Original Article

Enhanced Odorant Localization Abilities in Congenitally Blind but not in Late-Blind Individuals

Simona Manescu¹, Christine Chouinard-Leclaire¹, Olivier Collignon^{2,3}, Franco Lepore¹ and Johannes Frasnelli^{1,4,5,✉}

¹Centre de Recherche en Neuropsychologie et Cognition, Département de psychologie, Université de Montréal, Pavillon Marie-Victorin, CP 6128, succursale Centre-Ville, Montréal, Québec H3C 3J7, Canada, ²Center of Mind/Brain Sciences of University of Trento, Via Delle Regole 101, 38123 Mattarello, Trentino, Italy, ³Institutes for Research in Psychology and Neurosciences, University of Louvain, IPSY - Place du Cardinal Mercier, 10 bte L3.05.01, B-1348 Louvain-la-Neuve, Belgium, ⁴Centre d'études avancées en médecine du sommeil, Centre de Recherche de l'Hôpital du Sacré-Coeur de Montréal, Centre intégré universitaire de santé et de services sociaux du Nord-de-l'Île-de-Montréal, 5400 boulevard Gouin Ouest, Montréal, Québec H4J 1C5, Canada, and ⁵Department of Anatomy, Université du Québec à Trois-Rivières, 3351, C.P. 500, boulevard des Forges, Trois-Rivières, Québec G9A 5H7, Canada

Correspondence to be sent to: Johannes Frasnelli, Department of Anatomy, Université du Québec à Trois-Rivières, 3351, C.P. 500, boulevard des Forges, Trois-Rivières, Québec G9A 5H7, Canada. e-mail: johannes.a.frasnelli@uqtr.ca

Editorial Decision 22 October 2020.

Abstract

Although often considered a nondominant sense for spatial perception, chemosensory perception can be used to localize the source of an event and potentially help us navigate through our environment. Would blind people who lack the dominant spatial sense—vision—develop enhanced spatial chemosensation or suffer from the lack of visual calibration on spatial chemosensory perception? To investigate this question, we tested odorant localization abilities across nostrils in blind people compared to sighted controls and if the time of vision loss onset modulates those abilities. We observed that congenitally blind individuals (10 subjects) outperformed sighted (20 subjects) and late-blind subjects (10 subjects) in a binhinal localization task using mixed olfactory-trigeminal stimuli. This advantage in congenitally blind people was selective to olfactory localization but not observed for odorant detection or identification. We, therefore, showed that congenital blindness but not blindness acquired late in life is linked to enhanced localization of chemosensory stimuli across nostrils, most probably of the trigeminal component. In addition to previous studies highlighting enhanced localization abilities in auditory and tactile modalities, our current results extend such enhanced abilities to chemosensory localization.

Key words: congenitally blind, late blind, odor localization, sensory compensation, trigeminal function

Introduction

In humans, vision typically provides the most reliable information for the processing of spatial information (Alais and Burr 2004; Charbonneau et al. 2013). The prominent role of vision for space perception may, therefore, prevent individuals who are lacking visual

experience from developing normal spatial skills in the remaining senses (Voss et al. 2004; Collignon et al. 2009; Heller and Ballesteros 2016). Indeed, vision may be necessary to calibrate auditory or tactile spatial perception, at least for some specific abilities, as it was shown that congenitally blind people may be impaired in specific auditory

or tactile spatial tasks (Zwiers et al. 2001; Lewald 2002; Gori et al. 2010, 2014). Alternatively, some have suggested that greater weight is put on the sensory estimates obtained from the remaining senses in the absence of vision, which would trigger enhanced reliability in perceiving nonvisual spatial cues due to experience-dependent compensatory plasticity in perceptual networks (Voss et al. 2010; Heller and Ballesteros 2016; Voss 2016; Battal et al. 2019). Interestingly, the presence of these compensatory mechanisms appears to be strongly dependant on the onset time of visual deprivation (Bavelier and Neville 2002; Voss et al. 2013). Contrary to congenital blindness or blindness acquired during the first few years of life (i.e., early blindness), late-onset blindness typically gives rise to lower behavioral compensatory mechanisms (Dormal et al. 2016; for a review, see Voss et al. 2013).

Although they rely extensively on touch and audition to interact with their environment (Burton 2003), blind individuals also pay attention to other nonvisual cues, including odor cues. One may, therefore, postulate that chemosensation has an enhanced ecological value for blind individuals as olfactory stimuli provide them with crucial information about their environment (e.g., evaluation of the quality of food). In particular, olfaction may serve to locate objects and landmarks in navigation, providing useful points of reference and, thus, contributing to spatial cognition (Koutsoklenis and Papadopoulos 2011). However, only a few studies evaluated the sense of smell in blind individuals (e.g., (Murphy and Cain 1986; Beaulieu-Lefebvre et al. 2011; Kupers et al. 2011; Gagnon et al. 2014; Cornell Kärnekull et al. 2016) and did not find any superiority of blind individuals compared to sighted in olfactory tasks, such as odor detection thresholds, olfactory discrimination, and free or cued odor identification abilities (for a systematic review, see Sorokowska et al. 2018).

Chemosensory localization is based on stimulation of the trigeminal system and can be assessed by measuring the ability to determine if an odor is administered in the right or left nostril. Humans are not able to localize pure odorants, which stimulate the sense of smell exclusively and can only localize odorants that additionally stimulate the intranasal trigeminal system (Frasnelli et al. 2009; Kleemann et al. 2009; Frasnelli et al. 2010; Wise et al. 2012). As the trigeminal system is sensitive to irritant information and helps to discern between different chemical components (i.e., burning sensation from capsaicin in chilli peppers and cooling sensation from menthol in peppermint), we can hypothesize that this system could be, for adaptive reasons, specially developed in blind subjects compared to sighted individuals. For example, compared to sighted individuals, blind individuals might rely more on chemosensory information to protect their safety (i.e., detect the source of smoke in the case of a fire to retrieve to safety) and navigate in their environment. Only one recent study compared the ability to localize distant chemosensory stimuli between sighted and blind individuals but did not find evidence of any group differences (Sorokowska et al. 2019). Unfortunately, the authors did not report or differentiate the onset of the visual deprivation of their blind participants. Since an earlier onset of blindness is associated with better performances in nonvisual tasks (Gougoux et al. 2004) compared to later onset, mixing early and late-blind individuals could have masked any potential effect of blindness.

Therefore, the goal of the present study was to evaluate the ability to localize odorants across nostrils in congenitally and late-blind individuals. We hypothesized that congenitally blind individuals, but not late-blind individuals, outperform sighted controls on an odorant localization task. We additionally investigated differences in odorant detection and odorant identification tasks in order to see if blindness selectively alters spatial chemosensation or, alternatively, produces a generalized alteration of olfactory functions.

Experimental procedures

Participants

We included a total of 20 blind individuals. Of them, 10 were considered congenitally blind (CB; age mean $[M] = 41$, standard deviation (SD) = 14, range 21–62 years, 2 women) and 10 late-blind (LB; age $M = 56$, SD = 10, range 38–66 years, 7 women). Due to the significant age difference between the 2 groups, we established 2 separate control groups of subjects with normal vision: 1 for the congenitally blind (10 individuals; CB-C; age $M = 41$, SD = 14, range 23–58 years, 2 women) and 1 for the late blind (10 individuals; LB-C; age $M = 56$, SD = 9, range 37–63 years, 7 women), to match each blind individual, respectively, in terms of age, gender, and smoking habits. Within CB, all participants were born blind, and half of them had faint light perception in at least one of their eyes but never experienced pattern vision and never used their vision to recognize objects or navigate within their environment. Within LB, 2 out of 10 individuals had faint light perception in at least 1 of their eyes but also without functional use. An independent-samples (2-tailed) t -test was conducted to compare blindness duration across our 2 groups. The duration of blindness was slightly greater for the CB group ($M = 41$, SD = 14) compared to the LB group ($M = 28$, SD = 15), but the group difference was not statistically significant ($t(18) = 2.02$, $P = 0.059$). Further detailed description about both blind groups can be found in [Supplementary Table 1](#). All participants declared that they did not suffer from any medical condition that could affect their sense of smell at the time of the testing. Participants were instructed not to eat or drink anything besides water 1 h prior to the experiment. As depicted in [Supplementary Figure 1](#), all participants had normal olfactory function as ascertained by means of the Sniffin' Sticks identification test (Hummel et al. 1997, 2007). A 1-way ANOVA did not suggest a difference between any of the groups with regards to their average scores $F(3, 36) = 2.06$, $P = 0.12$, $\eta^2_{\text{partial}} = 0.15$.

Before taking part in the study, subjects gave their written informed consent and our study complies with the Declaration of Helsinki for Medical Research Involving Human Subjects. After completion, they received a \$40 monetary compensation for their participation, as well as reimbursement of their travel expenses. The ethics board of the Center for Interdisciplinary Research in Rehabilitation of Greater Montreal (CRIR) approved this study [CRIR-584-0211].

Chemosensory evaluation

Odorants

We evaluated participants' ability to localize odorants and to control for unspecific effects and also to identify and detect odorants. For odorant localization and identification, we used 2 mixed olfactory-trigeminal stimuli, that is, substances that stimulate both the olfactory and the trigeminal system (Doty et al. 1978; Viana 2011). Specifically, we used almond (benzaldehyde, almond odor with a burning/tingling sensation; Sigma-Aldrich) and eucalyptus (eucalyptol, eucalyptus odors with a cooling sensation; Galenova). Furthermore, for odorant detection, we used unrelated odorants related to edible objects, namely strawberry (strawberry aroma, Frey & Lau) and parmesan (parmesan cheese aroma).

Stimulator

Odorants were delivered with an adapted computer-controlled air compressor (IBB), which was used in past studies for the administration of time-controlled air pulses (Frasnelli et al. 2010; La Buissonnière-Ariza et al. 2012). The odorants were presented via a 6-channel air compressor. It delivered air puffs of 2.5 L/min per

channel as ascertained by a flow meter (Cole Parmer). A valve control unit directed air into the air compressor via polyurethane tubing with 8.0 mm outer diameter and an inner diameter of 4.8 mm (Fre-Thane 85A, Freelin-Wade). From the air compressor, polyurethane tubes were connected to bottles containing the odorants. Specifically, cotton balls were placed in 50-mL amber bottles and soaked with 10 mL of the respective odorant in neat concentrations. For odorant localization and identification, 6 tubes were connected to six 60-mL glass bottles containing the odorants: 2 bottles filled with almond, 2 bottles filled with eucalyptus, and 2 empty control bottles (Figure 1). From the 6 bottles, 3 polyurethane tubes were directly connected to

the left nostril and the other 3 polyurethane tubes were connected to the right nostril. For the detection task, 3 tubes were connected to three 30-mL glass bottles containing the odorants: strawberry, parmesan, and 1 empty control bottle.

To administer the odorants, an air stream was sent to the compressor, which delivered an air puff into 1 of the 4 odor-containing bottles and/or into the 2 control bottles for the identification and localization tasks or 1 of the 2 odorant-containing bottles and/or into the control bottle for the detection task. During the interstimulus interval, no air was delivered. The Presentation software (Neurobehavioral Systems, Inc) was used to deliver odorants, as well as to record participants' responses and reaction times.

Figure 1. Schematic view of the protocol.

Tasks and procedures

To test odorant localization, participants were placed in front of the computer on a comfortable chair with their chin on a chin rest in a ventilated testing booth. They were instructed to press one of 2 buttons on a keyboard if they smelled an odor in their left nostril and the other button if they smelled an odor in their right nostril, independent of the identity of the odorant (almond or eucalyptus). Participants were asked to respond as fast and accurately as they could. Two seconds before stimulation, a sound was emitted indicating that an odorant would be administered. This allowed participants to stop breathing during odorant delivery. Odorants (eucalyptus or almond, 500 ms, 2.5 L/min) were delivered to one nostril (randomly chosen per trial), while the other nostril received

Localization task

Figure 2. IE scores obtained in the odorant localization task (blue for almond and orange for eucalyptus). Panel A displays the results obtained by congenitally blind individuals (almond: $M = 2681.88$, $SD = 1284.83$; eucalyptus: $M = 2188.49$, $SD = 1649.44$) and their matched sighted counterparts (almond: $M = 3360.41$, $SD = 2183.12$; eucalyptus: $M = 5224.10$, $SD = 2658.49$). Panel B displays the results obtained by late-blind individuals (almond: $M = 3724.30$, $SD = 2565.03$; eucalyptus: $M = 4658.13$, $SD = 4045.63$) and their matched sighted counterparts (almond: $M = 3040.57$, $SD = 1862.84$; eucalyptus: $M = 4443.46$, $SD = 2947.03$). Panel C displays the standardized IE scores of blind individuals generated by their respective control groups (CB: almond: $M = -0.31$, $SD = 0.59$; eucalyptus: $M = -1.14$, $SD = 0.62$; LB: almond: $M = 0.56$, $SD = 1.68$; eucalyptus: $M = 0.07$, $SD = 1.37$).

an equivalent odor-free air puff. The interstimulus interval was set at 40 s to avoid habituation (Hummel and Kobal 1999). Each odorant was presented 16 times to each nostril, divided into 2 blocks with a 5-min break between blocks. We recorded response accuracy (% of total stimuli) and response time (in milliseconds) for correct stimuli.

We carried out 2 additional tasks to control for unspecific effects of blindness on olfactory processing. First, we measured participants' ability to identify the odorants used in the main task. In this task, conditions were identical as in the localization task, with the exception that participants had been instructed to press one button if they smelled almond and the other button if they smelled eucalyptus, independent of the stimulated nostril (left or right). Participants were asked to respond as fast and accurately as they could. We again recorded response accuracy (% of total stimuli) and response time for correct responses (milliseconds).

Second, we assessed participants' ability to detect odorants. For the odorant detection task, the same conditions as above applied with the following exceptions: stimuli (strawberry, parmesan, and odorless control condition) were delivered to both nostrils simultaneously; each stimulus was presented 15 times. Participants were asked to press on a button as soon as they smelled an odorant and refrain from pressing it if they did not smell anything. To avoid habituation, the interstimulus interval was set at 30 s. We again recorded response accuracy (% of total stimuli) and response time for correct responses (milliseconds).

Each participant completed practice trials before the start of each task to familiarize them with the protocol. The detection task was always administered first, followed by the identification task and then the localization task. The whole experiment took around 3 h from start to finish.

Data and statistical analysis

We investigated each variable (response accuracy and response times) for outliers beyond a z -score of 3.29 using the median absolute deviation method (Leys et al. 2013; Tabachnick and Fidell 2013). In 2.9% of trials, we observed outliers and set their value to 3.29 (Tabachnick and Fidell 2013).

In tasks such as the ones we used, there is a possibility of criterion shifts or speed/accuracy trade-offs (Spence et al. 2001; Röder et al. 2007). To account for this, we computed inverse efficiency scores (IES), which combine response time and accuracy rate into one measure (Townsend and Ashby 1978, 1983) and can, therefore, be considered as "corrected reaction times." As suggested by some authors (Townsend and Ashby 1978, 1983; Bruyer and Brysbaert 2011), we first evidenced the correlations between response time and accuracy rate of each variable (Supplementary Table 2) and then we divided response times by accuracy rates for each task separately (a higher value indicates worse performance). Accuracy and reaction time are illustrated in Supplementary Figures 2–4.

We conducted 2 sets of analyses to evaluate performance differences among our 4 groups of participants. First, we compared each blind group (CB or LB) with their respective control group on localization, identification, and detection. To do so, we conducted a separate 2-way ANOVA for each task (localization, identification, and detection), with IES as dependent variable and *odor* (2 levels: localization and identification: almond and eucalyptus; detection: strawberry and parmesan) as within-subject factors. Furthermore, we used *group* as between-subject factors (2 levels: CB and CB-C or LB and LB-C).

Second, in order to detect any effects of blindness onset, we directly compared CB and LB. Since both groups were not equivalent in terms of age, we used the scores of their respective control groups to generate standardized scores. Specifically, for each variable, we subtracted each data point in the blind group (CB or LB) from the average and divided the result by the SD of the respective control group (CB-C or LB-C). In doing so, every CB or LB participant had a z -score for both accuracy rate, and response time from which we could derive IES; we did this for each task (localization, identification, detection). We then again conducted 2-way ANOVAs for localization, identification and detection, separately, with *group* (2 levels: CB and LB) as between-subject factors and *odor* (2 levels: localization and identification: almond, eucalyptus; detection: strawberry, parmesan) as within-subject factors.

If F values were significant, we used t -tests with Bonferroni correction for post hoc comparisons. The significance level for all statistics was fixed at $P < 0.05$. All analyses were conducted with SPSS Statistics 25 (IBM, Corp, Armonk, NY).

Results

Odorant localization

The 2-way ANOVAs revealed a significant main effect of *group* for CB ($F(1, 18) = 7.011$, $P = 0.016$, $\eta_{\text{partial}}^2 = 0.280$) but not for LB ($P = 0.566$, $\eta_{\text{partial}}^2 = 0.019$). Post hoc tests showed that CB ($M = 2435$ ms, $SD = 1340$) were significantly more efficient at localizing odors than their sighted counterparts ($M = 4292$ ms, $SD = 2420$). We did not observe any significant effect of *odor* (CB: $P = 0.240$, $\eta_{\text{partial}}^2 = 0.076$, LB: $P = 0.218$, $\eta_{\text{partial}}^2 = 0.083$), nor any interaction between *odor* and *group* (CB: $P = 0.051$, $\eta_{\text{partial}}^2 = 0.195$, LB: $P = 0.463$, $\eta_{\text{partial}}^2 = 0.030$).

As a second step, we directly compared CB and LB. The 2-way ANOVA revealed a significant effect of *group* ($F(1, 18) = 4.665$, $P = 0.045$, $\eta_{\text{partial}}^2 = 0.206$); post hoc tests showed that CB ($M = -0.73$, $SD = 0.61$) were more efficient than LB ($M = 0.37$, $SD = 1.64$) at localizing the odors. Again, there was no interaction between *odor* and *group* ($P = 0.622$, $\eta_{\text{partial}}^2 = 0.014$). However, we found an effect of *odor* ($F(1, 18) = 9.649$, $P = 0.006$, $\eta_{\text{partial}}^2 = 0.349$). Post hoc tests showed that both blind participant groups were more efficient in localizing eucalyptus ($M = -0.53$, $SD = 1.21$) than almond ($M = 0.18$, $SD = 1.46$) (Figure 2).

Odorant identification

We conducted 2-way ANOVAs to evaluate the participants' ability to identify odors. As shown in Figure 3, we did not find any effects of *group* (CB: $P = 0.928$, $\eta_{\text{partial}}^2 = 0.000$; LB: $P = 0.263$, $\eta_{\text{partial}}^2 = 0.069$), *odor* (CB: $P = 0.586$, $\eta_{\text{partial}}^2 = 0.017$; LB: $P = 0.886$, $\eta_{\text{partial}}^2 = 0.001$) or interaction between *group* and *odor* (CB: $P = 0.864$, $\eta_{\text{partial}}^2 = 0.002$; LB: $P = 0.545$, $\eta_{\text{partial}}^2 = 0.021$). When directly comparing CB and LB, we again found no effect of *group* ($P = 0.268$, $\eta_{\text{partial}}^2 = 0.068$), *odor* ($P = 0.504$, $\eta_{\text{partial}}^2 = 0.025$), nor an interaction between *odor* and *group* ($P = 0.350$, $\eta_{\text{partial}}^2 = 0.049$).

Odorant detection

With regards to odor detection, we did not observe any effect of *group* (CB: $P = 0.243$, $\eta_{\text{partial}}^2 = 0.075$; LB: $P = 0.907$, $\eta_{\text{partial}}^2 = 0.001$), *odor* (CB groups: $P = 0.200$, $\eta_{\text{partial}}^2 = 0.090$; LB groups: $P = 0.277$, $\eta_{\text{partial}}^2 = 0.065$), nor any interaction (CB: $P = 0.279$, $\eta_{\text{partial}}^2 = 0.065$; LB: $P = 0.405$, $\eta_{\text{partial}}^2 = 0.039$).

Identification task

Figure 3. IE scores obtained in the odorant identification task (blue for almond and orange for eucalyptus). Panel A displays the results obtained by congenitally blind individuals (almond: $M = 1757.50$, $SD = 769.89$; eucalyptus: $M = 1671.44$, $SD = 669.07$) and their matched sighted counterparts (almond: $M = 1639.58$, $SD = 654.21$; eucalyptus: $M = 1535.39$, $SD = 630.14$). Panel B displays the results obtained by late-blind individuals (almond: $M = 1862.13$, $SD = 854.12$; eucalyptus: $M = 2025.25$, $SD = 788.88$) and their matched sighted counterparts (almond: $M = 1735.08$, $SD = 536.04$; eucalyptus: $M = 1806.24$, $SD = 581.25$). Panel C displays the standardized IE scores of blind individuals generated by their respective control groups (CB: almond: $M = 0.18$, $SD = 1.18$; eucalyptus: $M = 0.22$, $SD = 1.06$; LB: almond: $M = 0.24$, $SD = 1.59$; eucalyptus: $M = 0.38$, $SD = 1.36$).

When directly comparing CB and LB, we did not observe any effect of *group* ($P = 0.201$, $\eta_{\text{partial}}^2 = 0.089$), nor an interaction between *odor* and *group* ($P = 0.201$, $\eta_{\text{partial}}^2 = 0.089$). However, we observed an effect *odor* ($F(1, 18) = 4.858$, $P = 0.041$, $\eta_{\text{partial}}^2 = 0.213$); post hoc tests showed that both blind participant groups were more efficient to detect parmesan ($M = -0.30$, $SD = 0.39$) than strawberry ($M = 0.07$, $SD = 0.96$) (Figure 4).

Discussion

In the present study, we found that congenitally blind individuals are more efficient at extracting spatial information from chemosensory stimuli compared to late-blind individuals and sighted controls. More specifically, while all participants showed comparable performances in odor detection and identification, congenitally blind participants exhibited a selective improvement in localizing mixed trigeminal-olfactory odorants across nostrils over late-blind individuals, even when the age effect was accounted for.

Our results are in line with previous reports portraying enhanced localization abilities among congenitally, but not late-blind, individuals when soliciting auditory (Lessard et al. 1998; Röder et al. 1999; Voss et al. 2004; Collignon et al. 2006) and tactile (Van Boven et al. 2000; Goldreich and Kanics 2003) modalities. This enhanced ability could result from a training effect. More specifically, visual deprivations may lead to an increase in the recruitment of remaining healthy senses (here, chemosensory processing) and, thus, indirectly train them. In fact, training can improve chemosensory localization (Porter et al. 2007; Negoias et al. 2013) in sighted individuals. In blindness, such behavioral adjustments may relate to brain plasticity

of the chemosensory systems. Although odorant localization is primarily based on the activation of the intranasal trigeminal system (Frasnelli et al. 2009; Kleemann et al. 2009; Frasnelli et al. 2010; Wise et al. 2012), according to the olfactory spatial hypothesis of Jacobs (2012), the size of the olfactory bulb may reflect the ability to decode and map patterns of odorants for the purpose of spatial navigation. Early blind individuals do indeed have larger olfactory bulbs (Rombaix et al. 2010), and congenitally blind individuals recruit the olfactory cortex more strongly (Kupers et al. 2011) than sighted controls. This raises the hypothesis that the cerebral regions implicated in the processing of chemosensory objects can undergo significant changes due to visual deprivation and may be involved in odor localization.

Beyond intramodal plasticity, there is ample evidence that the occipital cortex of blind individuals activates when localizing stimuli in the remaining senses (Collignon et al. 2011, 2009; Dormal et al. 2012) and that such crossmodal recruitment may relate to performance (Gougoux et al. 2005). More particularly, localizing objects with the remaining senses selectively recruit regions of the right dorsal stream in blind people, areas known to process visuo-spatial information in the sighted. These results support the idea that crossmodal plasticity is constrained by the intrinsic computational bias of the deprived visual regions (Collignon et al. 2009, 2012; Heimler et al. 2015). However, whether the location of chemosensory information also preferentially recruits occipital regions typically assigned to visuo-spatial processing remains to be investigated.

In line with previous findings (Cuevas et al. 2010; Beaulieu-Lefebvre et al. 2011; Luers et al. 2014; Çomoğlu et al. 2015; Guducu et al. 2016; Sorokowska 2016; Majchrzak et al. 2017; Sorokowska

Detection task

Figure 4. IE scores obtained in the odorant detection task (blue for strawberry and orange for parmesan cheese). Panel A displays the results obtained by congenitally blind individuals (strawberry: $M = 967.90$, $SD = 210.30$; parmesan cheese: $M = 988.09$, $SD = 259.09$) and their matched sighted counterparts (strawberry: $M = 1070.00$, $SD = 357.57$; parmesan cheese: $M = 1300.42$, $SD = 725.73$). Panel B displays the results obtained by late-blind individuals (strawberry: $M = 1722.27$, $SD = 630.24$; parmesan cheese: $M = 1809.19$, $SD = 770.72$) and their matched sighted counterparts (strawberry: $M = 1493.51$, $SD = 544.28$; parmesan cheese: $M = 1717.39$, $SD = 790.65$). Panel C displays the standardized IE scores of blind individuals generated by their respective control groups (CB: strawberry: $M = -0.29$, $SD = 0.59$; parmesan cheese: $M = -0.43$, $SD = 0.36$; LB: strawberry: $M = 0.42$, $SD = 1.16$; parmesan cheese: $M = -0.16$, $SD = 0.39$).

and Karwowski 2017), we found no significant difference in olfactory performance between blind and sighted individuals on odor detection and identification tasks. It is, therefore, possible that the selective improvement of congenitally blind individuals for chemosensory localization reveals a selective pressure to further develop such spatial skills for coping with visual deprivation in daily life, potentially in relation to the dominant role vision typically plays in spatial processing and navigation. Perceptual enhancement in blind individuals should, therefore, not be considered as an automatic and general perceptual process but as a compensatory mechanism emerging depending on specific cognitive pressure created by the lack of vision early in life. The fact that such compensation does not emerge in late-blind people points toward the fact that such mechanisms interact with the developmental stage of the individual. Thus, our results support the importance of considering the age of onset of vision loss when doing research on compensatory mechanisms. Compared to the recent study conducted by Sorokowska et al. (2019) where no suprapercormances of chemosensory localization and lateralization were found in blind individuals, we evaluated 2 distinct groups of blind participants (i.e., congenitally vs. late blind). Consequently, our results highlight the importance of a sensitive period for the enhancement of odor localization abilities among visually deprived individuals. Moreover, it might be possible that this selective pressure solely enhances trigeminal rather than olfactory sensitivity among congenitally blind individuals. In order to test this hypothesis, future studies should investigate pure trigeminal stimuli, such as the odorless carbon dioxide (Cain and Murphy

1980) alone and in combination with pure olfactory stimuli. By independently modulating the concentrations of both components, it will be possible to determine individual thresholds (i.e., trigeminal sensitivity) and use subthreshold and suprathreshold concentrations to dissociate the trigeminal from the nontrigeminal effects in an intranasal localization task. The findings of our study suggest that there is likely no compensation effect on olfactory functions in general, but some specific chemosensory abilities, such as intranasal localization of odorants, may benefit from early onset of blindness.

The better performance of congenitally blind individuals could be explained by 2 different mechanisms. First, the effect may be purely trigeminal. For example, it is conceivable that congenitally blind individuals have a lower somatosensory threshold (Van Boven et al. 2000; Goldreich and Kanics 2003; Alary et al. 2009) and that this extends to sensations from the nasal mucosa. This would imply that congenitally blind individuals have a better ability to extract trigeminal information from the mixed olfactory/trigeminal stimuli we used; this improved ability may be linked to somatosensory thresholds, which may be evaluated in future studies. A second possibility is that congenitally blind individuals are able to localize the olfactory component of the mixed olfactory-trigeminal stimuli in contrast to controls. In fact, there are publications that suggest that some individuals are indeed able to localize pure olfactory stimuli (Von Békésy 1964; Porter et al. 2005). Future studies could evaluate this ability in congenitally blind individuals.

A few limitations should be noted. First, our study comprised small groups of participants and it is possible that individual

variations might influence our results. However, our group scores obtained with the Sniffin' Stick battery are coherent with the results of the meta-analysis of Sorokowska et al. (2018). Moreover, the absence of differences between groups for our own tasks of identification and detection is in line with the conclusions of this precedent meta-analysis. Therefore, we are confident that even with small groups of participants, which are common with clinical population studies, our results are robust. Second, it has already been said that the lack of differences between blind individuals and sighted ones on olfactory tasks might be due to the lack of sensitivity of the Sniffin' Sticks, which is commonly used for the examination of an olfactory deficit. Here, in addition to the Sniffin' Stick identification task, we used 3 new ways of evaluating olfactory abilities (i.e., detection, identification, and localization of odors). Our findings for the detection and identification tasks are coherent with previous studies in the domain and suggest that only olfactory localization abilities are enhanced in congenitally blind individuals but not the more traditionally assessed tasks, such as odor identification and/or detection. However, it remains unclear if the level of difficulty of our tasks, for which the detection and identification were performed better than the localization task, can explain the absence of difference between groups. Future studies should modulate odor threshold concentrations in their olfactory protocol in order to increase the difficulty of their tasks and avoid the ceiling effect. Last, the precise anatomic and physiologic mechanisms underlying our results are not yet clear. Relating odor detection, identification, and localization to magnetic resonance imaging (MRI) volumetric measures or functional imaging assessments (e.g., positron emission tomography and functional MRI) of the primary and secondary olfactory regions and visual cortices will also help to discern whether there is a structural or physiological component to the observed psychophysical results.

In summary, the findings of the present study suggest that the trigeminal component of chemosensory objects is processed differently among blind individuals, that is, congenitally blind individuals are better at localizing olfactory-trigeminal objects than late-blind subjects. Future neuroimaging studies could provide a better understanding of the underlying mechanisms of the current findings (i.e., the brain reorganization of congenitally blind individuals that contributes to the enhancement of trigeminal processing of chemosensory stimuli).

Supplementary material

Supplementary material can be found at *Chemical Senses* online.

Supplementary Table S1. Risk-of-bias assessment of selected articles.

Funding

This work was supported by the Natural Sciences and Engineering Research Council of Canada [NSERC 2014–05053] to F.L., the research center of Sacré-Coeur Hospital in Montreal (CIUSSS du Nord-de-l'Île-de-Montréal), the Université du Québec à Trois-Rivières, the Natural Sciences and Engineering Research Council of Canada [NSERC 2015–04597], the Canadian Institutes of Health Research [PJT-173514], and the Fonds de recherche du Québec – Santé to J.F., funding from the Natural Sciences and Engineering Research Council of Canada, and the Fonds de recherche du Québec – Nature et Technologies to S.M., funding from the Natural Sciences and Engineering Research Council of Canada to C.C.L., and the National Fund for Scientific Research of Belgium (FRS-FNRS) to O.C.

Conflict of interest

None declared.

References

- Alais D, Burr D. 2004. The ventriloquist effect results from near-optimal bimodal integration. *Curr Biol*. 14(3):257–262.
- Alary F, Duquette M, Goldstein R, Elaine Chapman C, Voss P, La Buissonnière-Ariza V, Lepore F. 2009. Tactile acuity in the blind: a closer look reveals superiority over the sighted in some but not all cutaneous tasks. *Neuropsychologia*. 47(10):2037–2043.
- Battal C, Occelli V, Bertoni G, Falagiarda F, Collignon O. 2019. “Ubiquitous enhancement of spatial hearing in congenitally blind people,” psyarxiv, doi:10.31234/osf.io/veh7t, 16 May 2017, preprint: not peer reviewed.
- Bavelier D, Neville HJ. 2002. Cross-modal plasticity: where and how? *Nat Rev Neurosci*. 3(6):443–452.
- Beaulieu-Lefebvre M, Schneider FC, Kupers R, Ptito M. 2011. Odor perception and odor awareness in congenital blindness. *Brain Res Bull*. 84(3):206–209.
- Bruyer R, Brysbaert M. 2011. Combining speed and accuracy in cognitive psychology: is the inverse efficiency score (IES) a better dependent variable than the mean reaction time (RT) and the percentage of errors (PE)? *Psychol Belg*. 51(1):5–13.
- Burton H. 2003. Visual cortex activity in early and late blind people. *J Neurosci*. 23(10):4005–4011.
- Cain WS, Murphy CL. 1980. Interaction between chemoreceptive modalities of odour and irritation. *Nature*. 284(5753):255–257.
- Charbonneau G, Veronneau M, Boudrias-Fournier C, Lepore F, Collignon O. 2013. The ventriloquist in periphery: impact of eccentricity-related reliability on audio-visual localization. *J Vis*. 13(12):20–20.
- Collignon O, Dormal G, Lepore F. 2012. Building the brain in the dark: Functional and specific crossmodal reorganization in the occipital cortex of blind individuals. In: Steeves JKE, Harris L editors, *Plasticity in Sensory Systems*, Cambridge (UK): Cambridge University Press. p. 114–137.
- Collignon O, Renier L, Bruyer R, Tranduy D, Veraart C. 2006. Improved selective and divided spatial attention in early blind subjects. *Brain Res*. 1075(1):175–182.
- Collignon O, Vandewalle G, Voss P, Albouy G, Charbonneau G, Lassonde M, Lepore F. 2011. Functional specialization for auditory–spatial processing in the occipital cortex of congenitally blind humans. *Proc Natl Acad Sci*. 108(11):4435–4440.
- Collignon O, Voss P, Lassonde M, Lepore F. 2009. Cross-modal plasticity for the spatial processing of sounds in visually deprived subjects. *Exp Brain Res*. 192(3):343–358.
- Çomoğlu Ş, Orhan KS, Kocaman SÜ, Çelik M, Keleş N, Değer K. 2015. Olfactory function assessment of blind subjects using the sniffin sticks test. *Otolaryngol Head Neck Surg*. 153(2):286–290.
- Cornell Kärnekull S, Arshamian A, Nilsson ME, Larsson M. 2016. From perception to metacognition: auditory and olfactory functions in early blind, late blind, and sighted individuals. *Front Psychol*. 7:1450.
- Cuevas I, Plaza P, Rombaix P, Collignon O, De Volder A, Renier L. 2010. Do people who became blind early in life develop a better sense of smell? A psychophysical study. *J Vis Impair Blind*. 104(6):369–379.
- Dormal V, Crollen V, Baumanns C, Lepore F, Collignon O. 2016. Early but not late blindness leads to enhanced arithmetic and working memory abilities. *Cortex*. 83:212–221.
- Dormal G, Lepore F, Collignon O. 2012. Plasticity of the dorsal “spatial” stream in visually deprived individuals. *Neural Plast*. 2012.
- Doty RL, Brugger WE, Jurs PC, Orndorff MA, Snyder PJ, Lowry LD. 1978. Intranasal trigeminal stimulation from odorous volatiles: psychometric responses from anosmic and normal humans. *Physiol Behav*. 20(2):175–185.
- Frasnelli J, Charbonneau G, Collignon O, Lepore F. 2009. Odor localization and sniffing. *Chem Senses*. 34(2):139–144.
- Frasnelli J, La Buissonnière Ariza V, Collignon O, Lepore F. 2010. Localisation of unilateral nasal stimuli across sensory systems. *Neurosci Lett*. 478(2):102–106.
- Gagnon L, Kupers R, Ptito M. 2014. Making sense of the chemical senses. *Multisens Res*. 27(5–6):399–419.
- Goldreich D, Kanics IM. 2003. Tactile acuity is enhanced in blindness. *J Neurosci*. 23(8):3439–3445.

- Gori M, Sandini G, Martinoli C, Burr D. 2010. Poor haptic orientation discrimination in nonsighted children may reflect disruption of cross-sensory calibration. *Curr Biol*. 20(3):223–225.
- Gori M, Sandini G, Martinoli C, Burr DC. 2014. Impairment of auditory spatial localization in congenitally blind human subjects. *Brain*. 137(Pt 1):288–293.
- Gougoux F, Lepore F, Lassonde M, Voss P, Zatorre RJ, Belin P. 2004. Pitch discrimination in the early blind. *Nature*. 430(6997):309–309.
- Gougoux F, Zatorre RJ, Lassonde M, Voss P, Lepore F. 2005. A functional neuroimaging study of sound localization: visual cortex activity predicts performance in early-blind individuals. *PLoS Biol*. 3(2):e27.
- Guducu C, Oniz A, Ikiz AO, Ozgoren M. 2016. Chemosensory function in congenitally blind or deaf teenagers. *Chemosens Percept*. 9(1):8–13.
- Heimler B, Striem-Amit E, Amedi A. 2015. Origins of task-specific sensory-independent organization in the visual and auditory brain: neuroscience evidence, open questions and clinical implications. *Curr Opin Neurol*. 35:169–177.
- Heller M, Ballesteros S. 2016. Visually-impaired touch. In: Prescott T, Ahissar E, Izhikevich E, editors. *Scholarpedia of touch*. Paris (France): Atlantis Press. p. 387–397.
- Hummel T, Kobal G. 1999. Chemosensory event-related potentials to trigeminal stimuli change in relation to the interval between repetitive stimulation of the nasal mucosa. *Eur Arch Oto-Rhino-L*. 256(1):16–21.
- 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. *Eur Arch Otorhinolaryngol*. 264(3):237–243.
- Hummel T, Sekinger B, Wolf SR, Pauli E, Kobal G, Hummel T. 1997. “Sniffin’ Sticks”: olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold. *Chem Senses*. 22:39–52.
- Jacobs LF. 2012. From chemotaxis to the cognitive map: the function of olfaction. *Proc Natl Acad Sci*. 109:10693–10700.
- Kleemann AM, Albrecht J, Schöpf V, Haegler K, Kopietz R, Hempel JM, Linn J, Flanagan VL, Fesl G, Wiesmann M. 2009. Trigeminal perception is necessary to localize odors. *Physiol Behav*. 97(3–4):401–405.
- Koutsoklenis A, Papadopoulos K. 2011. Olfactory cues used for wayfinding in urban environments by individuals. *J Vis Impair Blind*. 105(November):692–702.
- Kupers R, Beaulieu-Lefebvre M, Schneider FC, Kassuba T, Paulson OB, Siebner HR, Ptito M. 2011. Neural correlates of olfactory processing in congenital blindness. *Neuropsychologia*. 49(7):2037–2044.
- Kupers R, Ptito M. 2011. Insights from darkness: what the study of blindness has taught us about brain structure and function. *Prog Brain Res*. 192:17–31.
- La Buissonnière-Ariza V, Frasnelli J, Collignon O, Lepore F. 2012. Olfactory priming leads to faster sound localization. *Neurosci Lett*. 506(2):188–192.
- Lessard N, Paré M, Lepore F, Lassonde M. 1998. Early-blind human subjects localize sound sources better than sighted subjects. *Nature*. 395(6699):278–280.
- Lewald J. 2002. Vertical sound localization in blind humans. *Neuropsychologia*. 40(12):1868–1872.
- Leys C, Ley C, Klein O, Bernard P, Licata L. 2013. Detecting outliers: do not use standard deviation around the mean, use absolute deviation around the median. *J Exp Soc Psychol*. 49(4):764–766.
- Luers JC, Mikolajczak S, Hahn M, Wittekindt C, Beutner D, Hüttenbrink KB, Damm M. 2014. Do the blinds smell better? *Eur Arch Otorhinolaryngol*. 271(7):1933–1937.
- Majchrzak D, Eberhard J, Kalaus B, Wagner KH. 2017. Do visually impaired people develop superior smell ability? *Perception*. 46(10):1171–1182.

- Murphy C, Cain WS. 1986. Odor identification: the blind are better. *Physiol Behav.* 37(1):177–180.
- Negoias S, Aszmann O, Croy I, Hummel T. 2013. Localization of odors can be learned. *Chem Senses.* 38(7):553–562.
- Porter J, Anand T, Johnson B, Khan RM, Sobel N. 2005. Brain mechanisms for extracting spatial information from smell. *Neuron.* 47(4):581–592.
- Porter J, Craven B, Khan RM, Chang SJ, Kang I, Judkewitz B, Sobel N. 2007. Mechanisms of scent-tracking in humans. *Nat Neurosci.* 10(1):27–29.
- Röder B, Kusmirek A, Spence C, Schicke T. 2007. Developmental vision determines the reference frame for the multisensory control of action. *Proc Natl Acad Sci USA.* 104(11):4753–4758.
- Röder B, Teder-Sälejärvi W, Sterr A, Rösler F, Hillyard SA, Neville HJ. 1999. Improved auditory spatial tuning in blind humans. *Nature.* 400(6740):162–166.
- Rombaux P, Huart C, De Volder AG, Cuevas I, Renier L, Duprez T, Grandin C. 2010. Increased olfactory bulb volume and olfactory function in early blind subjects. *Neuroreport.* 21(17):1069–1073.
- Sorokowska A. 2016. Olfactory performance in a large sample of early-blind and late-blind individuals. *Chem Senses.* 41(8):703–709.
- Sorokowska A, Karwowski M. 2017. No sensory compensation for olfactory memory: differences between blind and sighted people. *Front Psychol.* 8:2127.
- Sorokowska A, Oleszkiewicz A, Stefańczyk M, Plachetka J, Dudójć O, Ziembik K, Hummel T. 2019. Odor lateralization and spatial localization: null effects of blindness. *Atten Percept Psychophys.* 81(6):2078–2087.
- Sorokowska A, Sorokowski P, Karwowski M, Larsson M, Hummel T. 2018. Olfactory perception and blindness: a systematic review and meta-analysis. *Psychol Res.* 83(8):1595–1611.
- Spence C, Shore DI, Gazzaniga MS, Soto-Faraco S, Kingstone A. 2001. Failure to remap visuotactile space across the midline in the split-brain. *Can J Exp Psychol.* 55(2):133–140.
- Tabachnick BG, Fidell LS. 2013. *Using multivariate statistics.* Boston (MA): Pearson Education.
- Townsend JT, Ashby FG. 1978. Methods of modeling capacity in simple processing systems. In: Castellan J., Restle F, editors. *Cognitive theory.* Vol. 3. Hillsdale (NJ): Erlbaum. p. 200–239.
- Townsend JT, Ashby FG. 1983. *Stochastic modeling of elementary psychological processes.* Cambridge (MA): Cambridge University Press.
- Van Boven RW, Hamilton RH, Kauffman T, Keenan JP, Pascual-Leone A. 2000. Tactile spatial resolution in blind braille readers. *Neurology.* 54(12):2230–2236.
- Viana F. 2011. Chemosensory properties of the trigeminal system. *ACS Chem Neurosci.* 2(1):38–50.
- Von Békésy, G. (1964). Olfactory analogue to directional hearing. *J Appl Physiol.* 19(3):369–373.
- Voss P. 2013. Sensitive and critical periods in visual sensory deprivation. *Front Psychol.* 4:664.
- Voss P. 2016. Auditory spatial perception without vision. *Front Psychol.* 7:1960.
- Voss P, Collignon O, Lassonde M, Lepore F. 2010. Adaptation to sensory loss. *Wiley Interdiscip Rev Cogn Sci.* 1(3):308–328.
- Voss P, Lassonde M, Gougoux F, Fortin M, Guillemot J.-P, Lepore F. 2004. Early- and late-onset blind individuals show supra-normal auditory abilities in far-space. *Curr Biol.* 14(19):1734–1738.
- Wise PM, Wysocki CJ, Lundström JN. 2012. Stimulus selection for intranasal sensory isolation: eugenol is an irritant. *Chem Senses.* 37(6):509–514.
- Zwiers M, Van Opstal A, Cruysberg J. 2001. Two-dimensional sound-localization behavior of early-blind humans. *Exp Brain Res.* 140(2):206–222.