Olfactory priming leads to faster sound localization

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ABSTRACT

Cross-modal interactions between vision, audition and touch have been extensively studied in the last decade. However, our understanding of how the chemical senses interact with other sensory modalities remains relatively scarce. We performed a cued auditory localization paradigm in healthy young adults by measuring reaction times to monaural auditory stimuli after subjects had been cued by unilateral olfactory stimuli, mixed olfactory/trigeminal stimuli or somatosensory stimuli. As expected, all cuing conditions led to enhanced performances in auditory localization. Further, both odors led to significantly shorter reaction times when compared to the somatosensory stimuli. We did not observe any effect of side-congruency between the cues and the targets. These results suggest facilitative effects of odorous cues independent of a possible trigeminal component in the interaction between olfaction and audition.

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1. Introduction

Environmental stimuli usually activate several sensory systems simultaneously. Hence, the different senses, such as audition, vision, and touch, interact with each other in our perception of the environment [26,41]. A well-known example of such interactions is the ventriloquism effect [49], a perceptual illusion in which the voice of the puppeteer is shifted to a congruent visual source, that is, the puppet, therefore seeming to emanate from it [26]. At the cortical level, higher neuronal responses to bimodal vs. unimodal stimuli provide evidence for multisensory integration [30,47]. Consequently, interactions between the senses may lead to changes in performance during the execution of perceptual tasks. Auditory cues improve the detection of a simultaneously presented visual target [29,50]. Analogous findings have been reported for vision and touch [51]. Similarly, the chemical senses, i.e., smell, taste and the trigeminal chemosensory system interact mutually. Here, most studies focused on flavor perception and thus the interactions between the chemical senses (e.g., olfactory and gustatory [14,45,52]; gustatory and trigeminal [8,10]; olfactory and trigeminal [7,27,28]).

Most odors are mixed olfactory/trigeminal stimuli, as they activate both systems [15,18]. Hence, it is difficult to isolate the effect of odors from their trigeminal component, and vice versa. Only few studies investigated cross-modal interactions between the chemical and other senses, the majority focusing on vision; even fewer compared pure odors with mixed olfactory/trigeminal odorants. Subjects who were exposed to pleasant or unpleasant background odors reacted faster to visual and auditory stimuli than control subjects who performed the test in an odor free environment, suggesting both odors induce increased arousal levels [34]. Both odors (lavender and pyridine) are considered olfactory/trigeminal stimuli [1,36] and no control condition with continuous stimulation of another sensory modality was applied, making it difficult to conclude that the observed effects are specific to olfaction. The same group investigated olfactory modulation of visual reaction times (RTs) [32,33] by exposing subjects to a mixed olfactory/trigeminal [6,16] or to a pure olfactory [15] stimulus, while performing a visual task. In partial contrast to the findings of the first study [34], subjects reacted slower when the pure olfactory stimulus was applied than in the no ambient odor baseline condition; in the mixed olfactory/trigeminal odor environment, RTs were not different from baseline. When the authors distracted the subjects with a luminance change, subjects reacted slower than in the no ambient odor baseline condition, and even more so in the mixed olfactory/trigeminal ambient odor condition. In the pure odor condition, however, subjects became significantly faster when distracted [32,33]. The authors speculated that odor exposure led to two distinct mechanisms: (1) a non-specific slowing of processing and an eventual ignorance of the distracter (pure odorant), and (2) an increase of arousal levels due to the irritant properties of the stimuli, leading to enhanced sensitivity to distracters

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(mixed olfactory/trigeminal odorant). Pure odorant cues were also found to induce priming effects during the presentation of emotionally valenced visual stimuli, illustrated by faster RTs to disgusted faces after the presentation of odorous cues vs. ambient air [43,44]. In summary, odors have effects on RTs to heteromodal stimuli, suggesting cross-modal interactions between olfaction and other senses.

In addition to temporal contiguity, spatial proximity is a critical feature of multisensory integration: in order to integrate two stimuli from two different sensory modalities and enhance performance, both stimuli need to co-occur in time, but also in space [26,39]. This is particularly salient in spatial localization tasks, where spatially congruent cues from a different modality enhance the detection of a stimulus, whereas incongruent cues may have no influence or impair performance [20,26].

In the present study, we planned to elucidate the impact of olfactory or trigeminal cuing on auditory processing. We performed a cued auditory localization paradigm by measuring RTs to monaural auditory stimuli after cuing subjects with unilateral chemosensory stimuli. Humans cannot lateralize odors unless the odors also activate the trigeminal system [17,19,25]; thus odor lateralization allows to dissociate between olfactory and trigeminal stimulation. Air puffs and a baseline condition served as controls.

We expected all cues to induce shorter RTs than in the baseline condition. We also hypothesized (1) the facilitative processing induced by cuing to be enhanced by both kinds of olfactory stimuli when compared to simple somatosensory stimulation [29]. Next we hypothesized (2) spatial congruency between cue and target to lead to faster RTs than incongruent stimulation [46], but only for stimuli which we can localize in a monorhinal stimulation design namely the mixed olfactory/trigeminal (b) and somatosensory (c) conditions. Pure olfactory stimuli, which cannot be localized [19,25], should not have any effect of side-congruent stimulation.

2. Materials and methods

The protocol was approved by the Ethics Board of the University of Montreal and subjects gave informed written consent prior to testing.

2.1. Subjects

Thirty-one subjects (14 women) aged between 18 and 35 years (mean age = 23; standard deviation [SD] = 3) participated in the study. Two subjects were removed from analysis because their mean RTs were more than two SD from global mean. No participant suffered of any medical condition at the time of the testing and did not report any olfactory or auditory problem.

2.2. Stimuli

2.2.1. Olfactory stimuli

We used pure eucalyptol (eucalyptus odor; Galenova, St.-Hyacinth, QC) and pure phenyl ethyl alcohol (PEA; rose odor; SAFC, St. Louis, MO) as chemosensory stimuli, and air puffs as somatosensory stimuli. Eucalyptol is considered a mixed olfactory/trigeminal stimulus [15,16], whereas PEA is considered a relatively pure odor [15]. Air puffs activate only somatosensory trigeminal fibers.

We used the same adapted stimulation computer controlled device (IBB, University of Münster, Germany), which delivers air pulses of well-defined duration, as in an earlier study [19], to deliver the nasal stimuli. We connected the outlet channels to odor chambers (50 mL glass bottles, filled with 4 mL of odorant) via polyurethane tubing with 8 mm outer diameter and an inner diameter of 4.8 mm (Fre-Thane 85A, Freelin-Wade, McMinnville, OR). The odor chambers were connected to the subjects' nose with the same polyurethane tubing of approximately 50 cm length inserted into the subjects' nostrils, and maintained there with an elastic band around subjects' head. Odor channels were completely separated to avoid cross contamination of odors. During odor presentation, air (2 L/min) was switched into the respective channel. All nasal stimuli lasted 750 ms.

2.2.2. Auditory stimuli

Unilateral white noise was presented to the right or to the left ear through headphones for 150 ms (5 ms rise/fall time) per trial at a comfortable hearing volume.

2.3. Procedure

Subjects were blindfolded and tested in one session of approximately 1.5 h. An alerting high-pitched sound (150 ms) was delivered via headphones to announce the next trial arising from 2000 to 4600 ms after the alerting sound. Subjects were asked to breathe in when hearing the alerting sound and hold the breath until after their response. Subjects had to localize left or right unilateral auditory stimuli (target stimulus), by pressing one of two buttons as fast as possible in order to indicate if they had perceived the auditory stimulus in the left or the right ear. We delivered cuing stimuli consisting of (1) air puffs (somatosensory stimulation), (2) PEA stimuli (olfactory stimulation), (3) eucalyptol stimuli (olfactory/trigeminal stimulation) 600 ms before the target stimulus; a control condition without cuing was also applied. When chemosensory stimuli (2 and 3) were presented to one nostril, an odorless air puff of same pressure and duration was simultaneously delivered to the other nostril to isolate the effects of chemosensory and somatosensory cues.

Subjects received a nasal-auditory stimulation each 15 s. Testing was done in 10 blocks of 28 stimuli (2 of each combination per block).

Stimulus delivery and responses recording were controlled by the "Presentation" software (Neurobs) running on a HP PC (AMD Phenom X3 processor) with Windows XP.

2.4. Statistical analysis

Subjects' performance was evaluated in terms of hit rates (proportion of correct responses) and RTs (only for correct responses in the range 100–1500 ms post stimuli (99.61% of correct trials)). To evaluate the effect of a cuing stimulus, we performed paired t-tests (cued stimulation vs. uncued stimulation). Next, we performed a repeated measures ANOVA with side of the auditory stimulus (left, right), modality of the cuing stimulus (somatosensory, olfactory–trigeminal, olfactory), and side congruency of the cuing stimulus (congruent, incongruent) as within subject factors and RT as the dependent variable. We performed post hoc paired t-tests with Bonferroni correction.

3. Results

On average, subjects were able to indicate the side of the auditory stimulation with very high accuracy (>93% of the trials in all conditions). They responded after 500 (SD: 97) ms and 489 (115) ms, for the left and the right auditory stimulus, respectively. Independent of its nature, preceding co-stimulation reduced RTs significantly (all $ps < 0.001$) to the auditory stimulus by over 100 ms.

We observed a significant effect of cuing stimulus ($F[2,27] = 6.26$; $p = 0.006$), in that both chemosensory stimuli led to shorter RTs than somatosensory air puffs. Post hoc comparisons showed that when alerted by the somatosensory air puffs, subjects reacted after 394 (standard error of the mean [SEM]: 88) ms, whereas they were significantly faster when alerted by either a mixed olfactory–trigeminal stimulus (382 (92) ms; $p = 0.027$) or a pure olfactory stimulus (381 (82) ms; $p = 0.026$) (Fig. 1). There was no significant difference between the two chemosensory alerting stimuli ($p = 1.0$). No other factor or interaction reached significance, most importantly side congruency of the alerting stimulus ($F[1,28]$ 1.06; $p = 0.31$) (Fig. 2).

3.1. Control experiment

We performed a second 25-min experiment in 31 subjects (14 women) to ensure effects would be specific to chemosensory properties of the costimulation and not to the amount of stimulation available (two vs. one air puff in the somatosensory condition), by comparing RTs following the presentation of 1 vs. 2 odor-free air puffs. Settings and parameters were the same as in the main experiment. No significant difference in mean RTs between unilateral (465 ms (146)) and bilateral (481 ms (149)) costimulations ($F[1,30] = 1.10$; $p = 0.302$) was found.

4. Discussion

We show that odorous cues, independent of a possible chemosensory-trigeminal component, lead to shorter RTs to auditory targets. This corroborates an earlier report, where ambient
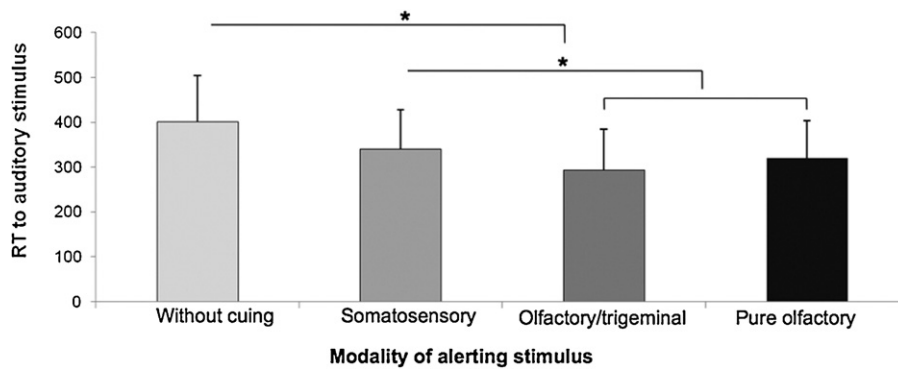
Fig. 1. Average reaction times with and without alerting stimulus (error bars indicate standard deviations).

odors induced shorter RTs to auditory and visual stimuli [34]. Two conditions of our experiment established the effect to be specific for olfactory stimulation. Firstly, cuing with a somatosensory stimulus, had a significantly weaker effect on RTs than chemosensory cuing. We excluded a possible effect of bilateral cuing in the control experiment. This suggests that chemosensory stimulation, whether pure olfactory or mixed olfactory–trigeminal, induces a specific reduction of RTs. We did not observe any difference between pure olfactory and mixed olfactory–trigeminal cuing; one can speculate that the observed facilitating effects of chemosensory stimuli are attributable to their olfactory properties.

Odorants may increase arousal levels, leading to faster responses to auditory stimuli, as alertness and information processing speed are closely related [38]. Michael et al. [32] suggested that pure odors may modulate the noradrenalin system influencing the alert state. However, one has to keep in mind that each odor presentation lasted 750 ms which may be short to influence arousal.

These results may seem contradictory to earlier findings reported by Michael and collaborators [33], in which a pure (ambient) odor increased RTs to visual targets, possibly by reducing subjects' arousal levels. Differences in experimental designs may account for this discrepancy, as we used a priming paradigm similar to Seubert et al. [43,44], who used odorant cues prior to the presentation of visual targets and also found facilitative effects of odors on sensory processing. Similarly, in our study the odorants were not constantly present in the environment as the nasal stimuli and the control condition were alternatively presented before auditory stimulation. We were therefore able to avoid potential effects of a constant presentation of the odorants, i.e., habituation and/or modulation of the arousal levels. However, using air puffs to deliver the odors might induce confounding effects, as the puff itself stimulates somatosensory trigeminal fibers. Due to this both odorous stimuli activated both the olfactory and the trigeminal system. We

know that strong (and painful) trigeminal stimuli [4,5] may inhibit the processing of olfactory component [5,21,23]. This may explain the absence of differences between both odorous stimuli; however, it is unlikely that the somatosensory stimulation per se led to the shorter reaction times, since the pure somatosensory stimulation did not induce such an effect. The interaction between more than two sensory systems (like olfactory, trigeminal and auditory) may be an interesting topic for future research.

A second finding supports our hypothesis of the odor component being responsible for RT reduction. In audiovisual cross-modal cueing paradigms, space congruency has been shown to influence performance on localization tasks. While auditory and visual localization are relatively easy, humans are not able to distinguish between a pure olfactory stimulation of the left and the right nostril [18,24,53]. Using the same stimulation methods, we previously showed that subjects are able to localize eucalyptol but not PEA [19]. If the trigeminal component was driving the effect, one would expect shorter reaction times following congruent olfactory/trigeminal cueing, and no effect or the opposite effect for incongruent olfactory/trigeminal cueing. For pure odor cueing, there should not be any effect of side congruency. However, the absence of side congruency effects for both chemosensory stimuli supports our conclusion of the olfactory component of both chemosensory stimuli being responsible for the observed effects.

Side congruency effects tend to increase with increases in the proportion of congruent trials [22]. In our experimental design, congruent and incongruent trials were equally likely to occur, which may not be optimal to observe the attended effects. Still, previous studies using similar paradigms to ours successfully demonstrated effects of side congruency of the cues [29,39].

It may, however, seem surprising that we did not observe any effect of side congruency even for the somatosensory cues, even if the subjects were able to localize these somatosensory stimuli as shown previously [19]. This is in contrast to previous findings
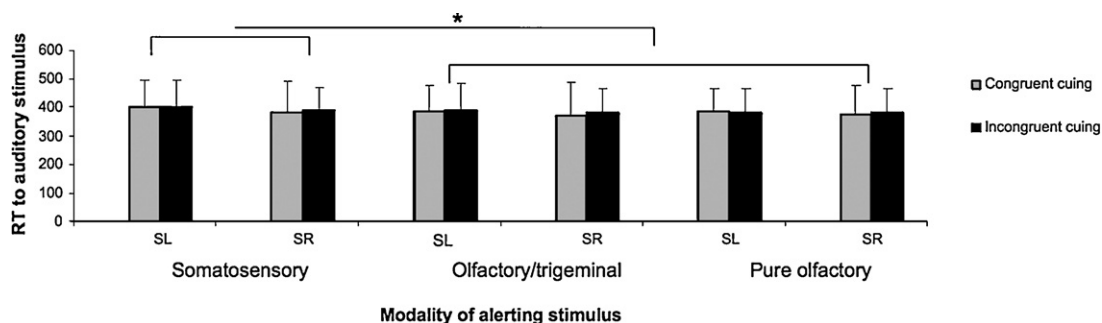

Fig. 2. Average reaction times with alerting congruent and incongruent stimulus (error bars indicate standard deviations). RT: reaction time; SL: target sound delivered to left ear; SR: target sound delivered to right ear.

of enhanced performances in detection of visual or auditory targets after the presentation of tactile cues [9,20]. Here, tactile and visual/auditory stimuli were presented simultaneously, whereas we separated cue from target presentation by 600 ms to ensure the subjects had enough time to perceive the odors. Chemosensory processing is slow compared to other sensory systems. For example, the P3 component of chemosensory event related potentials can be observed after 600–1200 ms; in the visual system they typically occur after 300 ms [24,35,37]. Similarly, odor detection occurs after more than 1500 ms [3]. Furthermore, subjects took more than 1500 ms [2] to rate intensity and/or pleasantness of odors and more than 1100 ms to discriminate between two odors [11]. The olfactory system therefore seems to be significantly slower than other sensory systems, where RTs in several discrimination tasks ranged between 200 and 800 ms [9,20,40,42].

We considered a delay of 600 ms between cue and target to be necessary for the subjects to perceive the olfactory components of the stimuli and lead to priming effects; in turn it may be too long to observe facilitating effects of spatial congruency of the somatosensory cues, as temporal contiguity is primordial for multisensory integration [13,26,50]. Besides, some studies reported side congruency-independent facilitating effects of tactile cues [31] or visual costimulation [48] on auditory spatial localization. Since subjects reacted faster when receiving olfactory stimuli as compared to pure air puffs, air puffs per se cannot be responsible for the decreased RTs.

Even if we controlled for the number of air puffs presented in the control experiment, odorless puffs are unimodal somatosensory stimuli, whereas odorous puffs could be bimodal (PEA containing air puffs stimulate trigeminal-somatosensory and olfactory fibers) or even trimodal (eucalyptol containing air puffs stimulates olfactory, trigeminal-somatosensory and trigeminal-chemosensory fibers). Thus the number of sensory modalities, which was superior in the odorous trials, may have an effect as the related cuing intensity increases [12]. Further, we did not measure perceived intensity of the odorants. Eucalyptol stimulates both the chemosensory-trigeminal and the olfactory nerve, whereas PEA stimulates the olfactory nerve exclusively. The percept evoked by eucalyptol has more dimensions (the trigeminal components); as a consequence, the subjects may perceive eucalyptol to be more intense, even if the olfactory component of both stimuli is equally intense; making it is thus difficult to compare both odors. However, some authors have suggested that odors with low (e.g., PEA) and high (e.g., mustard oil) trigeminal components can be matched at perceptual levels [32,33], Since we did not observe differential effects between both odorous, we assume that perceived intensity played a minor role in our findings. Future studies should address these issues.

Our findings suggest the existence of lower order olfactory processing mechanisms, which increase attention to auditory cues. To our knowledge, no neuroimaging studies have yet investigated cross-modal integration of olfactory–auditory information, so the underlying neural correlates remain unclear. However, a recent study showed anterior insula's, right anterior cingulate cortex's and fusiform gyrus's implication in the modulation and integration of olfactory-visual information [43]. Further imaging studies are required to assess the role of these structures in olfactory–auditory interactions specifically, and the multisensory integration of chemosensory stimuli in general.

5. Conclusion

Odorous cues presented shortly before auditory stimuli had a facilitative effect on the localization of the sounds, independent of a trigeminal component and/or spatial congruency of the cues,

suggesting the priming effects were due to the olfactory properties of the odors. Importantly, the speeding effects were superior to the ones observed when using only somatosensory cues, demonstrating the specificity of the effects of the olfactory stimuli. This intimates the existence of interactions between olfaction and audition and suggests information from both sensory modalities is integrated, resulting in behavioral changes, i.e., enhancement of performance in auditory localization. Spatial congruency, a critical factor for cross-modal interactions between other sensory modalities during spatial discrimination tasks [20], does not seem to play a mandatory role in the integration of olfactory–auditory information. Further studies are needed to better understand the psychophysical and neural correlates underlying these cross-modal mechanisms.

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