Research report

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

George A. Michael*, Solveig Relland, Hélène Galich

Laboratoire d’Étude des Mécanismes Cognitifs, Université Lyon 2, Lyon, France

A R T I C L E   I N F O

Article history:
Received 12 April 2011
Received in revised form 9 June 2011
Accepted 14 June 2011
Available online 21 June 2011

Keywords:
Hemispheric specialization
Nostril lateralization
Nasal Temperature
Color-temperature synaesthesia
Reciprocal inhibition

A B S T R A C T

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 processes between the hemispheres. If the inhibition–balance hypothesis were correct then 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.

© 2011 Elsevier B.V. All rights reserved.

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

* Corresponding author at: Université Lyon 2, Dpt. Psychologie Cognitive & Neuropsychologie, Laboratoire d’Étude des Mécanismes Cognitifs, 5, Avenue Pierre Mendès-France, 69676 Bron Cedex, France. Tel.: +33 4 78 77 30 53;
fax: +33 4 78 77 43 51.
E-mail address: George.Michael@univ-lyon2.fr (G.A. Michael).

0166-4328/ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.bbr.2011.06.015
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 [67], 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 the LH and RH are 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 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 in the third (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: 0.83 ± 0.15; range: 0.50–1.0). At the time of testing, they were non-smokers, free of sinus infection, allergy and heat 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 delivered to the subject’s nostril is the one used in the experiment. 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 smelles. 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.
2.4. Procedure

The experiment was carried out in a quiet room under normal lighting conditions, and with a mean ambient temperature of 23°C. The experimenter sat facing the subject, with a small table placed between them. On the table was a box containing the glass bottles and the ENDD. At the start of the test, the experimenter told the subject the box contained a large number of bottles and then proceeded to touch them in order to produce a chime, so that the subject believed the box really did contain a large number of bottles and that a different one was presented in each trial. Subjects were not allowed to handle the bottles and were told that they all contained chemical agents, half of which would elicit cooling sensations and half warming sensations, but that these were so diluted that intuitive judgments could help. This method proved effective in previous studies on visual-somatosensory [23] and color-nasal temperature interactions [2–4] since it induces non-random response biases. Participants were then invited to get close to the ENDD and to position their head in such a way that they could no longer see their nose. The experimenter checked that their nasal bone was correctly positioned in the receptacle and that their eyes were above the upper board of the stand with their nose below it (Fig. 1). One of the bottles containing a colored solution was placed just in front of the viewing midline, at a distance of 33 cm from subjects’ eyes. The experimenter refrained from giving any information about the relation between the exhibited bottle and the sniffed bottle. Each trial started with the participant being asked to fixate the bottle and to maintain fixation throughout the whole trial. The experimenter checked the bottle was fixated and then asked the subject to close a designated nostril using the index finger of the hand of the same side (left hand for left nostril, right hand for right nostril). The bottle containing the colorless solution was then held up to the other nostril, and the subject was required to smell by taking one deep, slow sniff and to report whether the solution induced a cooling or warming sensation in the nasal cavity. No other response was accepted. Subjects were completely unaware of the fact that they were always sniffing the same bottle containing a colorless, odorless and trigeminal-free solution (i.e., containing no agents that could induce thermal or pungent sensations) presented at ambient temperature. Two factors were manipulated, each having two levels: (a) the tested nostril (left or right), and (b) the color of the exhibited solution (red or green). Six trials were presented per condition, and each of the four conditions was counterbalanced across trials and across subjects in a complete Latin square order. The number of trials was based on pilot experiments conducted on healthy volunteers of different ages (ranging from the 20’s to mid-50’s) having shown that the expected nostril by color patterns were robust up until 6 trials per condition, diminished with 8 trials, and disappeared with 12 trials or more (up to 24 presented), a phenomenon mainly explained by decreasing motivation over time as retrospectively suggested by subjects. The test was preceded by a few training trials during which the exhibited bottle contained a yellow solution. The Experiment lasted 10 min. Responses were recorded by the experimenters.

3. Results

An analysis of variance (ANOVA) was carried out on the proportions of expected responses, that is, the number of red-warming and green-cooling associations. The tested nostril (left vs. right) and color of the exhibited solution (red vs. green) were the within-subject factors. The main effect of nostril failed to reach significance (left: 0.58; right: 0.58; F(1,190) = 0.44; P = 0.5), as did the main effect of color (red: 0.58; green: 0.58; F(1,190) = 0.002; P = 0.97). The nostril x color interaction was significant (F(1,190) = 7.4; P < 0.0063; Fig. 2A). Planned comparisons (t-tests) revealed that, when the left nostril was stimulated, the proportion of red-warming responses (0.61) was greater than the proportion of green-cooling responses (0.55; t(190) = 2.12; P = 0.036), and the exact opposite pattern was found when the right nostril was stimulated (red: 0.54; green: 0.61; t(190) = 2.16; P < 0.032). These results are very similar to those we have reported in our previous studies [2–4] and establish, for the fifth time, the difference between the two nostrils. Red-warming responses are more frequent for the left nostril, and green-cooling responses are more frequent for the right nostril. That red-warming and green-cooling responses are independent from each other is attested through the absence of correlation between them when considered independently from the tested nostril (r(189) = 0.03; P > 0.78), despite one may think that warming and cooling are parts of the same response continuum. Indeed, warm and cool can be considered as exclusive descriptors that do not combine on a single scale since subjects do not always respond “warming” when a red solution is presented, nor “cooling” whenever a green solution is presented. This is attested by the fact that expected responses for each color never reach a perfect proportion (i.e., 1.0) and they never coincide with such a proportion when they are combined. Finally, that expected responses for each color can be dissociated is supported by neuropsychological data [4].

The balance between the nostrils for each kind of response was investigated by submitting the dominance of the left nostril (i.e., left minus right nostril) for warming responses and the dominance of the right nostril (i.e., right minus left nostril) for cooling responses to a correlation analysis. As expected, a positive correlation (r(189) = 0.37; P < 0.000001; Fig. 2B) was found. The more pronounced the dominance of the left nostril for warming responses, the more pronounced is the dominance of the right nostril for cooling responses, and vice versa. As seen in Fig. 2B, most of the points are situated 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, revealing a continuum in the color-by-nostril interaction. Of importance, despite the link observed between the dominance of one nostril with that of the other, no correlation was found between the left and the right nostrils when each kind of response was taken independently (r(189) = −0.03; P > 0.68 for red-warming; r(189) = +0.02; P > 0.78 for green-cooling).

To investigate whether the point where the left nostril/warming pattern inverses coincides with the point where the right nostril/cooling inverses, subjects were ordered as a function of the left nostril minus right nostril difference for the red-warming responses (from the strongest to the weakest). The green-cooling responses given by each subjects were then plotted correspondingly and a

---

1 When “warming” responses alone are used to investigate the balance between the nostrils, submitting the dominance of the left nostril (i.e., left minus right nostril) and the dominance of the right nostril (i.e., right minus left nostril) to a correlation analysis yields results that are similar to those obtained with the expected responses. It is expected that the frequency of warming diminish in a left/red-right/green direction. We find, indeed, a negative correlation the value of which is strictly identical to the one observed when exploring expected responses (r(189) = −0.37; P < 0.00001). When the direction of warming responses for the red solutions shifts from the left nostril to the right, the same responses for the green solutions shift in the opposite direction, and vice versa.
The polynomial regression curve was fitted in order to find the overall tendency. The resulting scatterplot is presented in Fig. 3A. Three different results can be seen. First, the point where red-warming passes from the left nostril dominance to that of the right nostril coincides perfectly with the point where the mean tendency of the green-cooling responses pass from the dominance of the right nostril to that of the left nostril. Second, the strongest dominance of the left nostril for red-warming responses, the strongest the right nostril for green-cooling responses, and this link continues even beyond the inversion point of the two. Third, the number of subjects presenting the expected pattern of results (i.e., situated before the inversion point) is larger than that of subjects presenting the opposite pattern. The color-by-nostril interaction (i.e., the red-warming minus green-cooling difference) is depicted in Fig. 3B and it clearly shows the continuum in the subjects’ performance \((r(189) = 0.82; P < 0.000001)\) extending from the expected pattern to the opposite.

We further investigated this continuum by inspecting the distribution of the color-by-nostril interaction (Fig. 3C). The
Kolmogorov–Smirnov test revealed that the data followed the normal distribution ($K^S$ $d = 0.07$; $P > 0.79$) suggesting the existence of continuity from the expected pattern of interaction to the exact opposite. The frequency of interaction was investigated by submitting the proportion of subjects exhibiting a particular pattern (expected, opposite, or none; Fig. 3C) to a Q analysis [24]. Sixty-six percent of subjects showed the expected pattern of interaction (i.e., left nostril dominance for warming and right nostril dominance for cooling), while 23.6% exhibited the opposite pattern, and 10.5% exhibited no interaction ($Q(2) = 129.8; P < 0.000001$). The difference between the subjects exhibiting the expected pattern and those exhibiting the opposite one was highly significant ($q^2 = 3.46; P < 0.002$), and both groups differed significantly from that exhibiting no interaction (both $P$s $< 0.0001$).

4. Discussion

The present study evidenced the relationship that exists between each nostril and temperature judgments for the fifth time since such a relationship was discovered [2]. The left nostril dominated for warming judgments and the right nostril for cooling judgments. In our previous studies we suggested such effects might be determined by the activity of learned expectations and neurobiological wiring. For instance, learnt color-temperature pairings could elicit task-dependent percepts in another modality (i.e., if the judgment to be made concerned temperature the elicited percept would be thermosensory in nature, whereas if the judgment were olfactory the percept would be olfactory). Engagement in a task could therefore re-shape and enhance processing in modality-specific brain zones mainly as a result of the observer’s expectations [3]. This account has received extensive support from research in the fields of vision [25], audition [26], olfaction [27], somesthesia [23,28], and gustation [29,30]. Thermosensory percepts elicited by temperature-related colors in temperature judgment tasks are seemingly generated by lateralized neural pathways [4,19,20,31], which may explain why lateralization is observed only when color cues are available [2,3].

4.1. Swings: achieving lateralized performance

How is the lateralization of thermal processing achieved? Because trigeminal projections that convey information about the temperature of airborne molecules entering the nasal cavity are mainly contralateral, it was initially suggested the LH may be more involved in processing cooling and the RH more specialized in processing warming sensations [2]. This rather simplistic account assumes each hemisphere is more specialized than the other in one particular type of processing. Both of them process thermosensory signals but to differing degrees. The assumption is that warming and cooling signals are processed via selective pathways [6,7], because why otherwise would subjects link only one of these sensations with only one nostril? However, a subsequent study [3] proposed a different account, namely specialization through inhibition [21], according to which, in addition to their relative specialization, the two hemispheres would inhibit each other, so that each can correctly process the signals it is specialized to process and thus balancing the two hemispheres. The results obtained with a patient who had suffered a unilateral insular stroke (the insula being part of the thermosensory cortex [5]) helped to disentangle the two alternatives and lent support to the latter [4].

Cooling judgments were diminished for contralateral nostril stimulation and strikingly increased for ipsilateral nostril stimuli. It was as if the lesion of one hemisphere released the other hemisphere from inhibition. The key mechanism at play would be thus reciprocal inhibition between systems processing the same signals (e.g., the system of the LH that preferentially processes cooling signals would inhibit its counterpart in the RH, and vice versa for warming signals) [21]. Both hemispheres would be co-activated for the purpose of nasal thermal judgments, and this co-activation of the two would ensure the judgments were balanced. However, reciprocal inhibition would determine which hemisphere is most involved in a given trial, depending on its specialization.

In addition to our previous neuropsychological study [4] the present study lends further support to the inhibition-balance account. The large number of subjects we tested allows for a more thorough investigation of the relationship between the left nostril’s dominance for warming responses and that of the right nostril for cooling responses. It was found that the stronger the dominance of the left nostril for warming responses, the stronger that of the right nostril for cooling responses. Conversely, a diminished dominance of the left nostril for warming coincided with a diminished dominance of the right for cooling. Furthermore, the point where the left-warming pattern inverses and becomes left-cooling is the same as the point where the right-cooling pattern inverses despite the absence of correlation between responses and between nostrils. Reciprocal inhibition between hemispheric mechanisms processing the same signals [21] may account for this balance since activation of the LH would reduce activation of the RH during warming responses and vice versa. It is interesting that the lateralized effects are not absolute but distributed over a continuum, although, despite this continuum, the number of subjects exhibiting the left-warming and right-cooling dominance was greater than that exhibiting other patterns. This may explain why this particular pattern was found in the present study as well as in our previous studies [2-4]. Taken together, the results suggest strong lateralization of one nasal thermal judgment coincides with strong lateralization of the other judgment, although the warming responses were preferentially associated with the left nostril whereas the cooling responses were preferentially associated with the right nostril.

4.2. Dampening the swings: achieving balance

How is this balance achieved? We have to take into account two different aspects of the present data. First, subjects are required to chose one of two mutually exclusive responses: warming or cooling. The choice of one over the other is unequivocal, and from existing literature it is likely that processing warm and cold depend on two separate pathways [6] giving rise to hemispheric differences [19,20] and nostril-temperature dissociations [2-4]. One mechanism should thus make it possible to select which hemispheric system should be activated. Second, the data presented here, and some neuropsychological evidence [4], show that the choice of one response over the other is clearly graduated, ranging from the expected to the opposite pattern. A second mechanism should thus fine-tune, in precise balance, the dichotomies of choice contributed by opponent hemispheric systems. It would be the interaction between these two mechanisms that shapes the response patterns. Our data are fully accounted for by Kinsbourne’s model of interhemispheric interactions in attention and cognition [21] which assumes that lower-level all-or-nothing reciprocal inhibition between the hemispheres determines which hemisphere would be most activated, and graduated higher-level fine-tuning dampens the swings between hemispheres. According to Kinsbourne, underlying these two mechanisms are different neural pathways, with reciprocal inhibition subserved subcortically and fine-tuning mediated by the corpus callosum. We can therefore speculate about the neural pathways involved in the lateralized color-induced nasal thermal sensations (the cognitive aspects have been developed elsewhere [3]) and, by extension, about putative lateralized pathways involved in thermosensory processing.
Thermoreceptive-specific neurons of the superficial spinal and trigeminal dorsal horn project to the posterior part of the ventral medial nucleus (VMpo) of the thalamus and reach the posterior insula [5,7,34,35] where lies the thermosensory cortex [5,9,20,31–34,36]. The thalamus and insula are thus to be considered the specific thermosensory processors. During unilateral innocuous thermal stimulation the thalamus exhibits bilateral activity [8,34], with stronger contralateral activity [34]. The insula mostly exhibits contralateral activity [8], which rises gradually as a function of stimulus intensity [34], as well as signs of hemispheric specialization [4,19,20]. Interestingly, when the insula is activated bilaterally, ipsilateral activity arises later than contralateral activity [36,37], which is consistent with the extra time needed for interhemispheric transmission. Like Kinsbourne [21], we propose that interhemispheric crosstalk between thalamic nuclei mediates reciprocal inhibition allowing for unequivocal selection between activating the left or right hemisphere for preferentially processing warmth and cold. There is evidence to show that communication among different nuclei of the thalamus is established by the thalamic reticular nucleus (TRN). The TRN is reciprocally connected to and regulates the activity of thalamic projection neurons by exerting inhibitory influences [38]. The TRN also projects to contralateral thalamic targets mainly within the TRN itself, giving rise to the thalamic commissural fiber system [39,40], a commissural pathway devoted to crosstalk between the thalami of the two sides and therefore a potential candidate for mediating selection between the left or right hemisphere. The suggestion is that activation of the reticular nucleus inhibits the ipsilateral VMpo nucleus and its cortical sensory targets, among which the insula. It would also inhibit the contralateral TRN, thereby releasing the contralateral VMpo nucleus from inhibition, which, in turn, would activate its cortical targets. Activating callosal connections between the insulae of each hemisphere [41], on the other hand, would tune the activity pattern and confer graduated processing along the cold-warm continuum. This hypothesis is presented in Fig. 4. Neuroimaging studies in humans and neurophysiological investigations in animals should help to confirm or invalidate this hypothesis.

4.3 Cyclic breathing and cerebral dominance

Nostril differences in olfactory processing are linked to the nasal cycle in a way that airflow would allow one nostril to detect the odor of some substances better and the other nostril to detect others better [1]. According to this suggestion, the nostrils are like false twins, at least as far as olfactory processing is concerned, and if they just smell different things, may be they also process temperatures differently. The nasal cycle determines the efficiency of breathing predominantly through right or left nostril in an alternate fashion during varying periods. That this cycle is regulated by both parasympathetic and sympathetic branches of the autonomic nervous system is interesting since it was suggested that the left insula is associated with parasympathetic functions, and the right insula with sympathetic functions [42]. In the 80s, it was found that the nasal cycle, a peripheral autonomic nervous function, correlates with dominance of cerebral hemispheric activity [43]. More precisely, relatively greater electrocortical activity in one hemisphere is tightly linked with airflow in the contralateral nostril. Furthermore, unilateral forced nostril breathing produces an increased activity in the contralateral hemisphere [44]. Do our data the balance pattern most precisely reflect such an alternation in cerebral dominance as captured through the investigation of responses in a large sample? Clearly, we have no means of responding directly to this question. However, some of our previous investigations may shed some light. First of all, lateralized color-temperature dominances were absent when the solutions-to-judge were not colored [2,3], and in one occasion they even shifted towards effort demanding conditions [3]. It is quite hard to admit that an ultradian rhythm in cerebral dominance can be evidenced only when color cues are present. One possibility is that, if such a phenomenon were involved and determined the response patterns, then only color cues allowed detecting its occurrence. This is why we believe that if colors influence thermal nasal judgments, they do it most probably by way of higher order processes. Another argument that runs counter the involvement of the nasal cycle and the related alternations in cerebral dominance is that the results from a previous study [3] showed no differences in performance as a function of the nasal cycle. Besides, even though we used a kind of forced nostril method (e.g., the experimenter designated the nostril to close during a trial), the forced unilateral nostril breathing was of a very short duration since it changed from one trial to the other (except in [2]), by contrast to the duration necessary to produce changes in the cerebral dominance (11–30 min). This minimizes the possibility that the cerebral dominance changed from one trial to the next. Indeed, 34 subjects out of the 40 tested in that particular experiment (85%) exhibited a stable nasal cycle throughout the whole test [3].

5. Conclusion

In answer to the question “Why do we have two nostrils?”, Sobel and colleagues [1] posited it is because they serve to smell different things altogether as a function of the nasal cycle. Work conducted in our laboratory [2–4] suggests that peripheral factors alone, such as the nasal cycle, cannot account for all differences between the two nostrils, and in particular lateralized color-induced nasal thermal judgments. It is our proposal that the two nostrils may convey signals to distinct specialized hemispheric processing systems that are activated on the basis of task-related expectancies. Mutually inhibitory and excitatory interactions between such independent systems would create a balance and help subjects choose the most plausible response, based on available cues from other sensory modalities (e.g., vision).

Acknowledgments

This study was supported by a DERMSCAN convention. Many thanks to Maud Brard, Sivgin Arda Dalkılık, Nina Maroglou and Pauline Rolihon for their help in collecting the data.
References