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Research report

Interhemispheric balance sets nostril differences in color-induced nasal thermal judgments

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ABSTRACT

Sniffing out of sight always the same colorless and odorless solution containing no thermal agents while viewing a bottle with colored water increases sensitivity of the left nostril/right hemisphere (RH) for warming sensations and sensitivity of the right nostril/left hemisphere (LH) for cooling sensations. It is likely that engagement in a temperature judgment task and the development of specific expectancies due to the presence of color cues alter and enhance processing in brain areas involved in thermosensory processing. The lateralized patterns thus intimate hemispheric specialization for thermosensory processing probably originating in reciprocal inhibition that confers balance between the hemispheres. If the inhibition-balance hypothesis were correct then the more the left nostril proves sensitive to warming the more the right nostril would prove sensitive to cooling. One hundred and ninety one healthy volunteers were tested here. The left nostril dominance for warming and the right dominance for cooling were replicated once more. The dominance of the left nostril for warming (left *minus* right nostril) correlated highly with the dominance of the left nostril to cooling (right *minus* left nostril) and the individual patterns of results were distributed along an axis starting from the expected left nostril/warming – right nostril/cooling pattern and ending at the opposite left nostril/cooling – right nostril/warming pattern. Furthermore, the point where the left nostril dominance for warming responses dropped and inverted perfectly coincided with the point where the right nostril dominance for cooling responses inverted too. Such a good continuum between the expected and the opposite patterns supports the inhibition-balance hypothesis. Finally, 66% of subjects exhibited the expected left-warming/right-cooling pattern suggesting, therefore, that, despite this continuum, there is a dominant lateral specialization for temperature processing.

1. Introduction

The answer to the question “why do we have two eyes?” is known: Because binocular viewing allows us to perceive depth. But is there such a straightforward and clear answer to the question “why do we have two nostrils?”. Sobel and colleagues attempted a fascinating first answer [1], when they suggested that nostrils smell different things altogether and that the difference in their perception is very subtle. Theses differences in olfactory processing are linked to the nasal cycle in such a way that airflow allows one nostril to detect the odor of some substances better and the second nostril to detect the odor of others better. Yet, peripheral factors such as airflow cannot explain other differences between nostrils, such as lateralized patterns of nasal thermal judgments. Studies conducted in our laboratory [2–4] revealed and replicated intriguing color-induced nasal thermal judgments in healthy volunteers. When a bottle containing colorless, odorless water and free of any thermal agent is presented out of sight to one nostril while subjects are viewing another bottle containing a colored (red or green) solution, a subject's thermal judgment does not systematically match the color viewed (e.g., warming with red, and cooling with green). Instead, subjects more frequently associate warming responses with red when they sniff the bottle with their left nostril, whereas cooling responses are more frequently associated with green when they sniff it with their right nostril. Such response patterns depend on the difficulty of the task, the presence of colors, they are specific to unilateral nostril stimulation and are seemingly independent of the nasal cycle. It has been suggested that fairly high order cognitive processes, guided by color cues and likely to occur through the modulation of activity in areas specialized in temperature processing [4,5], could modulate nasal thermal judgments. Differences between nostrils would thus depend upon the specialization of the cerebral hemispheres in addition to peripheral factors [1].

Trigeminal projections arising in the nasal cavity and conveying thermal signals are mostly contralateral, i.e., signals from the right

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nostril are conveyed to the left cerebral hemisphere (LH), and those from the left nostril to the right hemisphere (RH). Warming and cooling signals may thus be processed *via* selective pathways [6,7], giving rise to hemispheric differences [2–4]. Neuroimaging studies suggest, however, that thermosensory processing is strictly contralateral whatever the stimulus – warm or cool – and this is quite difficult to reconcile with our idea of hemispheric differences [2–4]. Yet, those findings are sometimes hard to interpret mainly because methodological issues do not allow drawing a complete picture of what is going on. For instance, a mostly left-sided activity involving the posterior insula was found with cooling stimuli applied on the right side of the body [5]. Yet, it is difficult to accept the idea of a strict contralateral activity without applying the same stimulus on the left side to discover whether activation would be found in the RH. In another study [9] cooling stimuli delivered on the right side of the body activated the left posterior insula (just as in [5]), but stimuli delivered on the left side of the body did not yield contralateral insular activation. Along with the findings of other imaging studies, these results suggest that cooling sensitivity is represented bilaterally [10] with a dominance of the LH. Something equivalent may be said for warming. RH activities were reported with stimuli delivered on the left side of the body [9,11,12]. Interestingly, one study reported activities in the right posterior insula with stimuli applied on the right side of the body [13], and another one reported bilateral activation of a brain network regardless of the side of stimulation, with activation being greater in the RH [8]. The combination of these studies suggests that a bilateral representation of warming sensitivity is possible [14,15], with a dominance of the RH. Taken in isolation, all these studies shed little light on the lateralization of thermosensory processes. Yet, their combination clearly supports the LH-cooling/RH-warming pattern discovered through the color-induced nasal thermal sensations [2–4].

The hemispheric account is also supported by neuropsychological evidence. It is true that clinical studies sometimes report contralateral loss of warm and cool sensitivity, which is consistent with their equal representation in each hemisphere [16–18]. Unfortunately, these reports do not allow distinguishing two alternative hypotheses, that is, representation in both hemispheres with equal importance and with contralateral involvement, or representation in both hemispheres with unequal importance and lateral dominance as a function of the stimulus type. To our knowledge, there are two single-case studies that provide a double dissociation and support the second account. A selective loss of contralateral cold perception, without any loss of warmth perception, has been reported following a lesion of the left insula [19]. Conversely, a lesion of the right insula might be followed by the selective loss of contralateral warmth perception, without any loss of cold perception [20]. Thus, the overall picture that rises when neuroimaging and neuropsychological data are taken together is that cooling and warming signals are likely to be processed differently in the two hemispheres despite being represented in both hemispheres.

However, it is unlikely the lateralization of color-induced nasal thermal sensations is due to a simple exclusive specialization of the cerebral hemispheres. If it were the case, both hemispheres would process thermosensory signals, but the LH would specialize in processing cooling signals and the RH in warming signals, as initially suggested [2]. What we observed [4] was that the frequency of contralateral (i.e., right) nostril green-cooling responses decreased following a lesion of the left insula, whereas there was an increment in the frequency of green-cooling responses in the ipsilateral (i.e., left) nostril. No changes were observed for red-warming responses. The inference from this is that the lateralized patterns probably emerge as a result of reciprocal inhibition between the cerebral hemispheres [21], and that a unilateral cortical lesion releases the intact hemisphere from inhibition. In addition to their relative specialization, the specific thermosensory systems of the two hemispheres would thus be mutually inhibiting (e.g., the dominant LH processing of cooling signals would inhibit the non-dominant cooling system of the RH), so that each hemisphere could efficiently process those signals it is specialized to process. Behavior control would be achieved through balance between the selection of brain areas involved in thermosensory processing and the reciprocal inhibition enabling unequivocal choice between activating more the left or the right hemisphere [21]. The performance of healthy subjects should thus provide supporting evidence. If lateralized responses arise because of interhemispheric inhibition and balance, the variability of left nostril-warming and right nostril-cooling responses would follow a particular pattern. First, the notion of balance means that when one side goes up the other side goes down. Therefore, the more sensitive the left nostril is to warming, the more sensitive the right nostril would be to cooling. A positive correlation is thus expected between the dominance of the left nostril (i.e., left *minus* right) for warming and the dominance of the right nostril (i.e., right *minus* left) for cooling. Nostril differences would thus range from left-warming/right-cooling (i.e., the expected pattern) to left-cooling/right-warming (i.e., the opposite pattern). Second, a single center of mass is the point where changes in balance are observed. Thus, if there were a true balance between hemispheric processes, the point where the left nostril dominance for warming inverses and becomes a dominance for cooling would be the point where the dominance of the right nostril for cooling inverses. Third, as established by the previous studies [2–4], the subjects exhibiting the left-warming/right-cooling pattern would outnumber those exhibiting the opposite pattern, signifying that overall there is hemispheric specialization and that the center of mass does not coincide with the geometric center of the data. The present study aimed to investigate these hypotheses in healthy volunteers, and insofar as they all suggest that diverse patterns of nostril dominance are to be found in the population, we felt it was important to base our study on a large sample of subjects.

2. Methods

2.1. Subjects

The study was conducted in accordance with the declaration of Helsinki. One hundred and ninety one volunteers (age range: 17–69 years) took part in this study. All subjects were female for reasons of sample homogeneity and because previous investigations had shown that females are more sensitive to stimuli delivered in the nostrils. All had normal or corrected-to-normal vision and could correctly identify the colors of the stimuli. According to the Edinburgh laterality inventory [22], all were right-handed (mean laterality coefficient: 0.89 ± 0.15; range: 0.50–1.0). At the time of testing, they were non-smokers, free of sinus infection, allergy and head colds, and not under medication. Young participants were not pregnant. They all gave their written informed consent for their participation.

2.2. Stimuli

Three small 20 ml glass bottles (height: 5 cm; diameter: 3 cm) containing 10 ml of water were used as stimuli. One drop of odorless food coloring (Vahiné®) was added to two of these bottles to obtain one green solution (Munsell system Hue (H): 126°; saturation (S): 100%; brightness (B): 88%) and one red solution (H: 0°; S: 100%; B: 100%). The solution contained in the third bottle remained colorless. A yellow solution (H: 46°; S: 100%; B: 100%) was used during training trials. The bottles were placed in a 30 cm × 10 cm × 7 cm box with eight empty glass bottles and were not visible to the participant.

2.3. Apparatus

The Eyes/Nostrils Dissociation Device (ENDD; Fig. 1) was used, a white 40 cm high wooden stand specially designed for separating what the subject sees from what she smells. The detailed description of this device can be found in ref. [3]. It comprises two rectangular boards joined together; the lower one acts as a support while the upper one is used to present the colored solution and receives the subject's nasal bone. The nasal bone receptacle contains a small soft pad filled with cotton wool to maximize comfort, minimize thermal sensations on the skin caused by the wooden board, and, as far as possible, fit the shape of each subject's nasal bone, thereby separating the eyes from the nostrils. Another board is placed opposite the nasal bone receptacle to prevent the color of the objects behind the device interfering with the color of the solutions exhibited.