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LATERALIZATION OF OLFACTORY PERCEPTION IN THE SURGICALLY SEPARATED HEMISPHERES OF MAN

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Abstract—Five right-handed human subjects in whom the cerebral hemispheres had been surgically deconnected for alleviation of severe epileptic seizures were examined for lateralization of olfaction. As with vision and stereognosis, it was found that olfactory perception may be confined to a single hemisphere when the input is restricted to one side (i.e. to a single nostril). The fact that odors were recognized only in the hemisphere ipsilateral to the nostril stimulated was evidenced by the subject's ability to name odors from the left but not from the right nostril. Non-verbal tests demonstrated perceptual recognition of the right nostril odors in the non-speaking (right) hemisphere. The results were further substantiated in tasks that involved cross-modal olfacto-tactual matchings. Responses were successful when both the tactual and olfactory stimuli projected to the same hemisphere but not if they projected to opposite hemisphere.

INTRODUCTION

When cross communication between right and left hemispheres of the mammalian brain is disrupted by surgical section of the corpus callosum and other forebrain commissures, the two disconnected hemispheres tend thereafter to function independently in most mental activities [1]. This bisection of the normally unified stream of conscious awareness into two separate gnostic realms has been strikingly confirmed in recent years in studies on human patients in whom the forebrain commissures were sectioned by P. J. Vogel for control of severe epileptic convulsions [2]. In postsurgical studies these patients were found to respond as if each of the disengaged hemispheres had its own separate sphere of mental awareness, i.e. its own private sensations, percepts, images, concepts, memories, volitional and related mental experiences [3–8]. With appropriate tests the mental performances of each hemisphere could be shown to be dissociated or cut off from the corresponding activities and conscious awareness of the other hemisphere.

If the commissurotomized subject is engaged in behavior in which the activity in both hemispheres is similar or identical, the presence of the split-brain effect is difficult or impossible to demonstrate. Study of the mental properties of the separated hemispheres and analysis of their functional interrelations depends upon finding cerebral activities that can be lateralized to one or the other hemisphere. This may be accomplished by restricting specific sensory information to a single hemisphere, or by utilizing a preexistent asymmetry of cerebral capacity like that of language in man. In the past we have relied mainly on

stereognosis involving the right and left extremities, vision in the right and left visual halffields, auditory input to right and left ears [9], together with speech and writing. Many other functions are excluded because of bilateral representation, as for example tactile sensibility about face and head. Although an object touching one side of the face has been presumed to arouse a double set of sensations in the divided brain [10], the duality cannot

The aim of the present study was to investigate olfactory perception in the same group of commissurotomy patients to determine whether olfaction might not be added to those functions that can be lateralized to one hemisphere and hence be used in split-brain analyses of cerebral activity. Specifically the plan was to test separately the olfactory sensations from right and left nostrils to find out if a right-left separation of sensation and a doubling in olfactory perception might be demonstrated comparable to that already shown for the right and left hands and the right and left half-fields of vision. Since olfactory innervation of right and left nostrils is anatomically separate [11], and since all olfactory fibers of the anterior commissure had been sectioned in these patients (along with those of the corpus callosum and hippocampal commissures), it seemed likely that an odor presented to one nostril might be perceived in the homolateral hemisphere only. If so, one would predict that the same odor could not be remembered if sensed through the other nostril. Similarly left-nostril odors could be expected to be described in speech and writing whereas perception of right-nostril odors could be signified only through nonverbal responses. These and other indications of the dual nature of olfactory gnosis are exactly what has been found, along with an interesting lateralization in emotional responses to the olfactory sensations.

SUBJECTS AND PROCEDURE

The subjects were 5 patients of Drs. P. J. Vogel and J. E. Bogen, all of whom had undergone surgical section of the forebrain commissures for control of intractable epilepsy. The present test for olfaction were administered from October, 1967 to April, 1968 which was from 3 months to 5 years after the surgery in different cases as follows: M. K., 3 months: N. W., 10 months; C. C., 2-5 years; A. A., 4 years; N. G., 5 years. In all these patients, complete section of the corpus callosum and anterior commissure was visualized at the time of surgery and the small hippocampal commissure or psalterium that closely underlies the corpus callosum is presumed to have been divided along with the latter. Additional aspects of the individual case histories are mentioned below in context insofar as they seem relevant to differences in the test data.

The olfactory stimuli were contained one each in a series of uniform glass vials 0.5 inch in diameter and 2 inches high with plastic screw caps. The vials and caps were spray-painted uniformly and labeled. They were presented in such a way as to be indistinguishable by vision except to the examiner. Each odor was paired with an object that could easily be associated with that odor. The objects were roughly equated for size, temperature, and manipulation sounds, and were all small enough to be grasped easily in the hand.

The odors were presented by passing the open vial quickly under the subject's nose with instructions to sniff once gently. A fan was used in the majority of tests, and other precautions were taken to eliminate lingering odors in the air, on the vials, on the examiner's hands, etc. A minimum of 30 sec was allowed between trials with additional rest periods to minimize adaptation and interference. In preliminary trials with both nostrils clear, the subject was asked to identify by name a series of 8-13 scents presented one at a time. If at first the subject could not identify at least five of these smells, he was allowed to choose

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Odors	Objects for visual and tactual association			
Lemon extract Pincapple extract Banana extract Tomato juice Apple juice Peanut butter Coffee grounds Tobacco Arpege perfume Aftershave lotion Mint extract Fish oil Hydrogen sulfide Butyric acid Garlic Mentholatum Water	Plastic lemon Plastic pineapple Plastic banana Plastic tomato Plastic apple Peanut Small coffee cup Pipe Perfume bottle Safety razor Peppermint stick (glass) Carved fish Discolored hen egg made of plaster Triangular package simulating wedge of cheese Clove of garlic Tube of mentholatum No object			

his answer from the associated objects placed in free vision. Once he was able to recognize the smells he was again required to name the smells (still with both nostrils clear) without the help of the objects.

A battery of 5-8 odors plus a vial of water were selected from among those the subject could recognize and name correctly. The scents were then presented in a random sequence alternating every one to three trials to S's right or left nostril. The non-smelling nostril was pinched firmly shut with a finger or a bent spatula-shaped plastic rod held by the examiner. As each odor was presented the S was instructed to sniff once gently and make the required response. The sets of odors varied from S to S as well as from session to session with the

After a sequence of trials like the foregoing that involved naming the odors presented to the right and left nostrils, another similar sequence was run in which the S was instructed to remain silent but to respond by pointing with one or the other hand to one of the associated objects that were lined up in front of him in free sight. At this point the water vial was removed and the subject was advised that there was an object corresponding to each of the smells. He was instructed to make a guess even though in some cases he might not have thought he had smelled anything. After the pointing tests further naming tests were again carried out if time permitted. At no time during any of the naming tests could the Ss see the associated objects.

Finally, trials were run in which the subject was required to find only by tactual palpation with left or right hand the associated objects corresponding to the odors presented to the left or right nostrils. All nostril-hand combinations were tested.

The data from the above trial methods were taken from several test sessions since the number of trials that could be run in a single session was limited. The preliminary tests preceded each test session and any differences in physical condition (e.g. nasal congestion, fatigue) were noted.

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RESULTS

Verbal naming for left and right nostrils

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All 5 subjects showed a normal ability to name odors presented to the left nostril. This is sharply contrasted to the failure to name the same odors presented to the right nostril. Typically, near perfect scores were obtained any time the odors were presented to the left nostril, whereas the verbal responses to right nostril smells showed little or no correlation with what actually had been presented. In fact, M. K. and N. W. seemed hardly aware that any odor was present in the right nostril, to judge from their vocal responses (that speak for the left hemisphere only). The greater percentage of their answers were either "water" or a denial that they had smelled anything. The other subjects occasionally answered "water" or merely guessed at what the odor might be. At times the guesses were wild, and included odors never introduced into the series. Three of the patients (M. K., C. C., N. W.) consistently failed to name odors sensed through the right nostril, performing purely at the chance level (p>0.05) (Table 2). In the other two cases, however, early scores for the right nostril were at a level somewhat better than that expected by chance. This occurrence suggested that these two subjects were either able to recognize and name smells in their right nostril, or else the odors were able to cross peripherally in the nasal passages to the left nostril.

The testing procedure was accordingly changed somewhat to further extend precautions against possible crossing of odors in the posterior nasal passages. In this revised procedure the active nostril was also pinched shut immediately after presentation of the stimulus and was kept shut until after the subject had made his response. It was hoped that this would reduce turbulence in the posterior passages and thus help to eliminate possible leakage of the stimulus to the wrong nostril. It may be seen that under these conditions the right-sided verbal performance promptly fell to a chance level in A.A. and to near chance level for N. G. The left nostril performance, on the other hand, remained unimpaired in both patients with the altered testing procedure.

Three subjects, C. C., A. A. and N. G. appeared able in their verbal reports to distinguish water from most of the odors presented to the right nostril, suggesting awareness in the left hemisphere of the presence or absence of an olfactory response in the right hemisphere. In contrast, the two other cases (M. K. and N. W.) were not able to choose between water and the other odors presented to the right nostril. These latter two subjects were the most recently operated, whereas the two subjects, N. G. and A. A., who required a special technique to minimize spread of the olfactory vapors, had been operated more than 3 years previously.

Pointing to objects for right nostril odors

For odors presented to the right nostril which the patients were unable to name, it remained to be shown whether or not these right side stimuli were in fact being perceived and identified. Accordingly, further tests were applied that utilized manual rather than verbal readout. The subject was instructed to identify the right nostril stimuli by pointing to the correct one of the associated objects that were lined up in front of him in free view. It was clear that 4 of the 5 subjects were readily able to perform the test with few mistakes. At times the subjects were questioned about their responses after a choice had been made. Verbally they would express uncertainty as to the reasons for their answers and explained that the choice had only been a guess. When, on occasion, the examiner reassured a subject

<0.028 < 10-6 < 10-6 <10-6 N.S. <10-4 < 10-5 < 10-8 < 10-4 < 10-8 <10-7 <10-5 *ď \$-01 \ \$-01 \ \$-01 \ \$-01 \ Prob. for 1 trial Pointing Right nostril 1/5 1/6 1/8 1/5 1/5 Total number correct 34 20 20 20 18 No data . . No data . . . 20 20 18 31 No data 28 21 Total number trials Table 2. Naming and pointing responses to five or more olfactory stimuli presented 20 88=4 N.S.‡ 0.019 N.S.‡ 0.0044 0.0044 N.S. N.S. N.S. N.S. 0.025
 10-3
 10-3
 N.S.
 0.031
 N.S.
 N.S.
 N.S. Z Z S.S. <0.021 10⁻³ 10⁻³ *ď Z Z Z Z S. S. S. Prob. for 1 trial Right nostril 1/7 1/7 1/9 1/6 1/6 Verbal Total number correct Total number trials 8 15 10 ដូន 12 12 10 10 < 10-8 < 10⁻⁸ < 0.021 A 10-8 A 10-4 A 10-4 * 10 10 E Prob. for 1 trial Verbal Left nostril 1/6 1/8 1/8 1/8 1/8 1/6 1/6 1/7 1/7 Total number correct 7 4 91 8 $\omega \propto c \propto$ 31 23 20 13 18 No data . 20 20 Total number trials 22 20 20 15 9 7 Day 58 55† 64 77 84 22722 M.K. ×. C, S Z.G.

†The new method of presentation as described in text is used here.

†Nasal congestion.

* $P = \sum_{n}^{(N)} p^{n}q^{N-n}$ (N.S.=Not significant).

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that his series of responses had been mostly correct, he expressed surprise that his "guesses" should have been so accurate. It was thus evident that the subjects could not only identify manually the right nostril odors that they could not name but also that the speaking (left) hemisphere remained wholly unaware of the discriminatory experiences involved and that these were presumably confined to the mute (right) hemisphere.

The left hemisphere's lack of knowledge of the smells perceived in the right nostril was further exhibited in instances like the following that occurred in a session with N. W. about I year after the operation. During the pointing test when the stimulus vial containing coffee was presented to the right nostril, the speech hemisphere "forgot" to keep silent and gave the response "water". Simultaneously, the left hand immediately reached out toward the coffee cup. She then apologized for speaking the answer aloud but reminded the examiner he had earlier told her to say "water" whenever she did not smell anything. When asked about her left hand response to the coffee cup, she replied that she had simply let the hand go where it wanted, adding the comment that sometimes it seemed to "have a mind of its own".

When allowed to give verbal responses coincidentally with manual pointing, the subjects could then name correctly the odors presented to the right nostril. However, further testing showed that this occurred only under conditions where the eyes, or hand and eyes had first centered on the appropriate target. The object that was named aloud was always the same as that pointed to, correct or incorrect. It appeared that once the right hemisphere had perceived an odor and identified by vision the corresponding object, this fix on the proper target was transmitted automatically by various forms of feedback to the opposite hemisphere through centering movements involving the eyes, hand, and head, or through the general orienting response. Whereupon the speaking hemisphere merely named the target object which it found itself centered on. This kind of cross-cuing is used by commissurotomized subjects extensively in many situations. Actual overt movement toward the target is not always needed [12].

The patient that failed to perform on this test (M.K.) had been operated only 3-5 months previously. She was observed to have had an exceptionally thick corpus callosum at the time of surgery and she had had an enlarged right ventricle from age 8. Since she dragged the left leg in walking and had numerous head scars from previous seizures, it is not unlikely that there was appreciable right hemispheric brain damage. She pointed readily to associated objects when odors were presented to the left nostril. In trials with the right nostril, however, she insisted she smelled nothing. She claimed she must have a cold on that side, but no signs of nasal congestion were evident. Although she was strongly encouraged to allow her left hand to make a guess on its own, she constantly protested that it was senseless since she did not smell anything at all. On one occasion near the final day of testing, she began to respond with her hand and pointed to the correct one of six objects 10 times in the first 20 trials (p < 0.0026). In further testing on the same day and in a later session, however, her performances failed to rise above chance and the protestations increased.

Tactual retrieval of associated objects

Identification of objects by manual stereognosis with vision excluded is lateralized in these patients as a rule, to the contralateral hemisphere. Hence, a right-left difference in the ability to retrieve by touch alone the correct objects for different odors would give further information regarding the lateralization of olfaction. This type of test proved to be feasible in two of the subjects (N.W. and N.G.) that were available for testing at this stage

of the study. Both N.W. and N.G. performed above chance when the primary tactual information from the associated object was projected to the same hemisphere as the primary olfactory (e.g. the left nostril—right hand combination). Conversely, in the "crossed" condition where the primary projections of each modality arrived in opposite hemispheres, the scores remained at the chance level.

Occasionally, however, scores obtained with the ipsilateral nostril-hand combinations were found to be better than those expected for chance on the 5% level of significance (Table 3), as if the olfactory information were being perceived by the contralateral hemisphere or the tactual information by the ipsilateral hemisphere, or both. In an attempt to

Table 3. Olfactory cues with tactual retrieval

Subject	Day	Condition*	Total number of trials	Total number of correct trials	Probability for one trial	Probability of observed results
N.G.	1	RN-LH RN-RH	12 13	7 6	1/6 1/6	<0.0013 <0.0130
	2	RN-LH RN-RH LN-LH LN-RH	20 10 20 10	11 2 7 8	1/6 1/6 1/6 1/6	<10 ⁻⁴ >0.2907 <0.0258 <10 ⁻⁴
	3	RN-LH RN-RH LN-LH LN-RH	14 24 24 11	7 5 7 10	1/6 1/6 1/6 1/6	<0.005 >0.58 >0.09 <10-6
	4	RN-LH RN-RH LN-LH LN-RH	20 41 20 20	10 16 2 14	1/5 1/5 1/5 1/5	<0.0023 <0.004 >0.938 <10 ⁻⁵
N.W.	İ	RN-LH RN-RH LN-LH LN-RH	13 6 8 6	5 1 1 5	1/6 1/6 1/6 1/6	>0.05 >0.665 >0.767 <10 ⁻³
	2	RN-RH LN-RH	21 13	8 9	1/7 1/7	<0.0062 <10-4
	3	RN-LH LN-LH LN-RH	24 15 6	13 6 3	1/7 1/7 1/7	<10 ⁻⁵ <0.014<0.042
	4	LN-LH	11	5	1/6	< 0.025
	5	RN-LH RN-RH	15 15	11 3	1/5 1/5	<10 ⁻⁴ >0.601
	6	RN-RH LN-RH	20 8	6 8	1/5 1/5	>0.001 >0.19 <10-5
	7	RN-LH LN-LH	17 36	12 7	1/6 1/6	<10 ⁻⁵ >0.39

^{*}RN-LH: Right nostril, left hand; RN-RH: right nostril, right hand, etc.

check ipsilateral tactual pathways, a new series of objects, similar to the associated smell objects, were presented to the subject's left hand, out of sight for naming. It was found that in one subject, N.W., correct verbal responses above the 5% level of significance were recorded, but only when the subject had extensive pretrial and tactual familiarization. At no

time could novel objects be named nor could right nostril smells be identified. The other subject, N.G., could not verbalize the names of any object, novel or familiar, in the left hand. However, unlike N.W., N.G.'s scores for right nostril naming were close to 5% level of significance. Apparently N.W. was making use of tactual cues while N.G. seemed to have bilateral access to olfactory information.

In further checks on N.G. she was asked to decide mentally on a particular odor and its associated object without mentioning her choice to the examiner. She was then told to search out the given object by blind palpation with the left hand. When asked what object she had chosen and picked up, her verbal accounts failed to agree with the actual objects chosen by the left hand. This indicated that her correct left hand choices must have been guided by the minor (right) hemisphere, suggesting again that the olfactory information presented to the left nostril had reached the minor hemisphere in these exceptional trials in N.G.

Emotional and related responses

Some of the less pleasant test odors (e.g. H₂S, garlic, fish, etc.) commonly caused immediate reflex-like aversive responses that included wincing, head-withdrawal, facial grimaces and verbal exclamations like "ugh", "yuk", "phew", etc. For example, when fish was used in the battery of smells during a session with N.W. she consistently winced and said "yuk", distinguishing this smell from all others verbally and with either nostril. When reactions of this sort were evoked in the subjects through stimulation of the left nostril, the subsequent verbal identification of the stimulus was generally correct. When such responses were evoked through the right nostril, verbal identification was restricted, as a rule, to the extent of selecting an unpleasant odor. Discrimination between different unpleasant odors within a given series, however, was not significantly above chance. The left hemisphere, in other words, received information about the general affective property of the olfactory gnosis on the opposite side but the more specific olfactory information remained confined to the right hemisphere.

The simple exclamations and reflective grunts involved in the aversive responses could probably be prompted from either the major or minor hemisphere. The peripheral components of the response (shuddering, etc.) preceded any verbal description and would appear to have been sufficient in themselves, without any brain stem crossing, to cue in the major hemisphere regarding the general nature and intensity of the minor hemisphere sensation. Whether there may in addition have been some direct central nervous crossing of the unpleasant olfactory sensations was difficult to assess as long as the strong peripheral signals were also present.

In one session N.W. was asked by the examiner to try to refrain from making any overt responses to the distasteful or other stimuli. After a few trials no further shudders or exclamations were noted and a response of "water" was usually given for fish or garlic in the right nostril. Even after the left hand (minor hemisphere) had correctly selected the fish in the manual pointing test with free vision, N.W. remained outwardly unperturbed that she had experienced the displeasing odor.

R.Y., another commissurotomy patient (not included in the above categories because of his inability to detect at best any but the strongest odors) winced and withdrew his head on a number of occasions when garlic or H₂S were presented to either nostril. Nevertheless, in the case of the right nostril he reported "water" because he "couldn't smell anything". When asked why he had made such a face if it were only water, he answered that he did

not know or that he guessed it was "unconscious". However, he correctly named these same odors when they were presented to the left nostril. In these and similar responses the affective as well as the olfactory component appeared to have been confined to the one hemisphere.

SUMMARY AND DISCUSSION

The findings support the conclusion that olfactory stimulation of right and left nostrils is independently perceived in right and left hemispheres, respectively, in these commissurotomy patients with little or no interhemispheric cross-communication of olfactory gnosis. A doubling and right-left separation in the patients' inner olfactory experience was indicated in all the different tests used; these test findings generally confirm and reinforce each other.

The inability to verbally describe odors presented to the right nostril when the same odors were readily named from the left nostril fits the previous evidence that speech is confined in these patients almost exclusively to the disconnected left hemisphere. The right nostril odors that could not be named were nevertheless perceived in the right hemisphere as indicated in the subject's ability to point selectively to the correct associated object or to pick out the correct associated object by tactual palpation.

Failure of the olfactory sensation from the right nostril to cross to the speaking hemisphere was further indicated in the subject's tendency to simply report "water" or to make vague verbal guesses from among the test scents to be in use. It was only after the correct associated object had been fixated upon via orienting responses of the eyes, head, and hands that the left hemisphere could make a correct verbal response.

The same interpretation finds further support in the subjects' ability to retrieve the associated objects tactually when the contralateral but not when the ipsilateral hand was used. The ipsilateral nostril-hand combinations produced only chance scores with the few exceptions noted above that seem best accounted for in terms of ipsilateral tactual projection [13], subvocal cross-cueing [14], or trigeminal stimulation. The results favor the conclusion that cross-modal associations between touch and smell are successful if the two inputs enter the same hemisphere, but fail if the two are restricted each to opposite hemispheres.

With strongly unpleasant odors it was apparent in many trials that the accompanying affective component of the subject's reaction remained confined to the one hemisphere, and that typical emotional responses were aroused in the minor as well as in the major hemisphere. Whether emotion may be cross-communicated from one to the other hemisphere at brain stem levels in these patients has long remained an open question. Clear crossing of emotion in the present tests through peripheral cues like wincing or grunting and the absence of crossing where such peripheral cues were lacking suggest that the contralateral transfer of emotional effects in the present tests was dependent upon feedback from peripheral responses. Since a similar peripheral mediation could not be ruled out in our earlier observations, the present findings raise doubt about the suspected spread through the brain stem of emotional tone and favor the view that feeling and emotion like other components of gnostic experience are divided into separate right and left realms by forebrain commissurotomy.

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Résumé—Chez cinq sujets droitiers qui avaient subi une déconnection chirurgicale des hémisphères cérébraux dans le but de traiter une épilepsie grave, la latéralisation de l'olfaction a été examinée. De même que pour la vision et la stéréognosie, on a trouvé que la perception olfactive peut être confinée à un seul hémisphère si l'entrée est restreinte à ce seul côté (c'est-àdire à une seule narine). Le fait que les odeurs fussent reconnues seulement par l'hémisphère ipsilatéral à la narine stimulée, était mis en évidence par la possibilité qu'avaient les sujets de nommer les odeurs présentées à la narine gauche, tandis que celles présentées à la narine droite ne pouvaient être nommées. Des tests non verbaux démontrainent la reconnaissance perceptive des odeurs présentées à la narine droite par l'hémisphère qui ne parle pas (droit).

Ces résultats étaient en outre confirmés par des épreuves d'appariements inter-modaux olfacto-tactiles. Les réponses étaient correctes quant les stimuli tactiles et olfactifs étaient projetés au même hémisphère, mais ne l'étaient pas s'ils étaient projetés à l'un et l'autre

hémisphère.

Zusammenfassung-Fünf rechtshändige Patienten, bei denen die Verbindung zwischen den Hemisphären chirurgisch unterbrochen worden war, um schwere epileptische Anfälle zu mildern, wurden auf die Lateralisation der Geruchswahrnehmung hin untersucht. Es wurde festgestellt, daß-entsprechend der Stereognosie und dem optischen Erkennen-die Geruchswahrnehmung auf eine Hemisphäre beschränkt ist, wenn der Reiz nur auf einer Seite, d.h. nur durch ein Nasenloch, erfolgt. Die Tatsache, daß Gerüche nur über die ipsilaterale Hemisphäre erkannt werden, wurde dadurch bewiesen, daß die betreffenden Personen fähig waren, Geruchswahrnehmungen, die durch das linke Nasenloch erfolgten, zu benennen, nicht aber solche durch das rechte Nasenloch. Sprachfrieie Tests zeigten, daß die Geruchswahrnehmung durch das rechte Nasenloch von der nicht dominanten rechten Hemisphäre verarbeitet wird. Die Ergebnisse wurden weiter untermauert durch Aufgaben, die gekreuzte olfaktorische und taktile. Wahrnehmungen verbanden. Die Antworten waren richtig, wenn der taktile und der Geruchsreiz die selbe Hemisphäre, jedoch nicht, wenn sie verschiedene Hemisphären trafen.