Incomplete Gustatory Lateralization as Shown by Analysis of Taste Discrimination After Callosotomy

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Abstract

■ The lateral organization of the gustatory pathway in man is incompletely understood. Majority of the studies support an uncrossed projection from each side of the tongue to the cortex, but reports of an opposite crossed organization continue to appear in the neurological literature. We studied the lateral organization of the gustatory pathway in normal controls, a man with a complete callosal agenesis, and a man with a complete section of the corpus callosum, a right anterior-frontal lesion, and language in the left hemisphere. Sapid solutions were applied to one or the other side of the tongue, and subjects reported the taste of the stimulus either verbally or by manually pointing to the name of the taste. There were no differences in accuracy and reaction time between the right and left hemitongues of the controls and the genetically acallosal observer. By contrast, the callosotomy subject showed a constant marked advantage of the left hemitongue over the right for both accuracy and speed of response, though performance with right stimuli was clearly above chance. The left advantage can be attributed to the left hemisphere being favored by the essentially verbal nature of the task, or to the presence of a lesion in cortical gustatory areas in the right hemisphere, or to both factors. Whichever of these hypotheses turns out to be correct, the results unequivocally reject the notion of an exclusively crossed organization of the gustatory pathway from the tongue to the cortex, and favor the notion of a bilaterally distributed organization of this pathway with a marked predominance of the uncrossed over the crossed component. ■

INTRODUCTION

Notions about the lateral organization of the gustatory pathway in man are still incomplete and controversial. The afferent gustatory fibers from each half of the tongue are known to travel via the VIIth and IXth cranial nerves to the ipsilateral nucleus of the solitary tract (NST). The latter nucleus projects to the parvocellular part of the ventroposteromedial nucleus of the thalamus (VPMpc), which in turn projects ipsilaterally to the primary gustatory cortex in the frontal operculum and anterior insula (Kobayakawa et al., 1996; Murayama et al., 1996; Ogawa, 1994; Norgren, 1990; Burton & Benjamin, 1971).

The unsolved question is whether the projection from the NST to the VPMpc is crossed or uncrossed. Following unilateral brain lesions, gustatory impairments such as ageusias, hypogeusias, or dysgeusias can be localized to one side of the tongue. In some cases, with small unilateral lesions in the brainstem, tests with the four basic tastes—bitter, salty, sour, and sweet—have revealed taste impairments in the hemitongue ipsilateral to the lesion, suggesting an uncrossed projection from the NST to the VPMpc (Uesaka, Nose, Ida, & Takagi, 1998; Shikama et al., 1996). The results from other cases with midbrain (Lee, Hwang, Rison, & Chang, 1998), pontine (Fujikane, Nakazawa, Ogasawara, Hirata, & Tsudo, 1998), or thalamic lesions (Combarros, Mirò, & Berciano, 1994) suggest instead that the projection from the NST to the VPMpc crosses between the lower brainstem and the thalamus. Ageusias or hypogeusias

of one hemitongue have also been observed in patients with unilateral cortical damage, again with contradictory indications as to whether the gustatory inputs from the tongue to the cortex are crossed or uncrossed. Börnstein (1940) reported deficits in taste recognition in the hemitongue contralateral to traumatic cortical lesions in the perirolandic area, whereas, in a much more extensive series, Motta (1958) and Motta (1959) found taste recognition impairments on the side of the tongue ipsilateral to extensive surgical hemidecortications, or tumors or infarcts of the frontal and parietal lobes. The hypothesis of an ipsilateral organization is supported by a case of dysgeusia ipsilateral to a temporal tumor (El-Deiry & McCabe, 1990), and by recent limited experience with electrical stimulation of the thalamus in conscious neurosurgical patients, whereby stimulation on one side was found to evoke gustatory hallucinations in the ipsilateral hemitongue (Lenz et al., 1997).

To our knowledge, the lateral organization of the gustatory pathway has not, so far, been studied in commissurotomy or callosotomy patients whose disconnected cerebral hemispheres process sensory information that are independent from one another. Owing to the crossed organization of the visual and somesthesic pathways, objects in the right visual hemifield or the right hand of these patients are seen and felt by the left hemisphere only; and conversely for the left hemifield and hand, and the right hemisphere (Gazzaniga, 1995;

Bogen, 1993; Sperry, 1982; Sperry, Gazzaniga, & Bogen, 1969). Odors restricted to the right or left nostrils, however, are processed in the hemisphere of the same side, revealing the uncrossed organization of the olfactory pathway (Gordon & Sperry, 1969). All these lateral relations between peripheral sensory organs and the cerebral hemispheres are demonstrated by the different kinds of outputs utilized by the two hemispheres for signaling their recognition of various sensory inputs. The left hemisphere can use language for this purpose, while the right hemisphere, being able to express its knowledge only through nonverbal behaviors, cannot (Gazzaniga, 1995; Bogen, 1993; Sperry, 1982; Sperry et al., 1969).

In this paper, we describe a study of a callosotomy patient with language in the left hemisphere who was tested for the recognition of basic taste stimuli applied to the right and left sides of the tongue. The starting assumption was that successful verbal recognition of stimuli applied to the left but not the right hemitongue would indicate an uncrossed organization of the gustatory pathway, whereas the converse result would point to a crossed organization. The results from the callosotomy patient are compared with the outcome of similar tests on neurally intact observers and a subject with a total agenesis of the corpus callosum who, like other cases of callosal agenesis (Lassonde & Jeeves, 1994; Jeeves, 1990), is known to

Table 1. Percentages of Correct Responses and Mean RTs for the Two Hemitongues

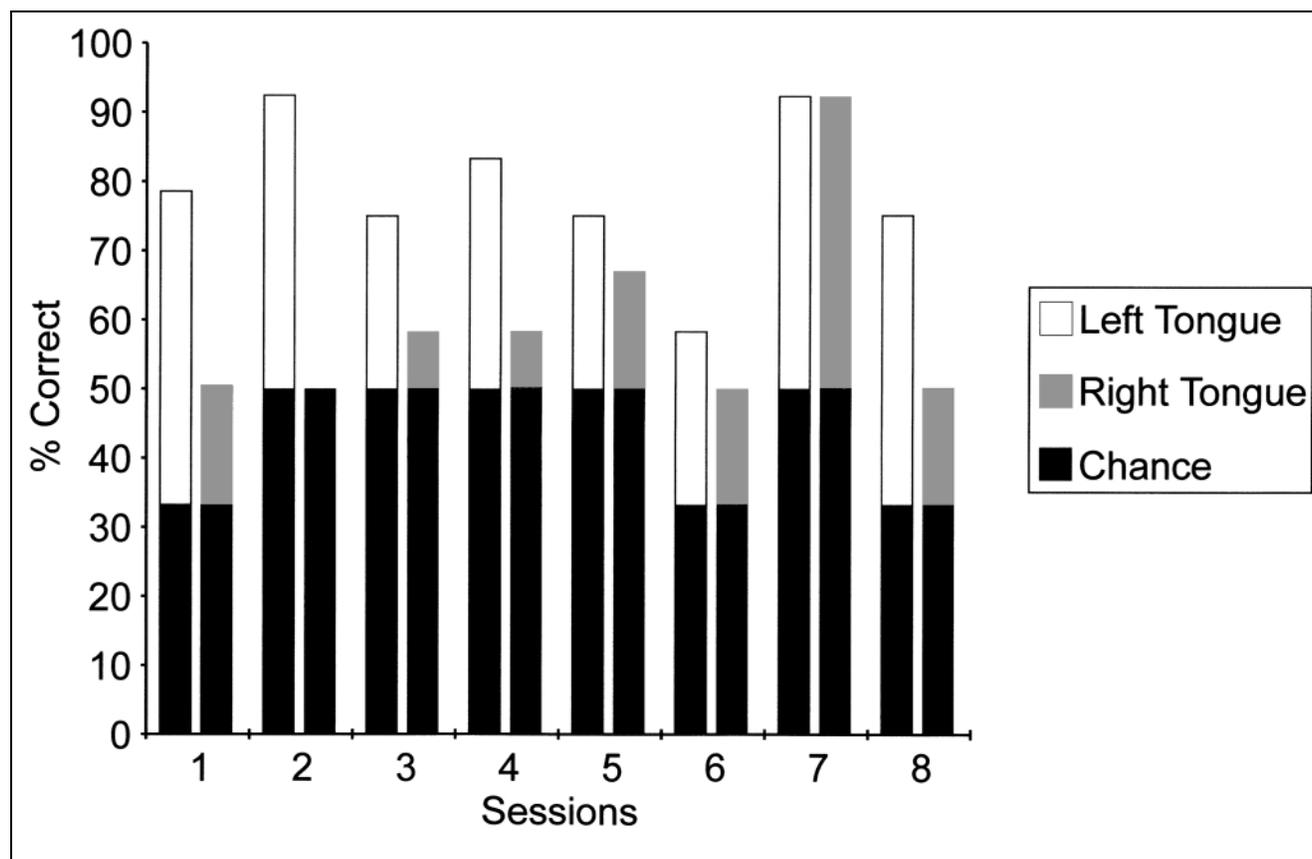|		L hemitongue	R hemitongue
Controls (one session per subject per task)			
Two taste discrimination (three subjects)	Verbal response	94.4% 2.9 sec	91.7% 2.9 sec
Three taste discrimination (three subjects)	Verbal response	88.9% 4.5 sec	83.3% 4.5 sec
Two taste discrimination (three subjects)	Pointing response	91.7% 3.6 sec	93.0% 4.7 sec
Three taste discrimination (one subject)	Pointing response	100% 3.0 sec	100% 2.6 sec
Patient R.B.			
Two taste discrimination	Verbal response	100% 2.3 sec	100% 2.1 sec
Three taste discrimination	Verbal response	91.7% 2.8 sec	91.7% 2.8 sec
Two taste discrimination	Pointing response	91.7% 4.9 sec	91.7% 5.3 sec
Three taste discrimination	Pointing response	91.7% 3.2 sec	91.7% 3.0 sec

show fewer and subtler signs of interhemispheric disconnection than callosotomy patients do (Forster & Corballis, 1998; Aglioti, Berlucchi, Pallini, Rossi, & Tassinari, 1993; Fiorentini, Berardi, Falsini, & Porciatti, 1992). While ruling out an exclusively crossed organization of the gustatory pathway, the results from the callosotomy patient are compatible with a bilateral, predominantly uncrossed organization of this pathway.

Part of the present results have been previously published in abstract form (Berlucchi, Tassinari, Aglioti, & Corballis, 1998a, Berlucchi, Tassinari, Aglioti, &, Corballis, 1998b).

RESULTS

A summary of the results from the controls and the acallosal subject, RB, presented in Table 1, with data collapsed across hands for pointing responses, shows that there were no marked and systematic differences between the right and the left hemitongues in both accuracy and reaction times (RTs). This was true in the controls as well as in R.B.

The results for the callosotomy subject, M.E., are presented in Figures 1 and 2. Figure 1 shows M.E.'s accuracy of performance in response to stimuli delivered to his right and left hemitongues. The six pairs of bars on the left refer to sessions with pointing responses, while the two pairs of bars on the right refer to the sessions with verbal responses. Each bar indicates the percentage of correct responses exceeding the percentage of successes expected on the basis of chance responding. It can be seen that in all sessions, performance was above chance for both hemitongues, except for session 2, in which performance with the right hemitongue was at chance. One sample t-tests run on the accuracy scores from the eight sessions showed that overall performance was above chance for both hemitongues (left hemitongue: $t(7)=12.2$, $p<.001$; right hemitongue: $t(7)=3.4$, $p=.01$). In all of the eight sessions, except one verbal response session, however, performance was better for the left hemitongue than for the right, and a paired t-test carried out on the means from all sessions showed that the difference was highly significant ($t(7)=4.0$, $p=.005$). There was no effect from the hand used for

Figure 1. Percentages of correct responses of the callosotomy subject, M.E., in eight experimental sessions, six of which (to the left) used pointing responses, and the other two used verbal responses. White=left hemitongue; gray=right hemitongue. The percentages of successes expected on the basis of chance responding are indicated in black for each session. The left–right ordering of the sessions in the figure corresponds to the temporal order in which they were run. The first two sessions were run on November 1, 1996, the third session was run on June 10, 1997, and the remaining sessions were run on June 11, 1997.
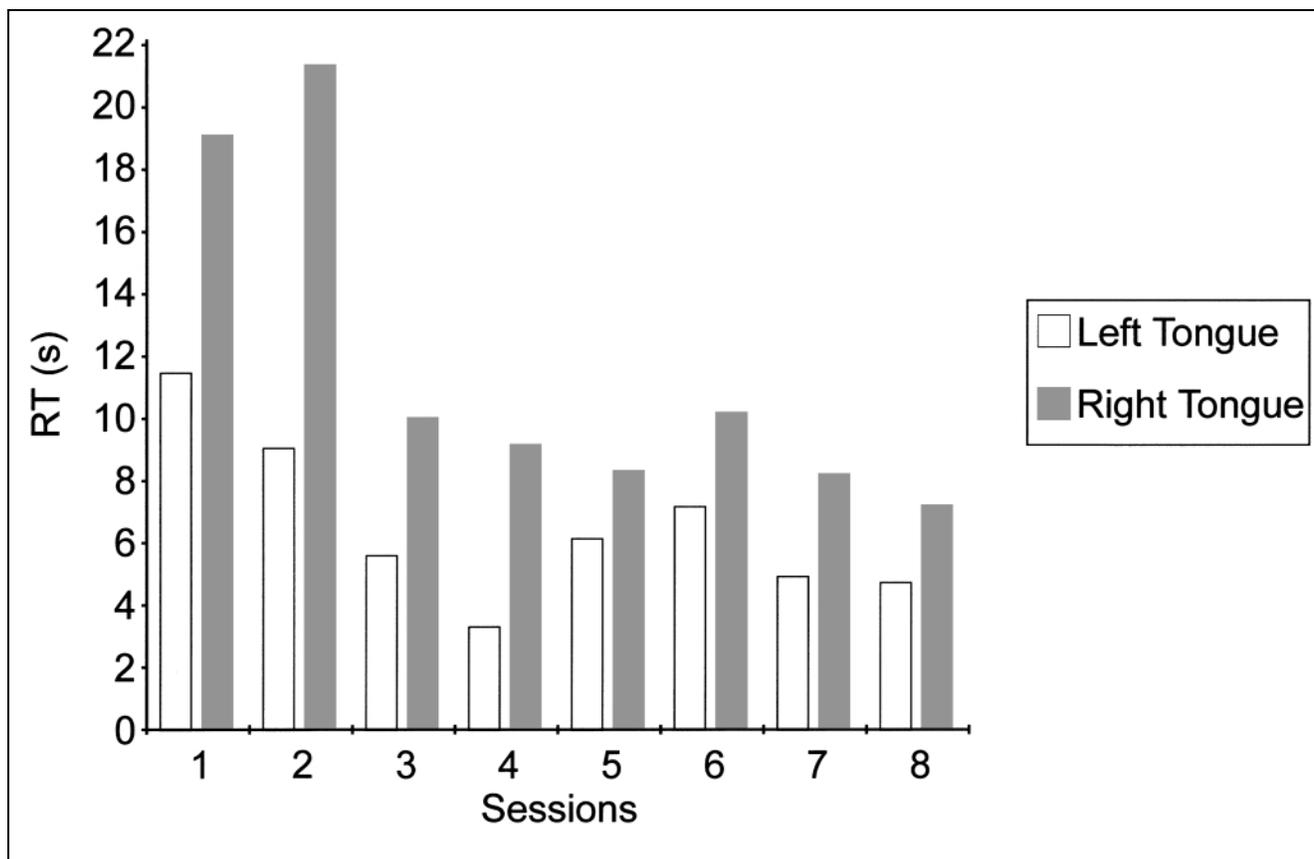
Figure 2. Reaction times of correct responses of the callosotomy subject, M.E., in the eight experimental sessions referred to in Figure 1. White bars=left hemitongue; gray bars=right hemitongue.

responding. Figure 2 shows RTs of correct responses to stimuli applied to the right and left hemitongues in sessions with pointing responses and sessions with verbal responses. A conspicuous advantage for the left hemitongue was present in all sessions, and highly significant in a paired t-test run on the mean RTs of each session ($t(7)=4.3$, $p=.004$), as well as in unpaired t-tests run on the available RTs of all correct responses in the six pointing sessions ($t(77)=3.7$, $p<.001$) and all correct responses in the two verbal sessions ($t(30)=2.5$, $p=.02$).

A few control experiments were run on M.E. to ascertain his ability to detect and recognize the side of tactile stimuli delivered to the two hemitongues. This was done by bringing two micropipettes simultaneously to the two margins of the tongue and by squirting tepid pure water from one of them, in such a way that the subject was unable to see on which side the stimulus was applied. Verbally, M.E. was consistently able to report the side of the tongue on which water was squirted. In the gustatory tests, he was also able to signal the absence of any stimulus on occasional blank trials in which the application of the sapid stimulus was feigned but not performed.

DISCUSSION

The results show that while the callosotomy subject, M.E., could recognize, at an above-chance level, lateralized gustatory stimuli from both the right and the left hemitongue, his performance was considerably better with left hemitongue stimuli than with right hemitongue stimuli, in terms of both accuracy and speed of response. This asymmetry was seen neither in neurally intact subjects nor in the genetically acallosal subject, R.B., confirming that R.B. can behave normally in at least some tests with lateralized sensory stimuli (Aglioti, Beltramello, Tassinari, & Berlucchi, 1998). The asymmetry between M.E.'s hemitongues in taste discrimination cannot be attributed to an attentional bias toward the tongue's left side, because attentional biases previously observed in visual and somesthetic tasks in this subject were all toward the right space, either personal or extrapersonal (Aglioti et al., 1998; Berlucchi, Aglioti, & Tassinari, 1997a). Preferential rightward attentional biases in visual tasks have been reported in other split brain studies (Marzi et al., 1997; Berlucchi, Gazzaniga, & Mangun, 1997b; Reuter-Lorenz, Nozawa, Gazzaniga, & Hughes, 1995; Proverbio, Zani, Gazzaniga, & Mangun, 1994). Incidentally, patients with unilateral left-visual and

tactile neglect from right-hemisphere lesions may show neglect for olfactory input from the left nostril as well, regardless of the fact that it projects to the intact left hemisphere (Bellas, Novelly, Eskenazy, & Wasserstein, 1988). This suggests that attentional biases tend to be spatially congruent in all sensory modalities, independent of the lateral organization of their cortical representation.

The results do not provide an unequivocal answer to the question of whether the gustatory pathways from the tongue to the cortex are crossed or uncrossed. We assumed that all types of responses employed in this study were based on linguistic abilities, since reading was required for pointing responses, and speech was required for naming responses. If, as suggested from previous studies (Aglioti et al., 1998), M.E.'s left hemisphere is totally responsible for these linguistic activities and, therefore, for his performance in the present task, his above-chance recognition of right and left stimuli implies that the left hemisphere was ultimately able to receive and process gustatory information from both hemitongues. The right anterior-temporal lobe has been implicated in the recognition of fine taste qualities (Small, Jones-Gotman, Zatorre, Petrides, & Evans, 1997), but the gross taste discriminations employed here should be within the capacity limits of the left hemisphere.

The advantage for the left hemitongue over the right can be accounted for in two ways. A possibility is that the gustatory pathways are entirely uncrossed and efficient interhemispheric transfer of taste information is normally ensured by the corpus callosum. M.E.'s reduced accuracy in processing taste stimuli to the right hemitongue would, thus, depend on a rather inefficient interhemispheric transfer to the left hemisphere, via an extracallosal pathway or through cross cuing. These possibilities for indirect interhemispheric communication have been invoked to account for M.E.'s limited ability to name objects presented in the left visual hemifield (Lauro-Grotto, Tassinari, & Shallice, in preparation). Processing of taste information by M.E.'s right hemisphere may also be defective due to its anterior-frontal lesion that encroaches on the primary cortical-gustatory area in the frontal operculum as well as on the caudolateral-orbitofrontal cortex, a secondary cortical taste area (Rolls & Baylis, 1994). Either of the above factors, or both of them, can also account for the latency to right side stimuli being considerably longer than that to left side stimuli. The anterior commissure, which is intact in M.E., is a likely candidate for providing the major route for the extracallosal interhemispheric transfer of gustatory information. Utilization of cross-cuing strategies (Gazzaniga, 1970) by M.E. is suggested by the fact that the left hemitongue advantage decreased in the verbal response sessions that were run last, after M.E. had achieved considerable experience with the task.

The other possibility is that there are both crossed and uncrossed gustatory pathways, and that the left hemitongue advantage in M.E. reflects an anatomo-functional predominance of the uncrossed over the crossed pathway, which, in neurally intact subjects, would normally be masked by the equalizing action of the corpus callosum. If this is the case, the left side advantage in M.E. would simply reflect the difference in strength of the signals reaching the left hemisphere via the uncrossed and crossed projections.

The two tentative explanations outlined above allow a firm conclusion insofar as they agree in rejecting the possibility of an exclusively crossed organization of the gustatory pathway as originally proposed by Börnstein (1940), and subsequently reiterated by other authors (Fujikane et al., 1998; Lee et al., 1998; Combarros et al., 1994). The possibility of a purely crossed organization is also indirectly contradicted by electrophysiological findings in monkeys, which support an ipsilateral representation of lingual taste receptors in the thalamus (and presumably in the cortex), as opposed to a bilateral thalamic representation of mechanical and thermal receptors of the tongue. Gustatory receptive fields of thalamic neurons appear indeed to be mostly confined to the ipsilateral hemitongue (Pritchard, Hamilton, & Norgren, 1989), in contrast with tactile lingual receptive fields of thalamic neurons, which are located on both ipsilateral and contralateral hemitongue, or extend bilaterally across the tongue midline (Jones, Schark, & Callahan, 1986). Mechanoreceptive fields with a similar spatial distribution on the tongue have been observed for a few single neurons in the human thalamus (Lenz et al., 1988), and the present evidence of a good verbal localization by M.E. of mechanical stimuli to the two hemitongues is also in agreement with a bilateral representation of lingual mechanoceptors. Finally, as mentioned in the Introduction, electrical stimulation of the thalamic taste relay in awake patients has recently been reported to evoke gustatory hallucinations in the ipsilateral hemitongue (Lenz et al., 1997).

Granted that the present data, taken together with other evidence, tend to favor an uncrossed organization, and to rule out a purely crossed organization of the gustatory pathways, it must be conceded that they do not exclude the existence of some crossed gustatory projections, along with more massive uncrossed projections, to each hemisphere. A bilateral organization of the gustatory pathways, with the ipsilateral projections largely outnumbering the contralateral projections, has been demonstrated in the rat brainstem (Williams, Murphy, Reynolds, Welch, & King, 1996). More definite conclusions than can be arrived at on the basis of a single case will of course be made possible by similar studies of lateralized taste discrimination in other callosotomy patients. If the hypothesis of the existence of both uncrossed and crossed gustatory projections is

supported, perhaps there may be an interindividual variability in the relative magnitude of the two components. This variability might account for the still unexplained discrepancies between studies that favor the uncrossed organization and those that support the crossed organization of the gustatory pathways.

METHODS

Subjects

Details of the callosotomy subject, M.E., and the callosal agenesis subject, R.B., have been provided in previous papers (Berlucchi et al., 1997a; Tassinari, Aglioti, Pallini, Berlucchi, & Rossi, 1994; Aglioti et al., 1993, Aglioti et al., 1998). The following description is limited to the essentials.

M.E., a male born in 1970, was submitted to a two-stage complete callosotomy in 1989 in an attempt to control drug-refractory daily complex partial seizures with secondary generalization. His epileptic condition had started in 1981, 3 years after a head trauma had required a removal of a right frontal-subdural hematoma and a partial-right frontal polectomy. The two stages of callosotomy were performed at a distance of 6 months by Prof. G. F. Rossi at the Neurosurgical Institute of the Catholic University in Rome, and the completeness of the callosal section and the integrity of the anterior commissure have been demonstrated by magnetic resonance imaging (MRI). MRI has also revealed a large defect in right prefrontal cortex, sparing most of the premotor cortex, the primary motor cortex, the basal ganglia, and the internal capsule, as well as a smaller lesion on the orbital aspect of the left frontal lobe with some undercutting of the lateral cortex of the frontal pole, presumably attributable to the old trauma. On the left side, the primary gustatory cortical areas in the frontal operculum and anterior insula appear intact, whereas on the right side the frontal lesion encroaches upon the frontal operculum but spares the insula. The completion of the callosal section, supplemented by pharmacological treatment with phenobarbital and phenytoin, has led to a marked favorable improvement in severity and frequency of the seizures. The patient, who is right-handed (Laterality Index = +16 according to Briggs & Nebes, 1975), shows typical signs of interhemispheric disconnection in vision, somesthesis, and praxic control, and there is definite evidence that language functions are lateralized to his left hemisphere (Aglioti et al., 1998). The tests reported in this study were performed in 1996 and 1997.

R.B., a male born in 1976, was diagnosed in March 1988 as congenitally lacking the corpus callosum and having a dilatation of the posterior portions of the lateral ventricles on the basis of an MRI examination. He is left-handed, and his intelligence is within normal limits, as shown by his successful graduation from a

technical high school. No clear manifestations of interhemispheric disconnection have been revealed by standard neurological examinations, though special experimental tests have borne out an abnormally slow interhemispheric visuomotor transfer in simple reaction time tasks (Forster & Corballis, 1998; Aglioti et al., 1993) and other subtle signs of defective interhemispheric visual communication (Fiorentini et al., 1992). Testing was carried out in July and October 1998.
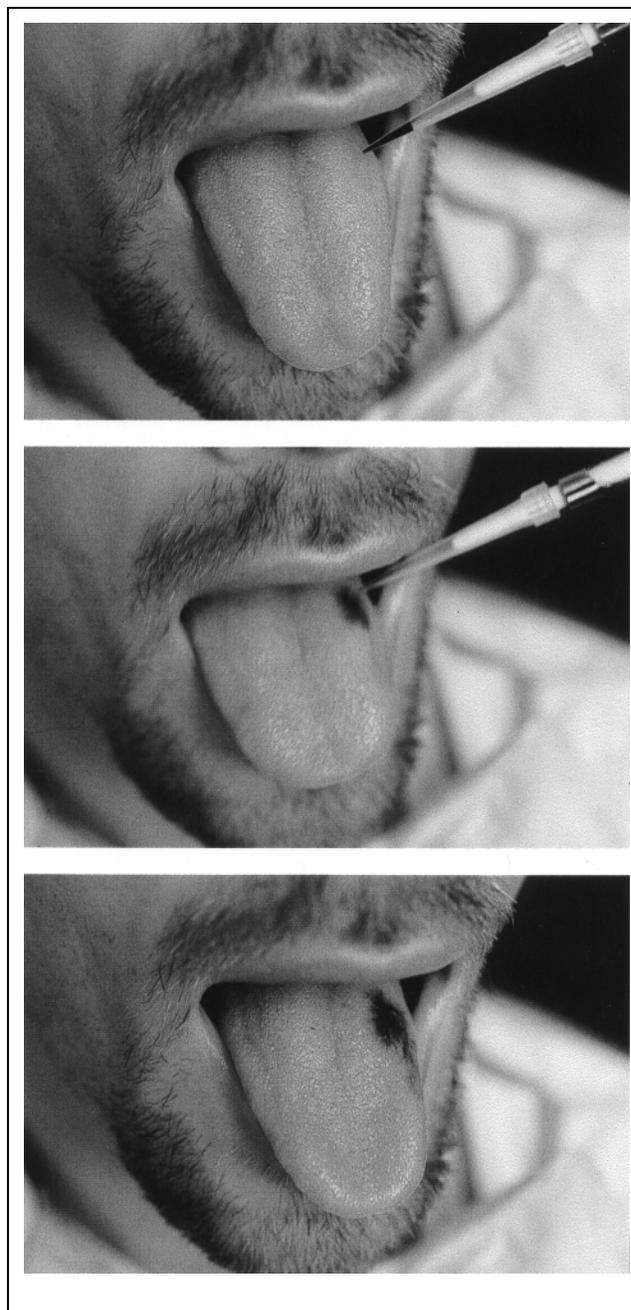
Figure 3. Photographs taken just before the ejection of methylene blue on the tongue (top), just after (middle) and about 1 min after the ejection (bottom).

Neurally intact control subjects were five males, ranging in age from 22 to 41 years. All subjects, either acallosals or controls, were non-smokers.

Procedure

Gustatory stimulation was performed by ejecting from a fixed-volume micropipette a 50-µl volume of a sapid solution on the right or left dorsal margins of the maximally protruded tongue in front of the foliate papillae. Four solutions were initially tested: .1 M citric acid for sour taste, 1 M fructose for sweet taste, 1 M NaCl for salty taste, .001 M quinine hydrochlorate for bitter taste. These concentrations are well above threshold for taste recognition when applied to the whole tongue. However, since it was realized early in the course of the study that a sweet sensation was very rarely evoked in all subjects by the fructose solution, the results reported here were obtained in discrimination tasks using the other three stimuli, or only the salty and sour stimuli. The diffusion on the tongue dorsum of the applied volume was preliminarily evaluated by squirting an equal amount of a methylene blue solution of similar concentration on the same location on the tongue margin. Photographs of the spatial spread of the dye taken at different intervals from the application showed that in spite of some diffusion, the ejected volume remained fully lateralized to the application side (Figure 3). An experimental session included 24 trials, and the intrasession order of taste stimuli and side of stimulation was randomized with the constraint that the number of presentations was the same for all taste stimuli, and each hemitongue received the same number of each of the taste stimuli employed in that session. Cards bearing the names of all stimuli employed in any particular session were attached to a panel in front of the subject, who was supposed to identify each stimulus by pointing to the card corresponding to it. The right/left or up/down positions of the cards were randomized from session to session, and pointing was performed by aiming at the chosen card a light beam from a microtorch tied to the right or left index finger. In other sessions, subjects were simply asked to name the stimulus. A forced response paradigm was adopted throughout. The subjects were instructed not to retract the tongue until after performing the response, either manual or verbal, to the sapid stimulus, and to rinse their mouth with pure water following each response. Accuracy, rather than speed of response, was encouraged, but approximate measurements of RTs were obtained by starting a stopwatch at the moment of the delivery of the sapid stimulus, and stopping it when a pointing or verbal response was produced. All sessions were video- and audiorecorded for data analysis.

Notes

After the present paper was accepted for publication, two relevant studies appeared which reiterate the controversy about the laterality of the gustatory pathways. Onoda & Ikeda's study in patients with unilateral brain damage suggests that the gustatory pathway ascends ipsilaterally from the medulla oblongata to the pons and then crosses to the contralateral midbrain, thalamus and cortex. By contrast, Pritchard, Macaluso, & Eslinger found that damage to the right rostrodorsal insula produced deficits in taste sensitivity and recognition in the right hemitongue, whereas damage to the left rostrodorsal insula impaired taste sensitivity on the left hemitongue and taste recognition in both hemitongues. Our data in callosotomy patient ME are compatible with Pritchard et al.'s claim that the predominant organization of the gustatory pathway is ipsilateral, with the left hemisphere processing information from both sides of the tongue because of an information transfer from the right hemisphere to the left hemisphere. While Pritchard et al. suggest that the transfer occurs through the corpus callosum, our present findings are compatible with an extracallosal transfer as well.

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