Cortical sensory representation of the human hand:

Size of finger regions and nonoverlapping digit somatotopy

William W. Sutherling, MD; Michel F. Levesque, MD; and Christoph Baumgartner, MD

Article abstract—Findings differ on cortical representation of fingers between human and animal studies, and on digit somatotopy among human studies. To resolve these differences, we mapped cortical sensory representation of each of the five digits and of median and ulnar nerves in three patients, using focal peripheral electrical shock stimuli. We compared locations and sizes of cortical regions among digits and nerves, using the model of a current dipole in a sphere applied to electrocorticography from subdural grids. Cortical representation was larger for the index finger than for the little finger and for the middle finger than for the ring finger, which are similar to findings in the monkey but different from Penfield's classic sensory homunculus. The thumb was larger than the middle finger, as in the homunculus. There was nonoverlapping somatotopy of all digits in each patient. These findings demonstrate a previously unrecognized similarity of cortical sensory organization of the fingers between humans and other primates.

NEUROLOGY 1992;42:1020-1028

There are differences between the classic cortical sensory homunculus of Penfield and recent reports of cortical sensory representation in monkey. The classic homunculus shows about equal cortical representation for the index finger compared with the little finger and for the middle finger compared with the ring finger.[1,2] In the macaque, however, cortical representation is larger for the index finger than for the little finger and larger for the middle finger than for the ring finger.[3-5] Although it is generally assumed that human studies clearly have shown a somatotopic sequence (somatotopy), there are differences among reports of somatotopy of the digits. The classic homunculus,[1,2] a composite diagram derived from intraoperative cortical stimulations in a large population of patients, apparently without identifying all of the five digits in the same brain and based on subjective reports that frequently included sensation in two or more digits during one stimulation, shows the five digits as separate and sequentially somatotopic. Noninvasive studies have reported evoked response separation of nonadjacent digits.[6-9] Previous studies with electrocorticography (ECoG) have been the most complete and have reported evoked potentials for all digits in the same brain; however, in all reported patients and figures, there is overlap or reverse sequence in the somatotopy for at least two digits in each patient.[10,11]

Dipole methods from physics recently have demonstrated cortical somatotopy in other modalities and have shown retinotopic organization in human visual cortex,[12] tonotopic organization in human auditory cortex,[13,14] and closely adjacent subregions in human hand somatosensory cortex.[15-20] Hence, dipole methods applied to ECoG appear to be an accurate strategy for localizing activity and resolving detail in human somatosensory cortex.

Due to discrepancies in the literature on cortical somatotopy in human and monkey hand, and to the demonstrated precision of dipole methods and of direct cortical recordings, we used ECoG dipole estimates to define cortical sensory representation of the hand by stimulating each of the five digits and the median and ulnar nerves in three patients, of whom two previously had verified cortical localization for the median nerve.[15,16]

Methods. *Recording of somatosensory evoked responses on ECoG.* Evoked responses were recorded from somatosensory cortex (somatosensory evoked responses; SERs) in three patients evaluated for epilepsy surgery using

From the Departments of Neurology (Dr. Sutherling) and Neurosurgery (Dr. Levesque), and the Brain Research Institute (Dr. Sutherling), University of California, Los Angeles, CA; the Cleveland Clinic (Dr. Baumgartner), Cleveland, OH; and Neurological University Clinic (Dr. Baumgartner), Vienna, Austria.

Supported by grants NS20806 and NS00678 from the National Institute of Neurological Disorders and Stroke, by Fonds zur Förderung der wissenshaftlichen Forschung Österreichs (P7434), by the Epilepsy Foundation of America, and by the Research Society for Parkinson's Disease and Movement Disorders.

Received August 19, 1991. Accepted for publication in final form October 9, 1991.

Address correspondence and reprint requests to Dr. William W. Sutherling, Reed Neurological Research Center, 710 Westwood Plaza, Los Angeles, CA 90024.

chronic subdural electrode arrays that were placed over sensorimotor cortex (Progress for Mankind Technology, Minneapolis, MN). All patients had seizures arising outside sensorimotor cortex and have had significant reduction of seizures after focal excision. Patient 3 had seizures that propagated rapidly to sensorimotor cortex. The location and extent of sensorimotor cortex were defined using cortical stimulations according to published procedures.[15] This study conformed to the Declaration of Helsinki and was approved by the UCLA Human Subject Protection Committee. All patients gave informed consent. ECoG was measured during the first 60 msec after shock stimulation of each contralateral digit at the proximal interphalangeal joint and of the median and ulnar nerves at the wrist. The first 5 msec were excluded from analysis to avoid contamination by stimulus artifact. The digits were stimulated with ring electrodes and were isolated from each other during stimulation by dry cotton pads between adjacent fingers. For median and ulnar nerves, 0.3-msec monophasic pulses at 3.1 Hz were applied to disks, which produced a thumb or little finger twitch. The same intensity was used for digits in the distribution of the respective nerve.[21] Appropriate stimulation distribution was checked in each patient. During stimulation of the thumb, patients reported tingling in the thumb. During stimulation of the median nerve, patients reported tingling in the thumb, index finger, middle finger, and often the ring finger, in the appropriate distribution. During stimulation of the ulnar nerve, patients reported tingling in the little and ring fingers. A 48-channel rectangular matrix covering somatosensory cortex was sampled simultaneously at 4,096 Hz (bandpass, 1 to 1,000 Hz; 12-bit resolution) on high-performance amplifiers (Grass Instruments, Quincy, MA). Two reproducible sets of 500 trials were averaged for each digit and nerve.

Original traces and isocontour maps. The original traces of the time series were plotted and isocontour maps were constructed at the estimated average latency of the initial amplitude peak for the digits and for the nerves. Not all digit evoked responses had well-defined early amplitude peaks in each patient, so the average latency was used at which most digits had an initial peak. These traces and isocontours were correlated with the composite image of electrode positions and functional anatomy from cortical stimulations, intraoperative photographs, skull x-rays, and MRIs (figures 1 and 2).

Current dipole model. A current dipole was used to localize the centroid of each cortical region with a model that we have previously shown to locate central fissure in hand sensorimotor cortex accurately, with a mean error of less than 3 mm.[15] The model allowed the dipole to move within a homogeneous sphere to obtain the smallest value of least squares between the model and the data using the nonlinear minimization simplex algorithm of Nelder and Mead,[22] as in our previous reports.[15-17] For the net current in a cortical region, the dipole model gave three parameters for location, two for angular orientation, and one for amplitude. The model calculated a "goodness-of-fit" measure of the percentage of variance in the data that was explained by the model ("reduced modified chi-square value"[23]).

The location of the dipole for digits and nerves was estimated by two methods. The localization estimates were robust, and both methods gave equivalent results. First, the dipole location was estimated at the latency of the initial amplitude peak, according to standard procedures. Second, the average or mean dipole location was estimated for the entire time series. We confirmed the localizations using both methods to avoid a biased comparison. Since not all digit evoked responses had uniformly large, initial cortical peaks like the N20-P30 or P25-N35 after median nerve stimulation, visual selection of the latency of cortical activity may have introduced bias for some digits. Inaccurate selection of latency would be expected to include more cortical activity for one digit than for another and might change the size of a cortical region and its centroid. Since the object of this study was to compare digit with digit and digit with nerve, we avoided bias from arbitrary visual selection of latency by comparing the entire time series for all digits and nerves. Modeling the entire time series has localized and separated multiple cortical sources after median nerve stimulation[16,17] without any detectable error from including small-amplitude subcortical activity.

The procedure of analyzing the entire times series was useful here because it allowed uniform analysis of all digits and nerves. The results for the entire time series were equivalent to those using a visual estimate of the latency of digit cortical activity. We also analyzed the entire time series starting from 5 msec after stimulation and the time series beginning at the initial amplitude peak. The results of these two analyses also were equivalent. For the locations in the study, the unbiased results for the entire time series were correlated with cortical functional anatomy. The mean location of the dipole was used as the measure of the centroid or center of mass of the cortical activity after stimulation. The data also were analyzed using the median statistic of all dipole locations. The results were similar using the mean or median statistic as a measure of central tendency.

The mean of the goodness-of-fit measure was calculated for the entire time series. The goodness of fit to a dipole is a measure of how well a cortical region corresponds to a point dipole. A dipole is a good approximation of a focal source and is the first approximation to the description of any source.[12] The goodness of fit, used in this way, is an objective measure of focality of a brain region. A small region would be expected to have a good fit to a point dipole, but a large region would be expected to have a poor fit to a dipole. The goodness-of-fit value has been shown to predict accurately the presence of an extended source based on comparison with recordings directly from neocortex.[24]

Construction of cortical anatomic maps. The mean locations of dipoles were mapped onto composite images of sensorimotor cortex from intraoperative photographs, skull x-rays, MRIs, and cortical stimulations performed extraoperatively with the same subdural electrode array used for recording ECoG (figure 3A). Electrode positions were verified on intraoperative photographs taken during initial ECoG electrode placement and during electrode removal 3 weeks later, and on skull x-rays taken before and after the recording period. There was no movement of the electrodes in relation to the underlying cortical sulci and veins. This use of intraoperative photographs allowed precise correlation of dipole location, with anatomy in a visualized reference frame.[15,16]

A two-dimensional graph of the cortical map was constructed for each patient. A line was drawn from each dipole location to the nearest point of central fissure. The line gave a reflection of the dipole location onto central fissure. We measured the absolute distance along central fissure between the reflection of one digit to the reflection of an adjacent digit. These distances were plotted on the vertical axis of the graph (figure 3B). The absolute

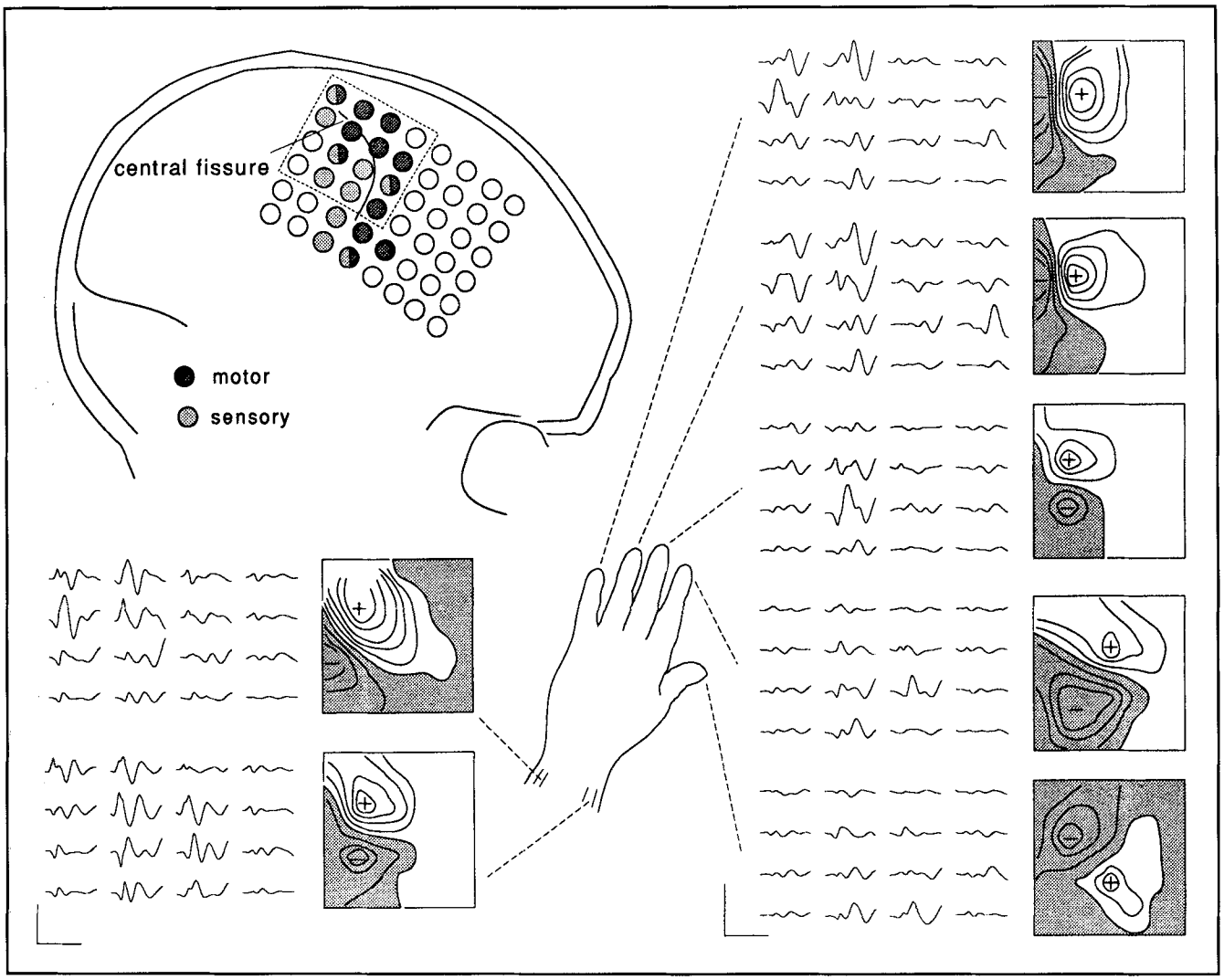

Figure 1. Patient 1. Recording matrix, original traces, and isocontour maps of right hemisphere. At top left is composite image from skull x-ray and intraoperative photograph with subdural electrode recording matrix (circles), results of behavioral testing during cortical stimulations at shaded electrode sites, and location of central fissure. At bottom center, diagram of contralateral hand shows sites stimulated. Traces and isocontour maps of sensory responses for median and ulnar nerves at bottom left and for digits at right. Traces are from electrodes enclosed by dotted rectangle above. Isocontour maps are from entire matrix: for nerves at initial peak of 15 msec poststimulus and for digits at initial peak of 17.5 msec poststimulus. Location of highest amplitude for digits and nerves shifts up and backward, along the direction of central fissure in a somatotopic sequence. Isocontours also show somatotopic sequence of polarity reversal with predominantly tangential dipolar pattern. Traces for 60 msec after stimulation, excluding the first 5 msec that contained stimulus artifact. Calibrations = 50 μV, 50 msec, positive up.

distance was measured from each dipole location to central fissure to estimate the size of the cortical representation of the digit or nerve, analogous to estimates of a "rostrocaudal band" in monkey.[25] These estimates of cortical representation were plotted on the horizontal axis of the graph.

Statistical analysis. The following hypotheses were tested to determine whether hand somatosensory cortex was identical in human and monkey. Is the index finger cortex larger than the little finger cortex? Is the middle finger cortex larger than the ring finger cortex? Do the digits show a somatotopic sequence, as expected, or is there overlap of the centroids of digit cortex for adjacent fingers?

The sizes of cortical representations of each digit were compared using two complementary measures. First, the distance from the mean location of the dipole to central fissure was used to estimate the size of digit cortex on the surface of the postcentral gyrus. Second, the goodness of fit measure between the cortical region compared with a point dipole was used as a measure of focality. The distance and goodness-of-fit criteria gave nonredundant confirmation. The distance to central fissure measures anterior-to-posterior length of an area on the surface of a gyrus, whereas the goodness of fit to a dipole measures the entire cortical volume activated. To analyze distances and goodness-of-fit values, we used repeated-measures analysis of variance with the post hoc *t* test.[26] We used repeated measures because the SDs of the dipole locations of each of the digits and of the nerves were similar. A one-tailed *t* test was used because our hypothesis addressed whether the index and the middle fingers were larger than or equal to the little and the ring fingers. To analyze somatotopic sequence, we used

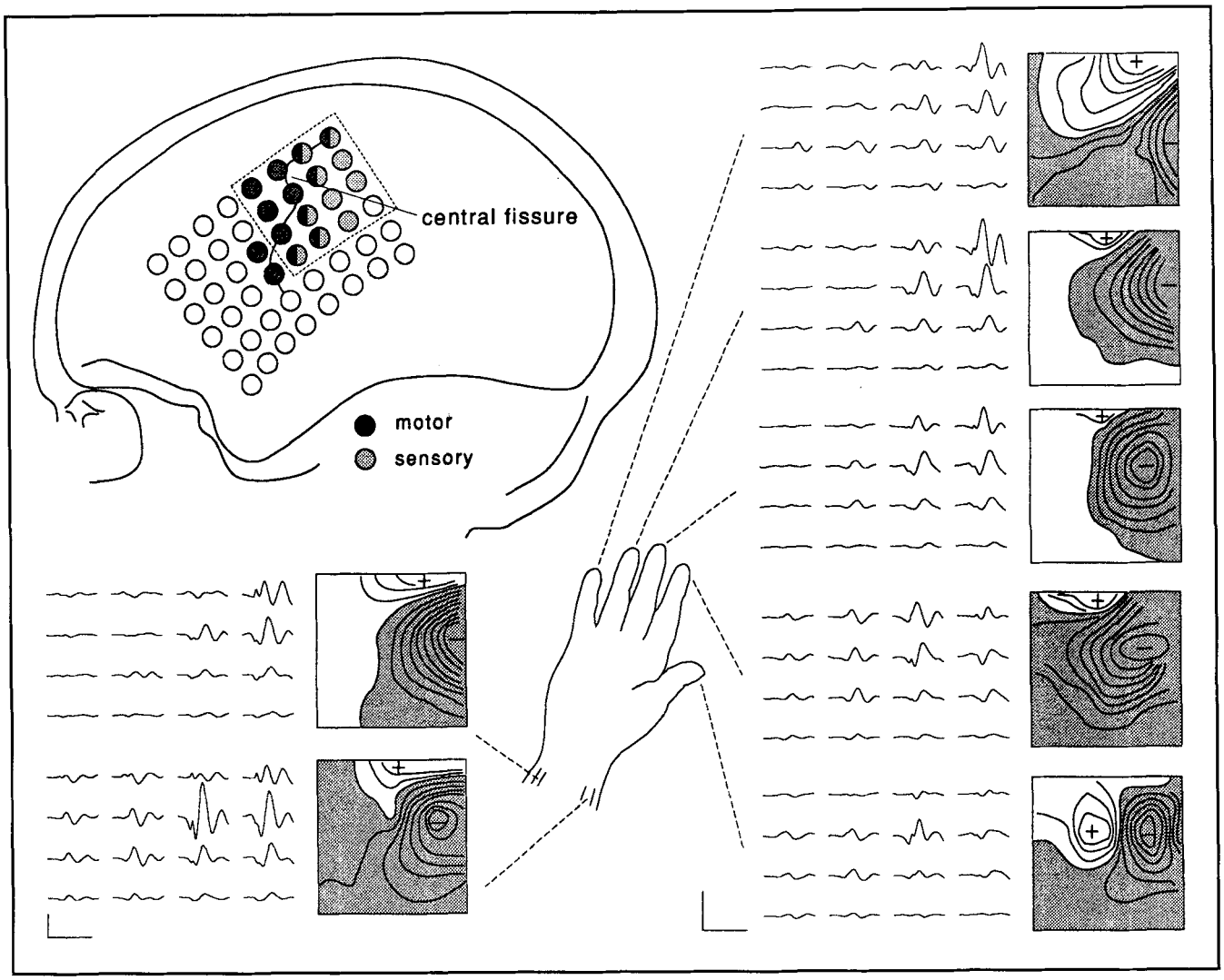

Figure 2. Patient 2. Recording matrix, original traces, and isocontour maps from left hemisphere presented like patient 1. Isocontour maps: for nerves at 20 msec poststimulus, for digits at 25 msec poststimulus. Traces and isocontours also show same somatotopic sequence for digits and nerves. Calibrations: 50 μV, 50 msec, positive up.

permutations. We determined whether the observed sequence of digits was different from chance by comparing the actual frequency to the expected probability of the observed sequences in the patients, considering the probabilities of all possible sequences.

Results. *Somatotopy.* The original time series traces and isocontour maps showed a gradual shift in location of amplitude peaks and of polarity reversal, up and backward along central fissure, consistent with a somatotopic sequence (figures 1 and 2). Most of the digits and nerves had time series traces that showed a contiguous area of high-amplitude peaks. For the ring and little fingers in patient 1, there was a spatial separation of high-amplitude peaks with the same polarity (figure 1). These separate peaks had different latencies, consistent with dipolar sources.

As expected, all mean locations of dipoles were in hand somatosensory cortex and agreed with cortical stimulations and intraoperative photographs (figure 3A). Figure 3B shows that, in each patient, each digit dipole was separate from every other digit dipole, with no overlap of two SEs of dipoles of any two digits ($p < 0.05$). The digit dipoles in all patients had identical somatotopic organizations from sylvian fissure to vertex in the sequence: thumb, index, middle, ring, little fingers. As expected, the median nerve dipole always was nearer the sylvian fissure than the ulnar nerve dipole. The digit locations tended to cluster near the location of the nerve in the appropriate distribution.[21]

We first analyzed all the digits together. The observed sequences were different from chance for all digits taken together. For all five digits together, in five positions in the same brain, there are 120 possible permutations of digit sequences. Given a specific digit sequence in the first brain sampled, the probability that the same sequence would occur again by chance in another two brains is small ($p < 0.0001$).

Since a major question in the literature concerns

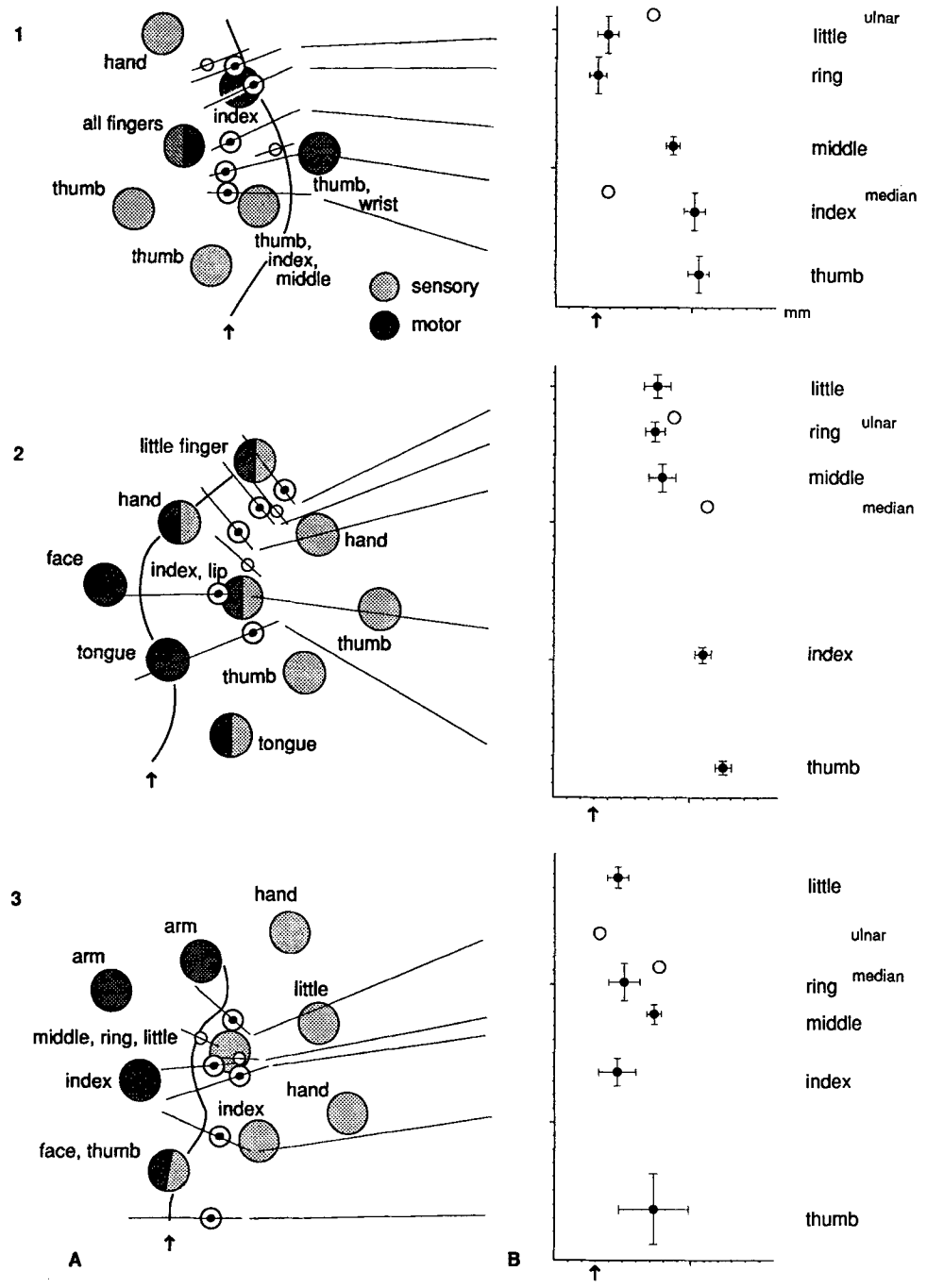

Figure 3. Cortical sensory anatomic maps of the hand for Patients 1, 2, and 3 from top to bottom. At left is original anatomic map with dipole locations; at right are dipole locations on graph of unfolded cortex in relation to central fissure (arrow). (A) Anatomic maps at left are enlargements of area of hand sensorimotor cortex where digit and nerve dipoles were located, constructed from intraoperative photographs of nearby electrode locations and central fissure. Areas shown for patients 1 and 2 are enlargements of hand area within dotted rectangles in figures 1 and 2, above. In anatomic maps, each large circle with a dot shows the mean location of the current dipole that best fits the cortical electrical activity after stimulation of one digit. The small unfilled circles indicate the dipoles for median and ulnar nerves. The mean locations of the dipoles agree with locations of sensory responses during cortical stimulation. A line is drawn between each dipole location to the nearest point of central fissure to derive the graphs at right. Distance is 10 mm between subdural electrode centers. The left hemisphere was studied in patient 3. (B) Graphs of digit dipole locations in relation to central fissure constructed from maps at left. The cortex has been unfolded to make central fissure parallel to the vertical axis. The vertical axis shows the distances between the reflections of digit dipoles onto central fissure. The horizontal axis shows the distance from each dipole location to central fissure, giving an estimate of cortical representation, analogous to an anterior-posterior rostrocaudal band.[25] Bars show ± 2 SEs of the mean of the dipole locations over the 60 msec after stimulation, excluding stimulus artifact. Each map shows a nonoverlapping somatotopic sequence from the thumb to the little finger and from the median to the ulnar nerve. Graphs in mm.

finger somatotopy and separation of adjacent fingers rather than the relative position of the thumb, we also analyzed the fingers only, with the thumb excluded from the analysis. The observed sequences were different from chance and from overlap of adjacent fingers. For the four fingers, there are five possible somatotopic sequences in which there is either complete separation of all fingers or overlap of two adjacent fingers: one with separation of the fingers and four with overlap of two adjacent fingers. Each of these sequences has 0.2 probability. Given a specific somatotopic finger sequence in the first brain, the chance that the same sequence would occur again by chance in the next two brains is small ($p = 0.04$).

Size of cortical representation. The size of cortical representation for fingers was like that of monkey and different from the classic sensory homun culus, based on anterior-posterior distance on the surface of the postcentral gyrus. The table shows the measurements for all patients with means and SEs. From largest to smallest, the size of cortical representation for all digits in the patient group was: thumb, index, middle, little, ring. Cortical representation was larger for the index finger than for the little finger ($p < 0.05$) and for the middle

Table. Anterior-posterior length of cortical representation (mm) *and goodness of fit between cortical representation and a dipole

Patient	Digit					Nerve	
	Thumb	Index	Middle	Ring	Little	Median	Ulnar
1	8	7	6	0	1	1	3
	*63**	*72*	*77*	*64*	*69*	*69*	*76*
2	9	8	5	4	5	8	6
	82	*81*	*77*	*85*	*80*	*83*	*79*
3	4	2	4	2	2	5	1
	66	*75*	*78*	*75*	*71*	*87*	*85*
Mean APL	**7.0**	**5.7**	**5.0**	**2.0**	**2.7**	**4.7**	**3.3**
SE#	(0.9)	(1.2)	(1.1)	(0.8)	(0.6)	(1.5)	(0.4)
Mean fit	***70***	***76***	***77***	***75***	***73***	***80***	***80***
SE	*(3.5)*	*(1.1)*	*(3.2)*	*(2.9)*	*(1.6)*	*(3.4)*	*(3.1)*

Thumb > ring, little, ulnar ($p < 0.05$)†
Index > ring, **little** ($p < 0.05$)
Middle > **ring** ($p < 0.05$)
Thumb < *middle*, ***median***, *ulnar* *(p < 0.05)*

Measurements coded as follows: plain roman = individual anterior-posterior lengths (APLs); bold roman = mean APLs; plain italics = individual goodness of fit values; and bold italics = mean goodness of fit values.

* Percent of data variance explained by a single current dipole.
# Standard error of mean in † repeated-measures analysis of variance and post hoc *t* test (one-tailed)[26] calculated separately for anterior-posterior lengths and *dipole fits*. F test (between/within groups) was significant, with $p = 0.03$ for APL and $p = 0.005$ *for fits*.

finger than for the ring finger ($p < 0.05$).

A single dipole did not explain all the data. The table also shows the goodness-of-fit values for all patients with means and SEs. The goodness of fit, or amount of data variance explained by the model, often was below the usual criterion of 80% for a focal region.[23] The distribution of goodness of fit among digits was similar in all patients ($p > 0.4$). The grand mean of the goodness of fit over the time series for all digits and nerves in all patients was 75.9% (SE = 1.6). Based on fit values, the thumb had a larger cortical representation than the middle finger did ($p < 0.05$), like the homunculus but different from monkey. An interesting but unexpected finding was that the median nerve and ulnar nerve both had significantly better goodness-of-fit values than did the thumb ($p < 0.05$). This appeared to be due to differences in two patients, whereas the third had about equal fit values for the thumb and the median nerve.

Multiple dipole model. We also tested a multiple dipole model for three reasons: (1) multiple cortical sources have been shown after median nerve stimulation,[15-20] (2) multiple sources would be expected for each digit in the two maps in areas 3b and 1,[4,5,27,28] and (3) there were lower values of goodness of fit for some digits than would be expected for a single dipole. We applied a new multiple dipole spatiotemporal model to the data.[16,17,29,30] The model used dipoles with fixed locations and time-varying amplitudes that were overlapping. This model has accurately identified two subregions in human somatosensory cortex.[16,17] The single dipole model, however, was more stable than the new multisource model for these digit evoked responses. We therefore used the more stable single dipole model for analysis to obtain unambiguous localizations that could be compared among digits. Since the two maps in areas 3b and 1 are contiguous and somatotopic in monkey,[4,5] combining them using a single dipole model appeared justified to compare mean locations of digits and nerves and would not be expected to affect the relative location of the center of a digit cortical region.

Discussion. These findings demonstrate that the size of cortical sensory representation of human fingers is similar to that in monkey and different in two respects from the homunculus of Penfield[1,2] and that there is nonoverlapping somatotopy in the individual human brain.

Size of cortical representation. Where prior human and monkey studies agreed, we found similar patterns of cortical representation. Where there were differences between human and monkey reports on cortical representation of fingers, our findings supported those in monkey and were different from those in the classic sensory homunculus.

Penfield and Boldrey[1] reported about the same number of positive subjective reports for sensation for the index finger compared with the little finger and for the middle finger compared with the ring finger. We found, however, that cortical representation estimated by anterior-posterior length of

exposed sensory cortex on gyral surface was larger for the index finger than for the little finger and for the middle finger than for the ring finger. These findings are analogous to those in macaque.[4,5] The anterior-posterior length for each digit is not apparent from illustrations published by Penfield and Boldrey,[1] which show a distribution of dots on a composite brain diagram without coding for individual digits or separation of all five digits in the same brain.

Our finding of a larger representation for the thumb than the ring and little fingers and for the index finger than the ring finger is similar to the classic homunculus and to macaque. Our finding of a larger representation for the thumb than for the middle finger, based on dipole fit, is different from studies of macaque[4,5] and similar to those of the classic homunculus. It is not surprising that the thumb had a larger gyral surface representation and a lower fit to a single dipole than did the other digits because the thumb had the largest cortical representation by cortical stimulations here (figure 3A) and in the literature.[1,2]

Our findings of extended cortical representations posterior to central fissure are similar to rostrocaudal bands in monkey studies[25] and to the classic homunculus. The absolute sizes of cortical representation for digits may be larger than our estimates. Size of surface cortical representation likely would be shown more accurately by a dipole estimate for only area 1 on the gyral cortical surface, since the first 60 msec of cortical somatosensory evoked activity combines activity from areas 3b and 1.[18] Since area 3b is buried in central fissure, combining ECoG activity from areas 3b and 1 would be expected to give a localization nearer central fissure than a dipole for area 1. Combining areas 3b and 1 would reduce an estimate of cortical representation from dipole distance to central fissure. We tried to isolate areas 3b and 1 for each digit with more complex procedures, including a new multiple dipole model, but this was less stable than the single dipole model. We are investigating additional methods of separating subunits of cortical representation.

An unexpected finding was that the median and ulnar nerves had better dipole goodness of fits than did the thumb in two patients, and a similar dipole fit in the third. The median nerve, however, represents the distribution of the thumb, two and a half fingers, and the palm[21]; therefore, the median nerve would be expected to have at least as large an area as the thumb and two fingers combined and, therefore, a lower dipole fit than that for the thumb. The opposite case observed here—a lower fit for the thumb compared with that for the median and ulnar nerves—has several possible explanations. It is unlikely that it is due to multiple sources for digits but not nerves, since multiple sources have been shown for the median nerve.[15-20] The differences between nerves and digits also are not likely due to lower signal-to-noise ratios for digit evoked responses, since nerves and digits had similar ratios (figures 1 and 2). Alternative explanations could be interactions in peripheral nerve,[31,32] spinal cord,[32,33] or cortex.[34] Since each patient reported tingling in three or four digits during stimulation of the median nerve, it is likely that the cortical representations of multiple digits were activated and that there was not cancellation or reduction of distribution of the receptive fields in peripheral nerve or spinal cord. A remaining possibility is a cortical interaction due either to a geometry of cortex that could produce self-cancellation of potentials or to an interaction among cortical receptive fields of the digits. There are changes in cortical representation due to cortical interactions in different states of peripheral stimulation in monkey.[34]

Somatotopy. Adjacent fingers had nonoverlapping centers in the same brain, unlike previous noninvasive and invasive studies. Although the report of somatotopy for all five digits is not new, we believe this study may be the first demonstration of nonoverlapping somatotopy of all five digits in the individual human brain. The finding of somatotopy of the median nerve, ulnar nerve, and digits in these patients is analogous to our previous study of the median nerve, ulnar nerve, and lip.[35]

These findings clarify work from prior human studies, which did not separate all digits in the same brain or showed variability in relative digit location. The separate somatotopic locations of the digits here confirm the classic sensory homunculus from cortical stimulations in composite maps from patient populations.[1,2] Noninvasive studies using scalp electric fields[6] and the magnetic fields[7,8] showed somatotopy for alternate digits but not for all digits in the same subject. PET studies focused on groups of digits rather than isolating each of the five digits.[9] Woolsey et al[11] showed somatotopy in individual patients using ECoG amplitude during finger tapping; however, all illustrations show widespread cortical activity during shocks or joint movement of fingers, producing at least one reverse or overlapping sequence in each patient. We found separate amplitude peaks for some digits, as did Woolsey et al[11] (figure 1); however, dipoles of adjacent digits were nonoverlapping.

The somatotopic map here is similar to that in monkey sensory cortex[4,5] but different from that in motor cortex, which is organized in muscle groups.[36] Primary sensory cortex of human digits appears to have an organization similar to primary essential, unimodal, agranular cortex in other modalities, with a one-to-one mapping of peripheral receptive fields onto cortex in a somatotopic sequence. This simple organization does not rule out more complex interactions among receptive fields, which is one explanation for our finding a lower dipole fit for the thumb than for the median nerve. Dipole modeling of the magnetic field has shown complex interaction among receptive fields in human primary auditory cortex, where pitch may be mapped as well as frequency.[14]

Possible causes of detection of new findings. The new findings in this study may arise from several factors. We used dipole models to derive current sources from cortical voltages. A dipole model avoided bias from subjective visual analysis and ambiguity of peak voltage amplitude, which can be distant from a source tilted from radial.[12,15,18,19] The dipole model would be expected to make more precise estimates than those from location of highest peak amplitude. Measurement of central tendency of early cortical activity over a time series, rather than a map at one instant, improved the stability of the estimates and increased spatial resolution to distinguish adjacent cortical regions.

We had large signal-to-noise ratios by averaging voltages directly from cortex in alert patients, which reduced errors inherent in noninvasive measurements such as distance[15,37] and skull smearing,[6,15,38] and those due to state changes from anesthesia or fatigue. Direct comparisons of current sources and cortical anatomy from photographs of the same grid used for stimulations and dipole localization aided accurate correlation. Precise correlation with central fissure geometry in patient 3 was necessary to determine sequence of middle and ring fingers. Electrical measurement from a 60-msec window avoided temporal averaging of initial localized and later propagated activity, which might have obscured organization of somatotopy. Initial evoked responses arise from areas 3b and 1.[18] Reports in monkey have shown somatotopy in areas 3b and 1[4,5] but overlapping representation in area 2, to which a somatosensory volley propagates.[27]

It is unlikely that the new findings here are due to pathology in epileptic brains. Although one patient had seizures that propagated rapidly to sensorimotor cortex, the findings in the other two patients were the same as the mean findings of the group and the new findings here. The other two patients had seizure foci distant from sensorimotor cortex.

Further research is warranted, using more realistic models on higher-resolution intracranial recordings. Dipole interpretation of the ECoG maps here is an abbreviated representation of cortical activity compared with single-cell recordings in animals. Although ethical constraints in humans prevent the detailed studies possible in animals, further correlations with primate cortex, smaller interelectrode distances, multiple dipole modeling of dynamic activation of cortical neuronal populations after peripheral afferent stimulation, and study of longer epochs could help resolve finer details of human digit cortical organization and test focused hypotheses of differences from other primates.

Acknowledgments

We thank Dr. J. Gornbein, UCLA Department of Biomathematics, for help with statistical analysis, Dr. Charles Wilson, Eric Behnke, Pat Glennon, and Jodi Schmidt for technical assistance, and Dr. Thomas Babb for his help in editing the manuscript.

References

1. Penfield WJ, Boldrey E. Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. Brain 1937;60:389-443.
2. Penfield WJ, Jasper HH. Epilepsy and the functional anatomy of the human brain. Boston: Little, Brown, 1954:70-73.
3. Woolsey CN. Organization of somatic sensory and motor areas of the cerebral cortex. In: Harlow HF, Woolsey CN, eds. Biological and biochemical basis of behavior. Madison: University of Wisconsin Press, 1958:63-81.
4. Paul RL, Merzenich MM, Goodman H. Representations of slowly and rapidly adapting cutaneous mechanoreceptors of the hand in Brodmann's areas 3 and 1 of macaca mulatta. Brain Res 1972;36:229-249.
5. Merzenich MM, Kaas JH, Sur M, Lin CS. Double representation of the body surface within cytoarchitectonic areas 3b and 1 in "SI" in the owl monkey (*Aotus trivirgatus*). J Comp Neurol 1978;181:41-74.
6. Duff TA. Topography of scalp recorded potentials evoked by stimulation of the digits. Electroencephalogr Clin Neurophysiol 1980;49:452-460.
7. Okada YC, Tanenbaum R, Williamson SJ, Kaufman L. Somatotopic organization of the human somatosensory cortex revealed by neuromagnetic measurements. Exp Brain Res 1984;56:197-205.
8. Hari R, Hamalainen M, Ilmoniemi R, Kaukoranta E, Reinikainen K. Magnetoencephalographic localization of cortical activity evoked by somatosensory and noxious stimulation. In: Bromm B, ed. New approaches to pain measurement in man. Amsterdam: Elsevier, 1984:317-324.
9. Fox PT, Burton H, Raichle ME. Mapping human somatosensory cortex with positron emission tomography. J Neurosurg 1987;67:34-43.
10. Woolsey CN, Erickson TC. Study of the postcentral gyrus of man by the evoked potential technique. Trans Am Neurol Assoc 1950;75:50-52.
11. Woolsey CN, Erickson T, Gilson WE. Localization in somatic sensory and motor areas of human cortex determined by direct recording of evoked potentials and electrical stimulation. J Neurosurg 1979;51:476-506.
12. Darcey TM, Ary JP, Fender DH. Methods for location of electrical sources in the human brain. Prog Brain Res 1980;54:128-134.
13. Romani GL, Williamson SJ, Kaufman L. Tonotopic organization of the human auditory cortex. Science 1982;216:1339-1340.
14. Pantev C, Hoke M, Lütkenhöner B, Lehnertz K. Tonotopic organization of the auditory cortex: pitch versus frequency representation. Science 1989;246:486-488.
15. Sutherling WW, Crandall PH, Darcey TM, Becker DP, Levesque MF, Barth DS. The magnetic and electric fields agree with intracranial localizations of somatosensory cortex. Neurology 1988;38:1705-1714.
16. Baumgartner C, Barth DS, Levesque MF, Sutherling WW. Functional anatomy of human hand sensorimotor cortex from spatiotemporal analysis of electrocorticography. Electroencephalogr Clin Neurophysiol 1991;78:56-65.
17. Baumgartner C, Sutherling WW, Di S, Barth DS. Spatiotemporal modeling of cerebral evoked magnetic fields to median nerve stimulation. Electroencephalogr Clin Neurophysiol 1991;79:27-35.
18. Allison T, McCarthy G, Wood CC, Darcey TM, Spencer DD, Williamson PD. Human cortical potentials evoked by stimulation of the median nerve: I. Cytoarchitectonic areas generating short-latency activity. J Neurophysiol 1989;62:694-710.
19. Wood CC, Spencer DD, Allison T, McCarthy G, Williamson PD, Goff WR. Localization of human sensorimotor cortex during surgery by cortical surface recordings of somatosensory evoked potentials. J Neurosurg 1988;68:99-111.
20. Wood CC, Cohen D, Cuffin BN, Yarita M, Allison T. Electrical sources in the human somatosensory cortex: identification by combined magnetic and electric potential recordings. Science 1985;227:1051-1053.
21. Medical Research Council. Aids to examination of the

peripheral nervous system. London: Her Majesty's Stationery Office, 1976:48-50.
22. Press WH, Flannery BP, Teukolsky SA, Vetterling WT. Numerical Recipes. New York: Cambridge University Press, 1986:289-293.
23. Stok CJ. The inverse problem in EEG and MEG with application to visual evoked responses. PhD thesis. Leiden: Netherlands, State University, 1986:77-79, 99-114.
24. Sutherling WW, Crandall PH, Cahan LD, Barth DS. The magnetic field of epileptic spikes agrees with intracranial localizations in complex partial epilepsy. Neurology 1988;38:778-786.
25. Powell TPS, Mountcastle VB. Some aspects of the functional organization of the cortex of the postcentral gyrus of the monkey. A correlation of findings obtained in a single unit analysis with cytoarchitecture. Bull Johns Hopkins Hosp 1959;105:133-162.
26. Dunn O, Clark V. Applied statistics: analysis of variance and regression, 2nd ed. New York: Wiley, 1986:236-260.
27. Iwamura Y, Tanaka M, Hikosaka O. Overlapping representation of fingers in the somatosensory cortex (area 2) of the conscious monkey. Brain Res 1980;197:516-520.
28. Zimmerman ID. A triple representation of the body surface in the sensorimotor cortex of the squirrel monkey. Exp Neurol 1968;20:415-431.
29. Baumgartner C, Sutherling WW, Di S, Barth DS. Investigation of multiple simultaneously active brain sources in the electroencephalogram. J Neurosci Methods 1989;30:175-184.
30. Barth DS, Baumgartner C, Sutherling WW. Neuromagnetic field modeling of multiple brain regions producing interictal spikes in human epilepsy. Electroencephalogr Clin Neurophysiol 1989;73:389-402.
31. Douglas WW, Ritchie JM. Non-medullated fibres in the saphenous nerve which signal touch. J Physiol (London) 1957;139:385-399.
32. Coderre TJ, Melzack R. Cutaneous hyperalgesia: contributions of the peripheral and central nervous systems to the increase in pain sensitivity after injury. Brain Res 1987;404:95-106.
33. Devor M, Wall PD. Plasticity in the spinal cord sensory map following peripheral nerve injury in rats. J Neurosci 1981;1:679-684.
34. Jenkins WM, Merzenich MM, Ochs MT, Allard T, Guic-Robles E. Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. J Neurophysiol 1990;63:82-104.
35. Baumgartner C, Barth DS, Levesque MF, Sutherling WW. Human hand and lip sensorimotor cortex as studied on electrocorticography. Electroencephalogr Clin Neurophysiol 1992;84:115-126.
36. Asanuma H. Cerebral cortical control of movement. Physiologist 1973;16:143-166.
37. DeLucchi MR, Garoutte B, Aird RB. The scalp as an electroencephalographic averager. Electroencephalogr Clin Neurophysiol 1962;14:191-196.
38. Cohen D, Cuffin BN. Demonstration of useful differences between the magnetoencephalogram and electroencephalogram. Electroencephalogr Clin Neurophysiol 1983;56:38-51.

Correction

In "^{123}I-iodobenzamide-SPECT predicts dopaminergic responsiveness in patients with de novo parkinsonism" by Schwarz et al, which appeared in the March issue (*Neurology* 1992;42:556-561), an error occurred in the identification and placement of figures 1A and 1B. The figures are correctly identified and oriented below. The editors apologize for the error.

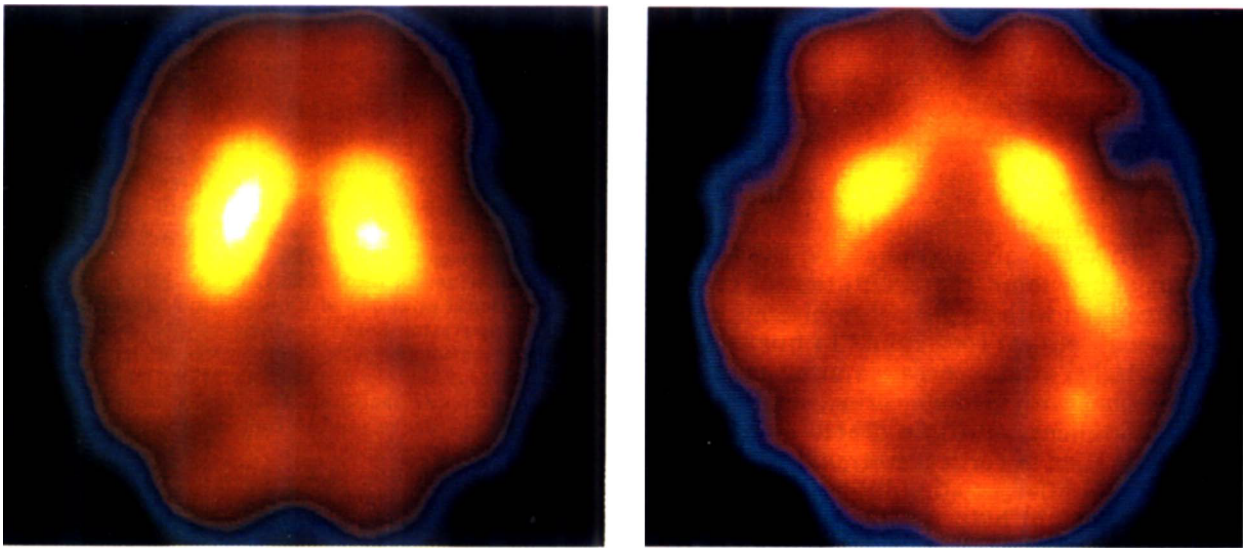

Figure 1. Transverse section of IBZM-SPECT obtained in a patient with parkinsonism and normal IBZM binding and a positive response to apomorphine (A), and decreased IBZM binding and a negative response to apomorphine (B). The images were generated by adding the two consecutive sections with the highest specific IBZM binding.

Cortical sensory representation of the human hand: Size of finger regions and nonoverlapping digit somatotopy

William W. Sutherling, Michel F. Levesque and Christoph Baumgartner

Neurology 1992;42;1020
DOI 10.1212/WNL.42.5.1020