor (regardless of odor type) had a disruptive effect on odor sampling behavior, which was interpreted as a
30 protective behavior in response to expectancy violation. Altogether, this second series of effects may serve an
31 adaptive function, especially the avoidance of, or simply vigilance towards, aversive and unpredictable stimuli.

32 **Keywords**

33 Olfaction, visual context, priming, intensity, pleasantness, sniffing

34

35 **Introduction**

36 Processing of environmental objects by our brain usually involves more than a single sensory input. A
37 given object possesses attributes that can be processed by vision (such as shape, color), somatosensory system
38 (e.g., softness, temperature, pain), audition (like sound volume, frequency), taste (e.g., bitter, sweet), trigeminal
39 system (e.g., freshness, irritation), and olfaction (e.g., odor intensity, localization). Such multimodal integration
40 contributes to the formation of percepts, where all pieces of solicited sensory information are associated together
41 and compared with previous mental representations.

42 Beside this multimodal integration, there is also evidence for interactions between sensory modalities
43 during the processing of environmental objects, including for instance auditory interferences on visual sensitivity
44 (Chen & Spence 2011) or between olfaction, verbal materials and/or vision which have also been shown to
45 interact with each other. These interactions can take two forms. The first form is an influence by *direct access*
46 whereby a sensory modality facilitates / interferes with the processing of another modality during a multimodal
47 perception (here, the two stimulations are presented concurrently) (Zellner and Kautz, 1990; Gottfried and
48 Dolan, 2003; Herz, 2003; Sakai, 2005; Bensafi et al., 2007a, 2014). The second form is an influence by
49 *reactivation* where a sensory modality facilitates / interferes with the processing of another modality via a
50 priming paradigm (here, the first stimulus – the prime – is presented before the second stimulus – the target).
51 Such priming paradigms are commonly used in psychological research to study how the prime can affect the
52 processing of, and behavioral/motor response to, the target. The target may or may not share with the prime
53 some sensory, affective or semantic properties. Priming tasks have been recurrently used in sensory studies in
54 order to explore how olfactory stimuli influence the processing of visual information (Grigor et al., 1999; Castle
55 et al., 2000; Bensafi et al., 2002a; Cook et al., 2015) and vice versa (van Beilen et al., 2011; Kowalewski and
56 Murphy, 2012).

57 On a theoretical level, such a mutual influence between olfaction and vision can be explained using
58 cognitive models of human memory, in particular the Activation-Integration ACT-IN model (Versace et al.,
59 2014). In this model, percepts are defined as representations characterized by multiple components: shape, color,
60 odor, sound, emotion, motor, etc. Such percepts are encoded in memory as multi-dimensional objects containing
61 these inter-related components which altogether form a “memory trace”. This model predicts that any salient
62 component of a given trace can reactivate the trace itself but also other components of the same trace. For
63 instance, for environmental objects that contain smells (i.e., a rose) one may assume that its visual characteristics
64 (materialized by, for instance, pictures of a rose or gardens) can influence the activation of the emotional (i.e.,

65 hedonicity of a rose, modulated by its intensity), semantic (i.e., smell of a rose) and motor (i.e., action of sniffing
66 a rose) attributes. The main aim of the present study was to test this prediction. Here, we hypothesized that a
67 visual image (prime) semantically associated with an odor would influence the subsequent processing of the odor
68 in a priming paradigm. We further assumed that such influence of the visual prime on the smell target would be
69 observed at different levels of processing, from emotional ratings, to semantic evaluations and olfactomotor
70 responses. The experimental design included 2 concentrations of 2 odors differing in hedonic valence. In
71 addition, the role of the semantic proximity between the prime and the target was examined: we predicted that
72 congruent associations might have a facilitating effect while incongruent associations might have a disrupting
73 effect on the processing of the target. During the experimental sessions, participants were required to perform a
74 series of tasks related to the odorant: following prime presentation, they were asked to detect the smell as fast as
75 possible after its presentation, to give estimates of intensity and pleasantness, and to qualify it using quality
76 descriptors, while sniffing behavior was recorded. Four variables were thus collected: emotional and semantic
77 ratings, olfactomotor response and response time.

78

79 **Material and Methods**

80

81 **Subjects**

82 Nineteen healthy participants (mean age \pm standard deviation: 28.9 ± 9.5 ; 9 men and 10 women) were recruited
83 at the University of Lyon, France. They declared having normal olfaction and *a posteriori* verification showed
84 that *i*) the participants perceived the experimental odors at a satisfactory level of intensity (4.6 ± 0.9 on a scale
85 from 1 to 9), and *ii*) none of the participants had lower intensity ratings than the others, as shown by a Grubbs
86 test for outliers ($G = 2.11$, $U = 0.72$, $p = 0.2257$). Participants provided written informed consent prior to
87 participation. They were tested individually and received monetary compensation for their participation. The
88 study was conducted in accordance with the Declaration of Helsinki and was approved by the local Lyon Sud-
89 Est II review board.

90

91

92 **Stimuli**

93 **Odors.** Two odorants were used (odorant code, « quality » with verbatim extracted from
94 www.thegoodscentscompany.com, CID): phenyl-2-ethanol (PEA, floral/rose/dried rose, 6054), terpinen-4-ol
95 (TER, earthy/musty/damp, 11230) both provided by Sigma Aldrich. Each odorant was used at 2 concentrations
96 (percentage in vol/vol): high (PEA: 1%; TER: 5%) and low (PEA: 0.5%; TER: 1%). Concentrations were chosen
97 based on previous studies (Kermen et al., 2011; Licon et al., 2018) so that each odor has a low and high
98 perceived intensity, that high concentrations of both odors are approximately iso-intense, and that low
99 concentrations remain high enough to allow odor identity to be recognized (explaining why concentration
100 intervals between high and low are not identical for both odors). Odorants were diluted in odorless mineral oil
101 (Sigma Aldrich), absorbed on a scentless polypropylene fabric (3 × 7 cm; 3M, Valley) to maximize air exchange
102 surface and dispensed in 15 mL brown glass jars (opening diameter: 1.8 cm; height: 5 cm; filled with 5 mL
103 odorous solution). We also used “blank” jars containing only odorless mineral oil, to limit participants’ olfactory
104 fatigue along the testing and to test for effective odor perception by comparing odorous vs. blank flasks. PEA
105 and TER were chosen because they were perceived as different in terms of pleasantness and because they
106 elicited distinct semantic descriptions in previous studies (Kermen et al., 2011). In that study, the analysis of
107 verbatims revealed that: (i) the two odors elicited no words in common, (ii) the most frequent words for PEA
108 were “Rose”, “Floral”, and “Alcohol” and for TER “Muddy”, “Woody”, “Damp”. These descriptions fit the
109 organoleptic characteristics of these molecules (see <http://www.thegoodscentscompany.com>).

110
111 **Pictures.** Visual cues were high-resolution pictures displayed on a computer screen. Pictures were either
112 copyright-free or from the authors’ personal shots. Two different contexts were used, and each context was
113 represented by 3 different pictures (Fig. 1A): Context 1 was a woody, damp, musty environment, congruent with
114 TER odor, and Context 2 was a floral, garden or perfume factory environment, congruent with PEA. The most
115 suitable pictures of a series were chosen during a pilot study, during which 5 participants were asked to evaluate
116 30 candidate pictures chosen by the experimenters to visually illustrate the odor descriptors. Participants were
117 asked to provide a rating of the congruence between the 6 descriptors given for PEA (3) and TER (3) and each
118 picture, on a scale from 0 (descriptor not suited at all) to 10 (descriptor very well suited). For each odor, we
119 identified and kept for the main study the 3 pictures with both the highest ratings of congruence with the target
120 odor’s descriptors and the lowest ratings of congruence with the other odor’s descriptors. We thus obtained 6
121 pictures in total, 3 for each odorant.

122 In the main protocol, each odor (PEA, TER) was presented after the 6 selected pictures (3 congruent, 3
123 incongruent), but also after a neutral context (grey rectangle). At the end of the experimental session (described
124 hereafter in the Procedure section), participants were asked to rate the congruency between each odor (at high
125 concentration) and the 6 pictures using a scale from 1 (not related at all) to 9 (very congruent). These evaluations
126 confirmed that the pictures were chosen in an appropriate manner (Fig. 1C) since TER was rated more congruent
127 with Context 1 than PEA (paired t-test: $t(17) = 2.41, p = 0.0274$), and PEA was rated more congruent with
128 Context 2 than TER ($t(17) = 3.77, p = 0.0015$).

129

130 **Procedure**

131 Each trial was characterized by a combination of 3 factors: Odor (PEA, TER), Concentration (high, low), and
132 Context (congruent, incongruent, neutral). A total of 36 olfactory trials were thus used (2 odorants \times 2
133 concentrations \times 3 contexts \times 3 pictures per context). Note that to limit olfactory fatigue and/or adaptation, an
134 empty flask was presented 9 times as a target (3 times per type of context, interspersed within the olfactory
135 targets). Thus, in total, the experiment lasted about 35 minutes and included 45 trials (36 odors + 9 empty
136 flasks). The presentation order of the 45 different combinations of odor/concentration/context/picture was fully
137 randomized. Participants were seated in a comfortable chair, equipped with the sniffing measurement apparatus
138 and facing an adjustable computer screen set at eye-level (1 m viewing distance). A nasal cannula (AirLife,
139 CareFusion, USA) positioned in both nostrils and connected to an airflow sensor (AWM720, Honeywell, France)
140 allowed to record sniffing behavior. The sniffing signal was amplified and digitally recorded at 256 Hz using
141 LabVIEW software®. To record response time during the odor detection task, participants' dominant, i.e., right
142 hand (all were right-handed) was placed on a button-box (see next paragraph). At the beginning of each trial (see
143 trial description in Fig. 1B), after a 1-second resting time, a circle was presented in the middle of the screen
144 during 4 s, followed by a picture presented for 5 s. The participant were then asked to breathe out (instruction
145 appearing for 2s), before a cross appeared in the middle of the screen for 5 s during which an odor was presented
146 by the experimenter. The flask was placed 1 cm under the participant's nostrils and the participant had to press a
147 key of the button-box with his/her index finger as soon as an odor was detected (and before the end of the 5-s
148 odor presentation). The flask was then removed, and a new screen was presented for 25 s, where the participants
149 were instructed to answer the questions of the experimenter. At this stage, participants were asked to rate
150 intensity, pleasantness, flowery note and damp note using scales from 1 (very little intense, very unpleasant, not
151 floral at all, not damp at all) to 9 (very intense, very pleasant, very flowery, very damp). The terms "flowery"

152 and “damp” were chosen among the other most frequent descriptors (see *Odors* section) because they referred to
153 perceptual characteristics of the odors rather than odor sources (like rose or mud). The responses of the
154 participants were given orally and written down by the experimenter.

155

156

Figure 1

157

158 **Data Analysis**

159 The analyzed variables were *i*) perceptual ratings of the odors (intensity, pleasantness, flowery note and damp
160 note), *ii*) characteristics of the first sniff during flask presentation, namely sniff volume (area under the curve)
161 and sniff duration in seconds (between the inhalation starting point and the point where the flow returned to
162 zero), and *iii*) reaction time (RT) during odor detection (i.e., time between the flask inhalation starting point and
163 the button-press to indicate that he/she detected an odor; these two time-points were recorded in milliseconds by
164 the sniff recording system described in the procedure). Only trials involving TER and PEA were considered in
165 the analyses (not the blank, $N=684$ trials). There were missing data described as follows. In case the odor was
166 not detected, participants made no perceptual ratings (6% of the ratings). Because of anticipated sniffing (i.e.,
167 inhalation starting point occurring before odor presentation) or because of technical issues, the olfactomotor data
168 of two participants were discarded (11 % of the trials, $N=17$ subjects). RTs below 200 ms were discarded (not
169 within the normal range of reactivity for this kind of task: Olofsson, 2014) as well as RTs above 5 s (which was
170 the maximum allocated time). It must be added that several aberrant observations that were deleterious for the
171 quality of the statistical models (see next paragraph) were identified by visual inspection of the graphs of
172 residuals and of Cook’s distances: they were removed (for sniff volume: 3 trials; for sniff duration: 3 trials with 2
173 being the same as for sniff volume) before recomputing the final model. Additional RTs were missing due to
174 technical problems or to non-usable sniffs (see above) since RT calculation was based on the start of the sniff
175 (16% of the trials missing, $N=17$ subjects).

176 We used RStudio 1.1.453 on R 3.5.0 (R Core Team, 2018) and lme4 package (Bates et al., 2015) to
177 perform a linear mixed effects analysis of the effects of Odor, Context and Concentration on participants’
178 responses, i.e. ratings of intensity, pleasantness, flowery and damp notes, sniff volume and duration, and odor
179 detection time. As fixed effects, we entered Odor (PEA, TER), Context (congruent, incongruent, neutral) and
180 Concentration (high, low) into the model, integrating only 2-way interactions because 3-way interactions were
181 not significant for any of the variables (likelihood ratio test – with the *anova* function – comparing models with

182 and without the triple interaction). As random effects, we had intercepts for subjects, which was found to be
183 highly relevant due to the important inter-individual variability (between 31 and 68% of the residual variance
184 depending on the variable considered). We also included the random intercept for pictures, but likelihood ratio
185 test model comparison showed that the complete model with both subjects and pictures was not significantly
186 better than the model with only subjects, which was thus used. Sniff parameters (duration and volume) as well as
187 RTs were log-transformed. Visual inspection of residual plots did not reveal any obvious deviations from
188 homoscedasticity or normality. Following (Luke, 2017), p-values were obtained using Kenward-Roger
189 approximation in the *anova* function of lmerTest package in R (Kuznetsova et al., 2017) and non-significant
190 interaction were removed to keep only the best model including the main effects and the significant interactions.
191 Post-hoc contrasts were performed using the *multcomp* function of the emmeans package in R (Lenth et al.,
192 2019) and are reported in the results section with a significance level of 0.05.

193

194 **Results**

195

196 Detailed statistics regarding the main effects and interactions are reported in Table 1, and post-hoc contrasts
197 allowing us to describe these significant effects are reported in Table 2 and illustrated in the Figures. Non-
198 significant main effects or interactions are not mentioned in the text and only appear in the tables.

199

200 **Emotional ratings**

201 **Intensity.** Linear mixed model showed a significant Odor \times Concentration interaction ($p < 0.0001$), as
202 well as main effects of Concentration ($p < 0.0001$) and Odor ($p < 0.0001$) (see Table 1). Both odors were
203 perceived as significantly more intense when they were at high concentrations compared to low concentrations
204 (significant post-hoc contrasts: PEA-high vs. PEA-low, and TER-high vs. TER-low), but TER at high
205 concentration received even higher intensity ratings (significant contrast: TER-high vs. PEA-high, while the
206 contrast TER-low vs. PEA-low was not significant).

207 **Pleasantness.** A main effect of Odor was found ($p < 0.0001$, see Table 1), due to PEA's higher
208 pleasantness ratings (Table 2).

209

210 **Semantic ratings**

211 **Flowery note.** The Odor \times Context interaction was found to be significant ($p < 0.05$, see Table 1). As
212 illustrated in Fig. 2A showing all significant post-hoc contrasts, while flowery ratings of TER were stable across
213 contexts, flowery ratings of PEA were significantly higher in the congruent (flowery) than in the incongruent
214 (damp) or neutral contexts (Table 2). In line with this, on average PEA was rated more flowery than TER (main
215 effect of Odor, $p < 0.0001$, see Tables 1 and 2). Also, the congruent context was associated to higher flowery
216 ratings (main effect of Context, $p < 0.01$, see Table 1; significant contrasts: congruent vs. neutral, and congruent
217 vs. incongruent, while the contrast neutral vs. incongruent was not significant, see Table 2).

218 **Damp note.** First, there was a significant Odor \times Context interaction ($p < 0.05$, see Table 1). As
219 illustrated in Fig.2B showing all significant post-hoc contrasts, while damp ratings of TER were stable across
220 contexts, damp ratings of PEA were significantly higher in the incongruent (damp) than in the congruent
221 (flowery) context (Table 2). Second, the Odor \times Concentration interaction was significant as well ($p < 0.01$, see
222 Table 1). Indeed, TER was rated damper at high compared to low concentration (significant TER-high vs. TER-
223 low contrast), while this was not the case for PEA (PEA-high vs. PEA-low contrast was not significant), and
224 TER received higher damp ratings than PEA at both concentrations (significant contrasts: TER-high vs. PEA-
225 high, and TER-low vs. PEA-low, see Table 2). In line with this, on average TER was rated more damp than PEA
226 (main effect of Odor, $p < 0.0001$, see Tables 1 and 2), and high concentrations were associated to higher damp
227 rating than low concentrations (main effect of Concentration, $p < 0.05$, see Tables 1 and 2).

228 *Figure 2*

229

230 **Olfactomotor responses**

231 **Sniff Volume.** Results on log-transformed sniff volume revealed a significant main effect of Context (p
232 < 0.01 , Table 1), due to the fact that sniff volume was smaller in the incongruent than the neutral context (Table
233 2, Fig. 3A: incongruent vs. neutral was the only significant post-hoc contrast). The Odor \times Concentration
234 interaction was significant ($p < 0.05$, Table 1). Indeed, sniffs had smaller volume when smelling TER at high
235 concentration compared to TER at low concentration (significant TER-high vs. TER-low contrast), and
236 compared to PEA at high concentration (significant TER-high vs. PEA-high contrast) (the other contrasts, PEA-
237 high vs. PEA-low, and TER-low vs. PEA-low, were not significant, see also Table 2). There were also
238 significant main effects of Odor ($p < 0.01$) and of Concentration ($p < 0.01$, Table 1), because sniff volume was
239 smaller for TER than for PEA, and smaller for high compared to low concentrations.

240 *Sniff Duration.* As for sniff volume, results on log-transformed sniff duration revealed a significant
241 main effect of Context ($p < 0.001$, Table 1), due to the fact that sniff duration was shorter in the incongruent than
242 the neutral context (Table 2, Fig. 3B: incongruent vs. neutral was the only significant post-hoc contrast). In
243 addition, there was also a significant main effect of Concentration ($p < 0.0001$, Table 1), because sniff duration
244 was shorter for high compared to low concentrations.

245 *Figure 3*

246

247 **Odor Detection Time**

248 There was a significant Odor \times Concentration interaction ($p < 0.01$, Table 1), due to the fact that TER at
249 high concentration was detected faster than TER at low concentration (significant TER-high vs. TER-low
250 contrast), and faster than PEA at high concentration (significant TER-high vs. PEA-high contrast) (the other
251 contrasts, PEA-high vs. PEA-low, and TER-low vs. PEA-low, were not significant, see also Table 2). Odor and
252 Concentration had significant main effects ($p < 0.0001$ and $p < 0.0001$ respectively, Table 1), due to faster
253 detection of TER than of PEA, and to faster detection of high compared to low concentrations (Table 2).

254

255

256 **Discussion**

257 In the present study, we aimed to test the hypothesis that a visual prime semantically associated with an
258 odor would modulate the subsequent processing of this odor. We tested this assumption by manipulating the
259 congruency between the visual prime and the olfactory target, and by measuring emotional, semantic and motor
260 responses to olfactory targets according to whether they were congruent or not with the visual prime. The visual
261 prime did influence odor processing, and this modulation depended on the nature of the odor. Indeed, when
262 considering the odor of PEA, which is rather pleasant and has a flowery quality, we found that a congruent visual
263 prime increased the flowery semantic quality attributed to this odor. Not only flowery but also damp ratings of
264 PEA were affected by visual context: PEA was evaluated as damper when presented after the damp context. On
265 the contrary, TER, which is a rather unpleasant odor that has damp/humid qualities, was unaffected by visual
266 priming since none of the perceptual ratings (intensity, pleasantness, flowery and damp ratings) for this odor
267 varied as a function of visual context congruency. The results on PEA are consistent with previous studies
268 reporting that visual environmental cues can prime odor processing and render odors more salient (Schifferstein

269 and Verlegh, 1996; Gottfried and Dolan, 2003). This also suggests a more vivid activation of the memory trace,
270 on several aspects including smell, by the related visual information (Versace et al., 2014). Note that, although
271 the damp visual context was clearly more congruent with TER than with PEA, it can still be part of memory
272 traces involving rose odor: indeed, plants and flowers, due to their vegetable nature, have a certain degree of
273 humidity that can express through olfactory notes. This would explain why the damp visual context increased
274 damp notes perceived when smelling PEA. The discrepancy observed between TER (unaffected) and PEA (more
275 flexible) with regards to visual priming may reflect that for unpleasant odors such as TER, their adaptive value
276 (i.e., indicating a potentially noxious odor source to be avoided) makes them less susceptible to cognitive
277 modulation. This asymmetry between positively and negatively valenced odors with regard to top-down
278 influences, with unpleasant odors being less prone to such influences, has been reported in previous studies
279 (Ferdenzi et al. 2013; Herz 2003).

280 Beyond the effects of visual context on participants' conscious responses (perceptual ratings), an
281 original finding of this study is that the olfactomotor behavior associated to the perception of the smell targets
282 was modulated as well. The volume and duration of the olfactomotor activity (sniffing) were significantly lower
283 after the participant was primed with an incongruent visual context (compared to a neutral context). Sniffing, i.e.
284 the active sampling of olfactory information, is an implicit behavior that accompanies odor perception in the
285 very first seconds after stimulus presentation (Ferdenzi et al., 2015). Its volume and duration determine the
286 amount of inhaled odor, which confers to sniffing behavior a function of protection against toxic substances
287 (decreased volume and duration in response to strong and unpleasant odors: Johnson et al., 2003; Bensafi et al.,
288 2007b). Here, the reduced sniffing behavior in the incongruent context may be explained by expectation effects.
289 When the target odor is inconsistent with the previous visual prime, participants may experience expectancy
290 violation and may therefore quickly stop sniffing as an expression of vigilance regarding an unpredictable
291 stimulus. It must be noted that this effect was disconnected from the nature of the odor (PEA or TER), probably
292 because this behavior occurs precociously in the chain of responses to the odor, before the more complex
293 cognitive processing measured through verbal evaluations.

294 In conclusion, this study showed the influence of the visual context on the processing of a smell
295 (semantic and motor attributes in particular). On the one hand, incongruity between a visual prime and an
296 olfactory target seems to have a disruptive effect on odor sampling behavior since it was associated with reduced
297 overall olfactomotor behavior. Congruency on the other hand increased the saliency of the trace only for the
298 pleasant odor PEA. Although our findings cannot be generalized to all pleasant and unpleasant odors, they make

299 sense in an adaptive perspective and should be tested in future studies by including more contrasted odorants and
300 a larger set of stimuli. Other observations were made in this experiment, namely that i) sniffing volume and
301 duration were lower for higher odor concentrations, which replicates previous findings (Mainland and Sobel,
302 2006), and ii) the most aversive odor TER was detected faster and sniffed less intensely (lower sniff volume), all
303 the more so that it was presented at high concentration, which is in line with Bensafi et al. (2002b) and
304 Boesveldt et al. (2010). These elements reinforce the validity of the protocol used in our study. We expected
305 visual congruent prime to shorten odor detection time, based on Olofsson et al. (2012)'s study, but this
306 assumption could not be verified. One explanation could be found in the nature of the primes (Loersch and
307 Payne 2011): indeed, congruency between the primes and the targets that we chose may have not been strong
308 enough to facilitate odor detection, and this parameter could be improved in the future (by reinforcing the
309 semantic content of the visual prime, e.g., with the addition of verbal information to the picture).

310 As a perspective, applications of this research could be developed for example in rehabilitation
311 strategies for patients with hyposmia (partial olfactory loss) where odors are perceived as relatively weak.
312 Several studies showed that the prevalence of hyposmia is relatively high (10-15 %) (Brämerson et al. 2004;
313 Landis et al. 2004; Hummel et al. 2007), and increases with aging (Gaines, 2010). Moreover, significant
314 alteration of the quality of life is typically associated with this sensory impairment (Croy et al., 2014; Manesse et
315 al., 2017). Concrete solutions to enhance olfactory perception would thus be extremely useful. Remediation of
316 olfactory perception through daily training has positive outcomes, both on the level of perception (Hummel et al.
317 2009) and on activation of brain areas involved in semantic and memory functioning (e.g. hippocampus)
318 (Gellrich et al., 2017). Therefore, setting up a training protocol that would enhance the saliency of the odor
319 memory trace (or at least some of its components), for example by combining odor with relevant visual contexts,
320 may be beneficial in improving olfaction in people with olfactory deficits.

321

322 **Acknowledgments**

323 This study was funded by a grant from the Auvergne-Rhone-Alpes French Region (ARC2 Program, Qualité de
324 vie et Vieillessement) to MB. The authors wish to thank Romain Bouet for helping with statistical analyzes and
325 two anonymous reviewers for their comments.

326

327

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415

Figure Legends

416

417 **Figure 1. Protocol.** (A) The experimental design comprised 45 trials that were combinations of the factors
418 Context (6 pictures + 1 neutral), Odor (2 odors + 1 blank) and Concentration (2 levels). (B) Sequence of a trial.
419 (C) Congruency ratings (Mean \pm SEM; * $p < 0.05$ in a paired t -test).

420

421 **Figure 2. Semantic ratings** (Mean \pm SEM). Odor by Context interaction for (A) Flowery ratings ($p = 0.0175$),
422 and (B) Damp ratings ($p = 0.0115$). * $p < 0.05$ post-hoc contrasts by pairs.

423

424 **Figure 3. Olfactomotor responses** (Mean \pm SEM). Effect of Context on (A) Sniff volume (Area Under the
425 Curve) ($p = 0.0082$), and (B) Sniff duration (in seconds) ($p = 0.0009$). * $p < 0.05$ post-hoc contrasts by pairs.