Tactile Discrimination Capacity in Relation to Size and Organization of Somatic Sensory Cortex in Primates: I. Old-World Prosimian, *Galago*; II. New-World Anthropoids, *Saimiri* and *Cebus*

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Living primates vary considerably in brain organization, in sensorimotor and cognitive abilities, and in natural behavioral repertoires. Comparative studies of primary (SI) and secondary (SII) somatic sensory cortex of primates reveal major differences in the size and in the complexity of topographic projection patterns. The separate projections of the glabrous hand to SI cytoarchitectonic areas 3b and 1 described in the Old World (OW) anthropoid *Macaca* and in New World (NW) anthropoids *Cebus*, *Saimiri*, and *Aotus* are lacking in NW *Saguinus* and in the prosimian *Galago*. The relationship between the size and complexity of SI organization and tactile abilities is explored in this study of four species of primates—*Galago*, *Macaca*, *Cebus*, and *Saimiri*. These species were trained to discriminate between pairs of objects differing either in cross-sectional diameter (size) or surface roughness (texture). The course of acquisition of such tactile discrimination in normal *Macaca* and the nature of deficits following SI or SII removals are known. Selective lesions of either cytoarchitectonic area 1 or 2 in *Macaca* affect only texture or size discriminations, respectively. Removal of area 3b in SI, or of SII, in *Macaca* affects both size and texture capacities. The single projection of the glabrous hand to area 3b–1 of *Galago* led to our expectation that the capacity of *Galago* to discriminate textures would be more similar to an area 1–lesioned than to a normal *Macaca*. The substantial and persistent differences between *Macaca* and *Galago* on texture, but not size, tasks lend support to the view that the evolution of a second projection of the glabrous hand to area 1 in *Macaca* contributes to increased texture discrimination capacity. The similarity in multiple projection patterns of the glabrous hand to areas 3b and 1 in *Macaca*, *Saimiri*, and *Cebus* led us to expect greater correspondence in texture discrimination capacity between these three anthropoids than to *Galago*. Contrary to expectations, *Saimiri* and *Cebus* showed a tactile capacity more similar to *Galago* than to *Macaca*. Furthermore, the texture discrimination capacity of *Cebus* actually improved substantially after re-

moval of area 1. This provides further evidence, together with the single SI hand area in NW *Saguinus* and *Galago*, that the separate cutaneous projections to area 1 in OW and NW primates are not homologous but evolved independently and possibly serve different tactile functions.

[Key words: tactile, discrimination, cortex, primates, behavior, evolution]

The comparative study of neural organization and of behavioral capacity has provided important insights into brain–behavior relations in a wide variety of vertebrates. By comparing species-typical features of the mammalian cerebral cortex with related sensory, motor, or cognitive functions, one can consider the role of localized cortical areas in specific behavioral capacities in this major class of vertebrates. Such an approach, in the order Carnivora, has been used to show that the density of peripheral receptors and relative enlargement of central projections from different skin surfaces to primary somatic sensory cortex (SI) correlate with the use of a surface in natural exploratory and discriminative behaviors in the family Procyonidae, which includes the raccoon, coati, and kinkajou (Welker et al., 1963, 1964).

The rich variety of existing primate species provides an unique opportunity for comparative studies of brain organization and behavior. The sizable number of field observations reported over past decades provides detailed information on the natural behavioral strategies of many species in current habitats. Continued examination of the taxonomic relations, based on both the fossil record and biomolecular evidence, between extinct and extant primates provides a firmer basis for the interpretation of comparative work on contemporary species. A major distinction in the study of primate phylogeny, critical to the interpretation of any comparative analysis of living primates, is that of the Old World (OW) and New World (NW) lineages.

The phylogenetic and geographical origin of the NW anthropoids and their taxonomic relationship to OW anthropoids remains one of the most intriguing questions in primate evolutionary biology. The first NW anthropoids appear abruptly in the fossil record in South America about 25 million years ago, without evidence that primates had previously existed on this continent. There are two alternative sources from which the NW anthropoids may have evolved—North American prosimian primates or early African anthropoids (Fleagle and Rosenberger, 1990). The few fossil remains recovered from South America do not provide conclusive evidence, but an African origin is favored because of shared morphological traits (Delson and Rosenberger, 1980; Fleagle, 1988). Through morphological

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Figure 1. This drawing of the prosimian *Galago crassicaudatus* (*G. garnettii*), commonly known as the greater bushbaby, presents a typical bipedal posture assumed in this species, characterized as a quadrupedal climber and upright leaper. *Galago* is a small primate, with a 32 cm average head-to-rump length (Macdonald, 1984). Average adult weight is 1 kg, with little or no sexual dimorphism (Bearder, 1987). The drawing of the glabrous hand indicates the thumb (D1) medial to digits (D2–D5) and palmar pads (P1–P7) (adapted from Biegert, 1961). *Galago* has a generalized primate hand, used mainly for locomotion, capture, and feeding on insects. *Galago*, like most other prosimians, have a stereotyped whole-hand grasp, in which the digit tips contact the palm (Bishop, 1964). During grooming the lower front teeth (forming a specialized tooth comb) are used rather than the hands. When in the bipedal stance frequently assumed during threat, hands are used in fisticuffs combat (Bishop, 1964). The drawing of the OW anthropoid *Macaca fascicularis*, or crab-eating macaque, illustrates the quadrupedal posture assumed during locomotion. *M. fascicularis* is medium sized, with a shorter head-to-rump length and more restricted range of body weights (upper numbers) than *Macaca mulatta* (lower numbers) or rhesus macaque (Macdonald, 1984). Both species are sexually dimorphic, with females on average 1–2 kg lighter than males.

comparisons of extant primate species it may be possible to infer phyletic relationships and evolutionary sequences. However, parallel evolutionary processes are not rare; therefore, it cannot be assumed that the presence of a shared morphological trait necessarily means that the functional aspects are homologous. This behavioral study compares the tactile discrimination capacity of *Galago*, a prosimian primate believed to have retained features of its brain and behavior that reflect an earlier stage of primate evolution 40–50 million years ago, to three anthropoid primates with more recent evolutionary histories: the OW *Macaca*, and NW *Saimiri* and *Cebus* (Napier and Walker, 1967; Radinsky, 1974; Carlson and Welt, 1981; Fleagle, 1988).

Among existing prosimians, presently found only in the Old World, *Galago* (family Lorisidae, subfamily Galaginae) is widely distributed across eastern and southern Africa. Its nervous sys-

Figure 2. This figure shows body and hand drawings of the NW anthropoids *Saimiri sciureus* and *Cebus apella*. Both species are widespread throughout South America. Weight ranges for both species are given in the figure along with head-to-rump lengths (from Macdonald, 1984). The average weight for adult *Saimiri* females (F) is 0.7 kg, and adult males (M), 1 kg. Average weight for adult *Cebus* females is 2.5 kg, and adult males, 3 kg (Robinson and Janson, 1987). The hand drawings identify the five glabrous digits (D1–D5), the palmar (P1–P7), thenar (TH), hypothenar (HP), and accessory hypothenar (HD) pads (Biegert, 1961). *Saimiri* has comparatively short fingers and a short thumb with limited opposability. When grasping insects, the mainstay of their diet, *Saimiri* flex the joints between digits and palm. *Cebus* also have short fingers, but the thumb is opposable, and they exploit their manual strength and dexterity to grasp foods unavailable to other species (Fleagle, 1988).

tem is the most extensively studied of the prosimians and its behavior has been studied in its natural habitat. Among the widely diverse OW anthropoids, *Macaca* (family Cercopithecidae, subfamily Cercopithecinae) is the most widely distributed of the nonhuman primate infraorder and the most commonly studied laboratory primate (Fig. 1).

The NW genera *Saimiri* and *Cebus* (family Cebidae, subfamily Cebinae) are found throughout most of Central and South America. Like all NW primates, *Saimiri* and *Cebus* are arboreal and the smaller-bodied *Saimiri* frequently form mixed groups with the larger-bodied *Cebus*. Both genera are frequently used in laboratory studies and have been studied extensively in their natural habitats (Fig. 2).

In the somatic sensory cortex of primates, the glabrous hand is the skin surface with the greatest relative enlargement compared to other body parts (Carlson, 1985, 1990). In addition to the differential enlargement of skin surfaces, research on the somatic sensory system in primates has come to focus on the importance of the relative complexity of topographic patterns in the SI area in different species. Early macroelectrode recordings in SI of *Macaca* defined only a single major topographic pattern in SI spanning several different cytoarchitectural fields in the postcentral gyrus (Woolsey et al., 1942). More recently, microelectrode studies in *Macaca* revealed multiple topographic

Figure 3. The drawings of the lateral surface of left hemispheres of *Macaca* and *Galago* show differences in number and orientation of sulci between the species. In *Galago*, SI is indicated by the shaded area located intermediate to the sagittally oriented rectus (*R*) and intraparietal sulcus (*IP*). Only a single hand area spans SI with the nonhairy or glabrous (*G*, white) projecting to area 3b and the hairy digits and ulnar (*UH*) and radial (*RH*) hand (*H*, hatched) projecting to area 1 and lateral 3b (*G. crassicaudatus*, Carlson and Welt, 1980; *G. senegalensis*, Sur et al., 1980). The location of the cutaneous input from the hand to the SI area in *Macaca* is indicated by shaded area behind the coronally oriented central sulcus (*CS*). The major cutaneous projection area, area 3b, is located in the posterior bank of the central sulcus, with the second SI cutaneous area, area 1, shown on the anterior crown of postcentral gyrus. In *Macaca*, the postcentral sulcus (*PCS*) lies medially midway between central sulcus and intraparietal sulcus (*IPS*) and near cytoarchitectonic division of areas 1 and 2. In *Macaca* two separate glabrous projection patterns (*G1* and *G2*, white) extend across areas 3b and 1, with a single, distributed hairy projection pattern (*H*, hatched) across the two cytoarchitectonic areas (*M. mulatta*, Paul et al., 1972; *M. fascicularis*, Nelson et al., 1980). The division between areas 3b and 1 is represented by a dashed line, while the curve from the crown to the anterior bank of the central sulcus is indicated by a solid line. The numbers under the anterior pole of each brain hemisphere indicate brain weights, for *Galago* (average) and separately for *Macaca* female (upper numbers) and male (lower numbers).

projection patterns from the glabrous hand to SI, corresponding to architectonic areas 3b, 1, and 2 (Paul et al., 1972; Nelson et al., 1980; Fig. 3). The use of "SI" in this article refers to the historical concept of the postcentral gyrus without reference to the debate about "SI proper" and issues of homology of areas 3a, 3b, 1, and 2 between primates and other mammals (Merzenich et al., 1978). Furthermore, these microelectrode mapping studies of SI have revealed differences in the size and topographic projection patterns of the glabrous hand and other body surfaces between prosimians, OW and NW anthropoids, as well as among the NW anthropoids.

In contrast to *Macaca*, we found only a single topographic pattern from the glabrous hand to area 3b and from the hairy hand to area 1 of the African prosimians *Galago* (Carlson and Welt, 1977, 1980; Sur et al., 1980; Fig. 3) and *Perodicticus* (FitzPatrick et al., 1982). In the Asian prosimian *Nycticebus*, we reported a minor second glabrous projection within the major projection of the hairy hand to area 1 (Carlson and FitzPatrick, 1982). Our subsequent studies of secondary somatic sensory cortex (SII) in *Galago* demonstrated a single hand and body projection pattern (Burton and Carlson, 1986) with features similar to the single area defined in SII of *Macaca* (Robinson and Burton, 1980).

Like *Macaca*, the NW anthropoids *Aotus* (Merzenich et al.,

1978), *Cebus* (Felleman et al., 1983), and *Saimiri* (Sur et al., 1982) have separate projections from glabrous hand and other body surfaces in areas 3b and 1 (Fig. 4), yet *Saguinus*, another NW species, has only a single hand and body projection area in SI, reminiscent of the *Galago* SI area (Carlson et al., 1986). Based on these results, it can be assumed that the last common ancestor of OW and NW anthropoids, whether of a prosimian or anthropoid grade, possessed only a single SI topography. Thus, when the existing comparative studies of SI cortical maps are examined relative to the phyletic relation between OW and NW species, it would appear that multiple SI areas seen in OW and NW species evolved independently after the divergence from a common ancestor.

The present studies were done to determine the capacity of these four species to acquire a series of size and texture discriminations of varying difficulty and to perform consistently on a composite task (the ALLS task) of the same series of discriminations. A comparison of the tactile capacity of *Galago* and *Macaca* relative to the size and complexity of their respective SI and SII hand areas allows for an estimation of the behavioral significance of the more recently acquired cutaneous projection to area 1 in SI in *Macaca*, which is lacking in *Galago*. By comparing the acquisition and performance scores of *Galago* and *Macaca* to *Saimiri* and *Cebus* and to the relative and ab-

Figure 4. The drawings of the lateral surface of left hemispheres of *Saimiri* and *Cebus* show the location of cutaneous input to the SI hand area (shaded). Maps of the hand areas show the general topographic features of the input from the glabrous (nonhairy) digits and palm (white) and hairy digits and hand (hatched). In *Saimiri* the central sulcus (CS) does not divide the somatic sensory from the more anterior motor cortex but rather the central sulcus lies within SI (Sur et al., 1982). Input from the glabrous areas form two topographic patterns, G1 and G2. The palm pads, hypothalar eminence (HP), and ulnar hand (UH) project to the margins of the 3b/1 border and digits to anterior area 3b and posterior area 1. The hairy surface of the hand and digits (H) projects primarily to the margins of the G1 and G2 patterns, though RFs on the dorsal hairy digits can be found within the areas 3b and 1 glabrous hand region (Merzenich et al., 1987). The area 3b/1 border is signified by a dashed line and the central sulcus by a solid line. The map of the *Cebus* SI hand area also shows two glabrous digit patterns (G1, G2) across areas 3b and 1. The topographic pattern of palm, hairy digits, ulnar (UH), and radial (RH) hand, and radial arm (RA) is compressed in the areas medial and lateral to G1 and G2 (*Cebus*, Felleman et al., 1983; *Saimiri*, Sur et al., 1982). In contrast to *Saimiri*, and similar to *Macaca*, the digits project across the anterior-posterior expanse of areas 3b and 1 and palm pads are located medial to the digit area. IP, intraparietal sulcus; LS, lateral sulcus.

solute expansion of their SI cortical hand areas, the behavioral significance of evolutionary changes in cortical expansion and organization may be better understood.

The current study also provides new information on the expansion of the SI hand area relative to the projection areas of other body surfaces and to the actual glabrous skin area of the hand and foot. By obtaining actual measures of glabrous skin areas of all four species in this study, we are able to make estimates of the magnification factors in SI (and SII in *Galago* and *Macaca*) of cortical projection areas for the hand and foot. Our previous maps of SI in the greater *Galago* (see Materials and Methods below, concerning species designation) were restricted to the hand area, with some adjoining receptive fields (RFs) from the arm and face area (Carlson and Welt, 1977, 1980). Those first maps of both awake and anesthetized *Galago* were intended to obtain the fine organizational detail of the cutaneous and noncutaneous input from the hand similar to microelectrode maps of the SI hand area in *Macaca* (Powell and Mountcastle, 1959; Paul et al., 1972). With an interest in estimating the relative expansion of the hand, foot, and other body surfaces projecting to SI in greater *Galago*, it was important we obtain maps of the remaining SI region, as had been done earlier for the lesser *Galago*, *G. senegalensis* (Sur et al., 1980). Comparative data on the relative and absolute expansion of the hand area (or areas) in cortex, relative to other body surfaces or to actual skin surface areas, provide another approach to the un-

derstanding of how evolutionary changes in neural structure and function are reflected in increased behavioral capacity.

Materials and Methods

Subjects. Eight adult *Galago garnettii* served as subjects in these studies (Table 1). This is the same species used in our previous studies of SI and SII and referred to as *Galago crassicaudatus* (Carlson and Welt, 1980; Burton and Carlson, 1986). The species designation of the greater *Galago* has changed over the past decade. The two types, which in the past were separated on the subspecies level, are presently considered as separate species. *Galago crassicaudatus* now refers to what was previously called *Galago crassicaudatus argentatus*. What was in the past referred to as *Galago crassicaudatus*, the species of our past and current studies, is now referred to as *Galago garnettii* (Bearder, 1987). All subjects were captive born and were within the normal size range for their gender. Behavioral data were obtained from *Galago* in this study and compared to data on *Macaca* described in a previous publication (Carlson, 1984).

All five *Saimiri* were normal adults, tested on their right hand. The two *Cebus* were first trained as normal and tested on their right hand (Table 1); Cb1 was later retested on the right hand after a single unilateral lesion in the left hemisphere, and Cb2 was retested on the right hand following an area 1 lesion in the left hemisphere, and on the left hand following a similar lesion in the right hemisphere. The lesions (*Cebus*-area 1) are illustrated in Figure 13, and intended to approximate the pattern of cutaneous projection from the hand defined as "area 1" by electrophysiological criteria in *Cebus albifrons* by Felleman et al. (1983; see Fig. 2). These data are also compared to previously published behavioral data from *Macaca* (Carlson, 1984).

Behavioral techniques. These behavioral data were obtained using

Table 1. Summary for the three primate species

Species	Origin	Gender	Age	Hand tested	Weight (g)	Lesioned hemisphere
<i>Galago garnettii</i>						
Gc1a	Captive born	Female	Adult	Right	920	None
Gc3a	Captive born	Male	Adult	Right	1065	None
Gc4a	Captive born	Male	Adult	Right	950	None
Gc5a	Captive born	Male	Adult	Right	1100	None
Gc6a	Captive born	Male	Adult	Right	790	None
Gc8a	Captive born	Male	Adult	Right	940	None
Gc9a	Captive born	Male	Adult	Right	915	None
Gc10a	Captive born	Female	Adult	Right	660	None
<i>Cebus apella</i>						
Cb1a	Captive born	Female	Adult	Right	2335	None
Cb1b				Right		Area 1, left
Cb2a	Captive born	Male	Juvenile	Right	1765	None
Cb2b				Right		Area 1, left
Cb2c				Left		Area 1, right
<i>Saimiri sciureus</i>						
Ss1a	Wild born	Female	Adult	Right	695	None
Ss2a	Wild born	Female	Adult	Right	670	None
Ss3a	Captive born	Male	Old	Right	1000	None
Ss4a	Captive born	Male	Adult	Right	1050	None
Ss5a	Wild born	Female	Adult	Right	595	None

techniques described in previous publications (Carlson, 1984, Carlson and Burton, 1988). Animals were tested in the dark, with a low-level "white noise" piped to the test chamber. Access to water was restricted during the week (except during testing), with subjects maintained at 90–100% of normal body weight. While in a primate restraint chair, they were presented a rotating carousel with 12 pairs of handles that differed either in size (cross-sectional diameter) or texture (covered with different grades of sandpaper). Size handles varied from the smallest handle of 7 mm diameter to 9, 12, and 18 mm in cross-sectional diameter. All texture handles were 14 mm in diameter and covered by different grades of aluminum oxide abrasive (3M), from the smooth 320 grains/linear inch (gr/in) grade to increasingly rough grades of 120, 80 and 40 gr/in. All handles were 3.8 cm long. Each of the six size and six texture pairs are referred to as a "comparison" throughout the article.

During the training phase, an animal was first presented with only the smallest (and correct) handle of the initial three size comparisons, with no handle in the other position. This same 7–0 mm comparison was presented, as a correction procedure, if an animal responded below 60% on the easiest comparison. During the "acquisition" phase the animal was presented pairs of vertically mounted handles (one above the other). The smallest or smoothest of the pair was designated as "correct" and is identified as the first value of a pair (i.e., 7–18 mm or 320–40 gr/in). To indicate a response the animal was required to pull forward on the handle to activate the microswitch attached to the lever on which it was mounted. Each single presentation of a comparison is referred to as a "trial." If a correct choice was made on a trial, the animal was reinforced by a small quantity of water delivered through a metal nipple mounted at mouth level on the chair. If an incorrect response was made, no fluid was delivered and a buzzer sounded briefly to indicate an error. After a response the carousel rotated to the next position to present the adjacent pair of handles. During the acquisition task, the animal was presented a series of 12 pairs of handles (of the same size or texture comparison), in which the "correct" handle was varied from the upper to lower position in a quasi-random order. If the animal performed correctly on 80% of the trials in a session (composed of at least 50 trials) it was given a more difficult comparison in the next daily session. If it performed at less than 60% correct for 2 d it was returned to an easier comparison for the next session and if between 60–80% correct it continued testing on the same comparison in the subsequent session. By such a procedure the six possible combinations of the four handles were presented in the order given in Figure 6 (order of testing).

During acquisition, two measures of learning efficiency were used: (1) the rate of learning, shown by the number of sessions required to reach the 80% correct criterion, and (2) the number of errors accumulated prior to reaching criterion on a comparison level. Total errors, not total trials, to criterion was used as the indicator of *efficiency of acquisition* in this and previous studies (Carlson, 1984; Carlson and Burton, 1988). If an animal performed at levels approaching but not exceeding the expected 80% criterion, or if criterion was reached early in a session, errors would accumulate at a lesser rate than total trials and thereby serve as a more sensitive accumulative measure of efficiency. If an animal failed to respond for at least 50 trials in a session, errors were included in the total for that comparison, but if the 80% correct criterion was achieved in less than 50 trials, it would not qualify as obtaining criterion. If the animal was returned to that comparison (as a correction procedure), errors made during those sessions were not counted toward error scores for the individual comparison or for the total errors to criterion. Total errors on size and texture acquisition tasks is the sum of errors required to reach criterion on each of the six individual comparisons, including comparisons on which criterion was not reached in at least 20 sessions. Some animals that failed to master the 320–120 gr/in comparison (in less than 20 sessions) were run on an intermediate-level comparison (320–100 gr/in) and errors to criterion on this task were included in total errors.

After being trained on the six combinations of the four handles during acquisition, the animal was tested on the ALLS task in which *all* six comparisons were presented together in the same session, as a measure of consistent performance on these previously learned discriminations. The animal was run for 120 trial sessions over 5 consecutive days on the ALLS task. Scores for individual animals consist of the average percentage correct over the five sessions on each individual comparison. The average score for individuals on the ALLS task is an average for the six tasks and these averages for individual comparisons and for the total of the six comparisons in the ALLS task are compared both within and between species.

Statistical significance was determined by using the nonparametric Mann-Whitney rank sum test. One-tailed *t* test was used when comparing the prosimian *Galago* to the anthropoids (*Macaca*, *Saimiri*, or *Cebus*) since they were expected to perform better than *Galago* on all measures. When comparing within the anthropoid sample a two-tailed *t* test was used since no directionality could be assumed. Only those tests with 0.05 probabilities or less were considered significant, though those less than 0.075 are included in the tables.

Surgical and recording procedures in Galago. Surgical and recording procedures were as described in Carlson and Welt (1980) and Burton and Carlson (1986). All procedures were performed under surgical levels of anesthesia. Premedication of 10 mg/kg of ketamine hydrochloride and 0.05 ml of atropine sulfate (administered intramuscularly) was followed by 20 mg/kg sodium pentobarbital (administered intraperitoneally), with subsequent doses of 5 mg/kg given as needed. The cornea was covered with Lacrilube. To maintain normal body temperature, the animal was placed on a hot water pad with rectal probe to monitor temperature.

The head was held in a Kopf stereotaxic instrument. After a scalp incision, and retraction of attached muscle, a large parietal bone flap was removed to expose the region of cortex between the rectus and intraparietal and from the midline to the lateral sulcus (Fig. 3). Prior to opening the dura, a shallow chamber of dental acrylic was attached to the skull margins to contain a pool of sterile silicone fluid (Dow Chemical) over the exposed cortex. The dura was opened and the cortical surface was photographed to provide vascular landmarks for placement of electrode penetrations.

Low-impedance tungsten microelectrodes (1.0–1.5 M Ω at 1000 Hz) were lowered 800–1200 μ m into the parietal region as the face, arm, and leg were briskly stimulated. When evoked activity was detected, receptive fields were defined by small probes to localize minimal receptive field to brushing or to punctate stimuli. Following complete exploration of the parietal cortex, the animal was anesthetized with a lethal dose of sodium pentobarbital. When spontaneous respiration ceased, it was perfused intracardially with 0.9% saline followed by 10% neutral buffered formalin-saline for histological processing of the cortex.

Cortical lesions in Cebus. Sterile surgical procedures were followed throughout, with the animals kept at surgical levels of anesthesia as described above. The scalp was shaved and scrubbed with Septisol, 70% alcohol, and 10% Betadine solutions. The scalp was incised from the brow to the occiput with the head held in the stereotaxic instrument. Skin margins were retracted and covered with damp saline-soaked sponges and a large skull flap was removed from over parietal cortex. The dura was opened laterally near the skull edges to expose the primary somatic sensory region, indicated by the configuration of the central and lateral sulci (Fig. 4).

Electrophysiological criteria were used to locate the hand area. Responses of cell clusters were recorded with sterile microelectrodes lowered 800–1200 μ m into the parietal region over the expanse of the postcentral crown and 1–2 mm into the central sulcus. The active sites were noted on drawings of the cortical vasculature, to delineate the extent of area 1 corresponding to the distal to proximal sequence of receptive fields found in a posterior to anterior axis of the postcentral gyrus (Felleman et al., 1983). Cortical lesions were made by subpial aspiration of the gray matter through a 16 gauge suction tube. After filling the lesion site with an absorbable gelatin sponge (GelFoam), the dura was repositioned and sutured with 4-0 coated Vicryl and covered with gelatin film (GelFilm). Small holes were drilled into the bone flap and skull margins, the flap was then reinserted and stabilized with Vicryl sutures. Connective tissue was sutured with absorbable sutures and the scalp closed with interrupted 4.0 silk sutures, which were removed 5–7 d later. The animal's temperature and vital signs were monitored until recovery from anesthesia was complete. Prophylactic administration of antibiotic Combi-Pen (0.25 ml/kg) was given in a single dose. A 1–2 week recovery period followed before tactile discrimination tasks were initiated. After completion of behavioral testing, the animal was killed and the brain prepared for histological processing.

Histological processing and computer reconstruction of cortex. Cortical blocks through the pre- and postcentral gyrus were cut in 50 μ m sections in the sagittal plane and stained for Nissl substance with cresylecht violet. Every 10th section was drawn with a camera lucida, and the drawings were digitized. Computer reconstructions of the drawings and of the estimated area of cortical removal are shown in Figure 13. Three-dimensional reconstructions of the lesions and remaining postcentral gyrus were obtained by outlining a contour from the remaining crown to the anterior bank of the gyrus of each section. Other details in the drawings include layer VI, layer IV, and the precentral gyrus. The full mediolateral profile of the lesion was created by the computer based on the magnification factor of the drawing, the thickness of sections, the interval between sections, and the viewing angle specified by the x,y,z-coordinates of the three-dimensional image. The illustrated profile was chosen to best visualize the full mediolateral expanse of the removal.

Measurement of skin area and cortical projection area of glabrous

hand and foot. Three of the behavioral animals (Gc5, Gc8, and Gc10) were among the 12 adult *Galago* used to determine the surface area of the glabrous hand and feet by direct carbon powder prints (Phillips-Conroy et al., 1986). Two juvenile male *Macaca mulatta* were used for the hand and foot prints (and from enlarged photographs of the hand in an additional juvenile) to determine the surface of the glabrous skin. To obtain the direct hand and foot prints, animals were tranquilized with a single dose of ketamine hydrochloride (10 mg/kg) and atropine sulfate (0.05 ml) administered intramuscularly. Glabrous surfaces were cleaned and dried prior to the dusting of carbon powder. With the digits spread apart, the hand or foot was flattened against 5 inch wide cellophane tape (book tape, 3M) and pressed firmly against the tape to leave a complete impression of the glabrous print. The tape was fixed to plain white paper for preservation. From photocopies of hand and foot prints (or of hand photographs) outlines of the glabrous surface were traced on a digitizing pad and the area of each digital, palmar, or volar surface was calculated.

The SI surface areas for the hand, foot, and other body areas in *Galago* were calculated by digitizing the outline of the complete SI maps obtained in this study (Gc5-83, Gc6-84, Gc7-84) and from our maps of the SI hand area in a previous publication (146-77, 333-73; Carlson and Welt, 1980). From our previous publication of *Galago* SII, estimates of the size of the hand and foot areas were obtained from animals G2 and G3 (Burton and Carlson, 1986). Maps of SI in *Macaca mulatta* were obtained from the published figures of Paul et al. (1972) and for *Macaca fascicularis* from Nelson et al. (1980). Estimates of the hand and foot areas in SII of *Macaca* were taken from published figures in Friedman et al. (1986) and Robinson and Burton (1980).

Direct prints of the skin surfaces of the hand and foot in five *Saimiri* and four *Cebus* (including two adult animals not used for behavioral testing) were digitized as for the other species. Measurements of the SI surface of the hand and foot areas were obtained from previously published maps of *Saimiri* (Sur et al., 1982) and *Cebus* (Felleman et al., 1983). At least three measurements were made of hand and foot projection areas, with an average value calculated in SI (and SII in *Galago* and *Macaca*) in each species.

Results

1. *Galago* and *Macaca*

Size discrimination

Size acquisition. Seven adult *Galago* were initially trained to the 80% correct criterion on the six size acquisition comparisons, followed by five sessions on the size ALLS task. The acquisition profiles of individual animals on the first three size comparisons, shown as percentage correct for each comparison on each session, are illustrated in Figure 5. By reference to Table 2, it is possible to characterize both the individual (Gc1–Gc9) and the species average (Gc AVG and Mm AVG) error scores.

As a group *Galago* required two or three sessions on each of the first two tasks, the easy (7–18 mm) and moderate (7–12 mm) level comparisons. On the third and least discrepant (defined by absolute physical difference between handles, 7–9 mm comparison, i.e., 2 mm difference), two to seven sessions were required to reach criterion (Fig. 5). When error scores on individual size comparisons for *Galago* were compared to those for *Macaca*, *Galago* was found to make significantly more errors on the first three tasks in order of testing and on the total over all six comparisons (Table 2, top; Fig. 6).

Size ALLS. Following the acquisition task, all animals were tested on the ALLS task. The level of performance on the ALLS task is shown as percentage correct for the six comparisons averaged over the five sessions (Table 2, bottom; Fig. 6, right). On average *Galago* attained above 90% on the two easy (7–18 mm, 9–18 mm) and two moderate (12–18 mm, 7–12 mm) level tasks. They performed over 80% on one difficult (9–12 mm), but under 60% correct of the most difficult (7–9 mm), comparison. The efficiency of acquisition for *Galago* was significantly

SIZE ACQUISITION

Figure 5. The course of acquisition for size tasks by normal *Galago garnettii* is shown for Gc1, Gc3–Gc6, Gc8, and Gc9. See Carlson (1984) for normal *Macaca mulatta*. These data show the percentage correct on the discrimination of the cross-sectional diameter of handles by each animal over individual sessions on the first three size comparisons in the order of testing. Weeks of testing indicates the length of time an animal was tested on size acquisition.

worse than that of *Macaca* on the first three tasks in order of testing and on the total errors over the six tasks, but when the error scores were ranked by order of difficulty (defined by physical differences between the handles) rather than order of testing, the combined contribution of these factors to errors scores can be appreciated (Fig. 6). On the size ALLS task there was no contribution of “order of testing” as the same six comparisons were presented together repeatedly in the same session. On the ALLS task where “order of difficulty” was the remaining influence on performance, *Galago* was significantly inferior to *Macaca* only on the difficult 7–9 mm comparison.

Texture discrimination

Texture acquisition. Following completion of the size discrimination tasks, the same seven *Galago* and one additional animal (Gc10) were trained to discriminate between a series of six texture comparisons. The acquisition profiles for the first three comparisons are illustrated in Figure 7. On average *Galago* required about six sessions to reach criterion on the first and easy task (320–40 gr/in, 386 μ m difference in grain size) and averaged more than 200 errors prior to criterion (Table 3, top). On the second task (320–80 gr/in), three or four sessions were

required and only 65 errors on average were made prior to criterion. The third task (320–120 gr/in and 91 μ m grain difference) was the second most discrepant in terms of grain size but consistently the most difficult in terms of errors to criterion for both species. On this task, two *Galago* (Gc9 and Gc10) failed to reach criterion after more than 40 sessions but mastered an easier (320–100 gr/in) comparison in only four sessions (Fig. 7). When tested further on the more difficult discrimination (320–120 gr/in), they once again failed, whereas the six animals that reached criterion made an average of 766.8 errors.

As a group *Galago* made significantly more errors than *Macaca* on the first (320–40 gr/in), second (320–80 gr/in), and third (320–120 gr/in) texture acquisition tasks in order of testing (Fig. 8), yet these differences do not reflect entirely the order of difficulty as no significant difference was found on the 120–80 gr/in (52 μ m difference) comparison. Significant group differences were obtained on total errors over all 6 tasks (Table 3, top; Fig. 8).

Texture ALLS. Following the acquisition task, seven of the original animals were tested on texture ALLS task. On average *Galago* scored over 90% correct on the easy and over 80% correct on the moderate level tasks. On the difficult 320–120

Figure 6. The bar graphs illustrate the average number of errors made during size acquisition and ALLS performance tasks, prior to reaching the 80% correct criterion for *Galago* (see Table 2) and *Macaca* (see Carlson, 1984). The accumulated errors for the two species on the different size tasks are given both in the order of testing and when rearranged by order of difficulty (difficulty being a physical, but not necessarily the psychological, difference between handles). The ALLS performance data are presented as average percentage correct for individual comparisons by order of difficulty. The asterisks found over some bars indicate significant differences (Mann-Whitney one-tailed tests; *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$; see Materials and Methods).

Table 2. Size discrimination by *Galago* (in order of difficulty)

	Size comparison (difference)						Total	Average
	7-18	9-18	12-18	7-12	9-12	7-9		
	mm (11 mm)	mm (9 mm)	mm (6 mm)	mm (5 mm)	mm (3 mm)	mm (2 mm)		
Errors to criterion on size acquisition task								
Gc1	239	1	64	174	34	81	593	—
Gc3	33	0	3	14	20	321	391	—
Gc4	129	0	73	173	17	86	478	—
Gc5	50	0	0	96	2	190	338	—
Gc6	28	6	69	44	68	60	275	—
Gc8	89	1	10	10	9	72	191	—
Gc9	44	6	119	29	31	103	332	—
Gc AVG	87.4	2	48.3	77.1	25.9	130.4	371.1	—
Mm AVG	7.8	3.3	21.6	5.2	23.2	54	115.1	—
<i>p</i>	0.0003***	NS	NS	0.0006***	NS	0.028*	0.001***	—
Percentage correct on size ALLS task								
Gc1	100	97.5	97.44	97.37	92.11	71.79	—	92.67
Gc3	100	100	91	89	78.79	55	—	85.64
Gc4	100	100	97.98	97	89	58	—	90.32
Gc5	100	100	94.87	98.67	96.05	53.95	—	90.57
Gc6	96.7	98.89	92.13	90.22	80.9	49.45	—	84.69
Gc8	96.55	91.38	80.7	91.23	82.76	54.39	—	82.9
Gc9	96.88	96.92	93.44	90.91	90.63	56.72	—	87.34
Gc AVG	98.5	97.8	92.5	93.5	87.2	57	—	87.7
Mm AVG	98.5	97	93.1	95.5	89.1	72.4	—	90.5
<i>p</i>	NS	NS	NS	NS	NS	0.0017**	—	NS

*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

gr/in task (composed of smaller grain sizes but with greater grain size difference, i.e., 91 μm difference), they performed under 60% correct compared to the 120–80 gr/in comparison (52 μm difference), on which they averaged over 70% (Table 3, bottom; Fig. 8). Although six of the eight *Galago* reached the 80% criterion on the 320–120 gr/in during acquisition, none performed over 60% on that comparison on average over the five ALLS sessions. *Galago* consistently performed below *Macaca* on all six texture comparisons. Statistical comparison of *Galago* and *Macaca* performance revealed significant differences on four of six individual comparisons (including the three most difficult tasks) and on the average over the six comparisons (Table 3, bottom).

Microelectrode mapping of the SI head, trunk, leg, and foot areas

A composite obtained from the three animals mapped in this study, combined with highly detailed hand maps from two animals in the previous study (Carlson and Welt, 1980), is given in Figure 9A. Within each of the projection areas for the different body surfaces, the progression of RFs was highly consistent from one animal to the next and to those progressions seen in *G. senegalensis* (Sur et al., 1980). As shown in Figure 9B, the posterior portion of the head and ear projects to the posterior region of the SI head area, with the eye, snout, and nose each projecting more anteriorly. Fields on the glabrous and hairy hand were intermediate to a split arm area as seen in Figure 9B but RFs on the hand were not extensively examined in these studies. From a row of penetrations extending from lateral to medial SI, RFs progressed from the glabrous hand to fields on the ventral and dorsal arm and then to the trunk, leg, and foot.

The organization of the foot area resembled that described earlier for the hand, with RFs on the dorsal and ventral digit tips located at the anterior border and fields on the proximal digits and plantar surfaces intermediate to those on the dorsal, hairy surface of the hand and foot. In spite of the major size differences between the greater *Galago*, *G. garnetti* (average 1000 gm), and the lesser *Galago*, *G. senegalensis* (average 250 gm; Sur et al., 1980), the relative proportion of SI devoted to the different body surfaces, and the general topographic details were highly similar in the two prosimian species.

Glabrous hand and foot area and SI and SII magnification factors for *Galago* and *Macaca*

From enlarged photographs of individual body parts of an adult *Galago*, it was determined that the head represented approximately 11.4% of the body surface. In our recent complete maps of SI, we found that the head projected to 37% of the total SI area—a threefold increase in the relative representation. Similarly, the skin surface of the glabrous hand represented only 2% of the total body surface area but the cortical projection area for the hand represented 11.2% of the total SI area. This represents more than a fivefold elaboration of cortical surface as compared to the skin surface. The skin of the glabrous foot represented 3.1% of body surface area and 8.7% of total SI surface area, less of an elaboration than for the glabrous hand. In addition, the area of glabrous skin on the hands and feet was estimated from direct prints of 12 adult *Galago* and 2 juvenile *M. mulatta* (and photographs of another *Macaca*) chosen to approximate the size of animals used in previous electrophysiological recording experiments (Paul et al., 1972; Nelson et al.,

TEXTURE ACQUISITION

Figure 7. The course of acquisition for texture tasks by normal *Galago* Gc1, Gc3–Gc6, and Gc8–Gc10 is shown. These data show the percentage correct on the discrimination of the different grades of sandpaper-covered handles by individual animals on all sessions on the first three texture comparisons in the order of testing. *Weeks of testing* is in reference to the first day of size acquisition training.

Table 3. Texture discrimination by *Galago* (in order of difficulty)

	Size comparison (difference)						Total	Average
	320–40 gr/in. (386 μm)	120–40 gr/in. (295 μm)	80–40 gr/in. (243 μm)	320–80 gr/in. (143 μm)	320–120 gr/in. (91 μm)	120–80 gr/in. (52 μm)		
Errors to criterion on texture acquisition task								
Gc1	174	39	59	34	1084	306	1696	—
Gc3	125	9	22	29	305	22	512	—
Gc4	192	20	520	62	254	—	1048	—
Gc5	285	2	7	139	1167	238	1838	—
Gc6	87	3	3	61	821	96	1071	—
Gc8	89	4	18	13	970	28	1122	—
Gc9	490	6	12	147	2099 ^a	24	2913	—
Gc10	374	11	75	41	1786 ^a	13	2465	—
Gc AVG	227	11.8	89.5	65.8	1060.8	103.9	1583.1	—
Mm AVG	77.2	5.2	11.3	26.5	92.2	42.4	316	—
<i>p</i>	0.0043**	0.0566	NS	0.0227*	0.0008***	NS	0.0001***	—
Percentage correct on texture ALLS task								
Gc1	78.72	82.22	77.27	82.61	57.78	67.39	—	74.36
Gc3	94.00	88.00	71.00	85.00	58.00	74.00	—	78.33
Gc5	98.00	100.00	96.00	71.00	57.00	77.00	—	83.17
Gc6	96.94	95.92	94.00	79.59	51.52	76.53	—	82.40
Gc8	98.91	97.06	85.15	92.16	55.88	86.14	—	85.67
Gc9	93.18	89.89	69.32	82.76	50.00	85.23	—	78.20
Gc10	96.63	94.38	67.42	88.64	52.81	82.95	—	80.45
Gc AVG	93.8	92.5	80	83.1	54.7	78.5	—	80.4
Mm AVG	96.9	97.8	90.5	94.8	63.7	90.5	—	89
<i>p</i>	NS	0.05*	NS	0.0087**	0.0189*	0.002**	—	0.002**

^a Failed to reach criterion in <30 sessions.

*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

Figure 8. The bar graphs illustrate the average number of errors made during texture acquisition and ALLS performance tasks, for *Galago* (see Table 3) and *Macaca* (see Carlson, 1984). The accumulated errors for the two species on the different texture tasks are given in the order in which they were presented (order of testing) and in order of difficulty. See Figure 6 for additional details.

1980). The average of these measures, along with body weight for each species, is given in Table 4.

For *Galago* the skin area of the glabrous hand was 73% of the skin area for the foot area, yet the hand projection area in

SI was about 125% that of the SI foot area. Although the SII hand area was seven times the size of the SII foot area, the SII hand area was only about half the size of the SI hand area. The largest cortical magnification factor for glabrous skin in *Galago*

Figure 9. Stylized map of the entire body area (A), head (B), trunk (C), and foot (D) areas in SI of *G. garnetti*. These are microelectrode maps of the entire medial (M) to lateral (L) and anterior (A) to posterior (P) extent of the projection of glabrous and hairy body surfaces to SI. A, The summary drawing of the maps of three animals from the present study (Gc5-83, Gc6-84, and Gc7-84) and two animals (146-77, 333-73) from a previous study of the SI hand area (Carlson and Welt, 1980) were used to construct the composite and individual maps illustrated. These same maps were used to determine the individual SI areas for the hand and foot given in Table 4. The drawing of the lateral view of the left hemisphere includes a stippled region indicating the general location of the SI body map, between the sagittally oriented sulci in the frontal and posterior parietal regions (see Fig. 3 for more details). The symbols used to denote receptive fields (RF) from specific body parts are shown in the expanded SI map summary. The RFs illustrated in B–D are designated by the large solid circles and the NIL (no response) recording sites are represented by the asterisks, as shown in A. B, In Gc5-83, a posterior–anterior progression of recording sites in the most lateral region of SI is associated with RFs beginning at the ear, moving to the eye, snout, nose, upper lip, and chin. This pattern of subdivisions in the SI head (solid triangles) area in *G. garnetti* is similar to that in *G. senegalensis* (Sur et al., 1980). C, A lateral–medial progression of RFs through the middle region of SI illustrates the progression from the glabrous hand (see Carlson and Welt, 1980), to ventral and dorsal arm (open squares), and finally dorsal and ventral trunk (solid diamonds) and leg (solid squares). The six-pointed stars designate RFs on the hand and the asterisks indicate NIL recording sites. D, An anterior–posterior series of penetrations (in Gc6-84) illustrate an RF sequence through the foot area beginning medially on the glabrous tip of D1, moving to the nail and to proximal fields on the volar surface. Finally, in the most posterior region RFs on the distal, then proximal, hairy surface of the digits are found. The small circles indicate RFs on the foot.

Table 4. Cortical magnification factors for SI and SII

	Skin area (mm ²)	SI area (mm ²)	Mag (10 ⁻³)	SII area (mm ²)	Mag (10 ⁻³)
<i>Galago garnettii</i>					
G hand	1215.63 ^a	5.6 ^b	(4.61)	2.9 ^c	(2.39)
G foot	1517.43 ^a	4.1 ^b	(2.71)	0.4 ^c	(0.26)
Weight	967.5 ^a				
<i>Macaca mulatta</i>					
G hand	2812.54 ^d	44 ^e	(15.64)	35 ^f	(12.44)
G foot	4365.17 ^d	21 ^e	(4.81)	5.5 ^f	(1.26)
Weight	3500 ^d				

^a Average of 12 adult *Galago*.^b From Gc7-84, Gc6-84, and Carlson and Welt (1980).^c From Burton and Carlson (1986).^d From three juvenile *Macaca mulatta*.^e From Paul et al. (1972).^f From Robinson and Burton (1980).

was for SI hand and the smallest magnification factor was for SII foot.

For *Macaca*, a similar pattern was seen for the glabrous skin of hand and foot and cortical areas. However, the absolute skin and cortical areas and cortex/skin ratios were all larger than for *Galago*. The actual skin area of the surface of the glabrous hand in *Macaca* was only 63% of the skin area of the foot, yet the SI projection of the glabrous hand to SI (areas 3b and 1) was about six to seven times that of the foot. By contrast, the absolute size of the SII hand area was about 80% that of the SI hand area, rather than 50% as in *Galago*. In both species the actual skin area of the foot exceeded that of the hand but cortical projections area of hand areas to SI and SII were larger than for the foot. The cortical magnification factor for SI and SII hand areas for *Macaca* was four to five times greater than for *Galago*. This indicates that the projection of cutaneous input from the hand to the two major cortical areas necessary for normal tactile function is vastly expanded in *Macaca* relative to *Galago*, as well as being organized into a more complicated topographic pattern across areas 3b and 1.

II. *Saimiri* and *Cebus*

Size discrimination, *Saimiri*

Size acquisition. The percentage of correct responses for each session and the number of sessions required to reach criterion on the first three size acquisition tasks is illustrated as acquisition curves (Fig. 10). Comparison of errors to criterion for *Saimiri* and *Galago* indicates a similar efficiency of acquisition. However, when compared to *Macaca*, *Saimiri* made significantly more errors on the three first tasks (order of testing, not order of difficulty) and for the total of the six comparisons (see Table 5, top; Figs. 11A, 12A).

Size ALLS. On average all *Saimiri*, except for Ss3, scored above 80% correct across the six comparisons (Table 5, bottom). The average error scores on the size ALLS task for *Saimiri* and *Galago* were not significantly different, but on the difficult 7–9 mm comparison, *Saimiri* scored significantly better than *Galago* (Fig. 11A). Although *Saimiri* showed significantly lower efficiency of acquisition compared to *Macaca*, this did not carry over to the performance on the size ALLS task. There was no

SIZE ACQUISITION

Figure 10. Individual size acquisition profiles for normal *Saimiri* (Ss1–Ss5) are shown at the top, normal *Cebus* (Cb1a, Cb2a) in the middle, and *Cebus*-area-1 (Cb1b, Cb2b/c) at the bottom. Only the first three tasks presented in order of testing are illustrated. See Figure 5 for more detail.

significant difference between the two species overall or for any of the individual size comparisons on the ALLS task.

Size discrimination, *Cebus*

Size acquisition. The two *Cebus* (Cb1a, Cb2a) were initially trained as normal animals on the size discrimination tasks. The percentage correct for the individual animals is illustrated in Figure 10 and errors to criterion are presented in Table 6 (top). No significant difference in the overall learning efficiency was evident (but *Cebus* made roughly half the total number of errors over all six comparisons as *Galago*), except for the 7–12 mm comparison where *Cebus* made many fewer errors than *Galago* ($p = 0.056$; Fig. 11B). Compared to *Macaca*, *Cebus* acquired the size discriminations with less overall efficiency (*Cebus* made twice the total number of errors over all six comparisons as *Galago*), but no statistical differences on individual comparisons or total errors were detected (Table 6, top). The small sample size for *Cebus* ($n = 2$) may have contributed toward the lack of statistical significance.

Size ALLS. The percentage correct for the two normal *Cebus* on the size ALLS task is shown in Table 6 (bottom). *Cebus* and *Galago* showed the same performance ability on size tasks, with no significant species difference. *Saimiri* performed on average about 7% above *Galago* and about 7% lower than *Macaca* on the difficult size comparisons, but no statistical differences were

Figure 11. Bar graphs show the average number of errors made during size acquisition and ALLS performance tasks, comparing *Galago* to *Saimiri* (A), *Cebus* (B), and *Cebus-area 1* (C). See Figure 6 for more detail.

found between species either on individual comparisons or over all six comparisons (see Table 6, bottom; Figs. 11B, 12B).

Although statistical comparisons were not made between *Saimiri* and *Cebus* because of the small number of animals in each group, it is possible to rank species by total errors to criterion during acquisition and average performance on the ALLS task. Over the course of size acquisition, species differed by approximately 100 total errors, with *Saimiri* showing the most errors, followed by *Galago*, *Cebus*, and *Macaca* (see Tables 5A, 6A). The same ranking is seen for size ALLS performance.

Size discrimination, *Cebus-area 1*

Size acquisition. A comparison of the acquisition profiles for the two *Cebus* before and after lesions shows fewer sessions were required to criterion postoperatively on the first three comparisons (Fig. 10). Postoperative error scores for *Cebus-area 1* (on the hand contralateral to the area 1 lesion) were half those made on the same hand prior to the lesions. When Cb1 was tested on the previously trained right hand after a left hemisphere lesion (Cb1b), it made half the number of errors as during original learning (Cb1a). Whereas Cb2 made about the same number of errors postoperatively as preoperatively on the previously trained right hand (Cb2b), following a left hemisphere lesion of the same magnitude as Cb1b (Table 6, top). However, the total errors for Cb2 on the untrained left hand following an even larger right hemisphere lesion (Cb2c) were a third of those for original learning (Cb2a).

The only difference that approached significance between nor-

mal *Cebus* and *Galago* was the moderate 7-12mm comparison, whereas *Cebus-area 1* had significantly fewer errors on total errors for the six comparisons as well as on the initial 7-18 mm comparison relative to *Galago* (Table 6, top; Fig. 11C). *Cebus-area 1* and *Macaca* had virtually identical total errors over the six tasks, with no statistically significant differences found on individual comparisons (Table 6, top; Fig. 12C).

Size ALLS. Compared to their own preoperative performance on size ALLS, *Cebus-area 1* performed the same on most of the size comparisons, with little indication that either the lesion or the preoperative experience strongly influenced their capacity. Cb1b performed slightly below the preoperative level when retested on the right hand after the left hemisphere lesion (4.3%) while Cb2b performed at the preoperative level on its right hand. Percentage correct on the untrained left hand (following a right hemisphere lesion; Cb2c) was 5.3% higher than its preoperative performance on the right hand (Cb2a; Table 6, bottom). It is evident that *Cebus-area 1* and *Galago* performed in a similar range, with *Cebus-area 1* doing strikingly better than *Galago* only on the most difficult comparison ($p = 0.058$). There were no statistically significant differences between *Cebus-area 1* and *Macaca*. Performance on the size ALLS task was very similar for all four primate species and for *Cebus-area 1*.

Texture discrimination, *Saimiri*

Texture acquisition. Four of the original animals tested on size acquisition and ALLS performance were also trained on texture comparisons. Acquisition profiles are presented in Figure 14

Figure 12. Bar graphs show the average number of errors made during size acquisition and ALLS performance tasks, comparing *Macaca* (Carlson, 1984) to *Saimiri* (A), *Cebus* (B), and *Cebus-area 1* (C). See Figure 6 for more detail.

and errors to criterion are summarized in Table 7 (top). All four *Saimiri* had difficulty with learning the texture discrimination comparisons and made between 23% and 63% more errors than *Galago* on the first three comparisons presented (Fig. 15A). During training, Ss4 ran over 40 sessions without mastering the difficult level comparison (320–120 gr/in), but did reach criterion on the intermediate level comparison (320–100 gr/in) after more than 20 sessions. Ss5 required 40 sessions to reach criterion on that intermediate level, but next showed little evidence of being able to acquire the 320–120 gr/in comparison.

The only statistically significant difference between *Saimiri* and *Galago* on individual comparisons was for the 320–80 gr/in comparison. When combining the errors made over all six comparisons, *Saimiri* made 43% more errors than *Galago*, though this difference did not reach statistical significance. The efficiency with which *Saimiri* mastered the first three texture comparison was significantly below that of *Macaca* but with no important differences in their scores on the last three comparisons. (Table 7, top; Fig. 16A). The total errors during texture acquisition by *Saimiri* were also significantly higher than for *Macaca*.

Texture ALLS. Although *Saimiri* performed below *Galago* on all but the easiest of texture comparisons there were no statistical significant differences between *Saimiri* and *Galago* on the texture ALLS task (Table 7, bottom; Fig. 15A). On average *Saimiri* performed more than 10% below the level of *Macaca*, with significant differences found for four of the six comparisons

and for the average over all comparisons (Table 7, bottom; Fig. 16A).

Texture discrimination *Cebus*

Texture acquisition. The two *Cebus* were also tested on texture discrimination tasks. The first animal to be tested, Cb1a, had difficulty mastering the initial texture comparisons, and because of continued poor performance this animal was given a interruption in testing from week 20 to week 40 (Fig. 14). When testing resumed, Cb1a was retrained on the first two comparisons prior to presenting the third and difficult comparison (320–120 gr/in). After many sessions at below 60% correct performance on that comparison (and repeated presentations of easier comparisons), an intermediate difficult comparison (320–100 gr/in) was presented and mastered in 12 sessions. After seven more sessions on the 320–120 gr/in comparison with near chance performance, it was decided to proceed with the three remaining comparisons.

The second *Cebus* to be tested, Cb2a, was more proficient in learning the different texture comparisons. However, during training on the difficult comparison it developed a position habit, and had to be taken back to easier tasks for eight sessions before it reached criterion. Cb2a never mastered the last comparison (120–80 gr/in) after 10 sessions.

The efficiency with which the two *Cebus* mastered the texture discrimination comparisons was not significantly different from *Galago*, except for the 320–80 gr/in comparison (which was also

Table 5. Size discrimination by *Saimiri* (in order of difficulty)

	Size comparisons (difference)						Total	Average
	7-18	9-18	12-18	7-12	9-12	7-9		
	mm (11 mm)	mm (9 mm)	mm (6 mm)	mm (5 mm)	mm (3 mm)	mm (2 mm)		
Errors to criterion on size acquisition task								
Ss1a	40	4	3	91	6	182	326	—
Ss2a	40	5	31	39	61	63	239	—
Ss3a	254	35	97	328	58	205	977	—
Ss4a	97	4	13	12	5	306	437	—
Ss5a	59	4	7	74	5	22	171	—
AVG Ss	98.0	10.4	30.2	108.8	27.0	155.6	430.0	—
AVG Gc	87.4	2.0	48.3	77.1	25.9	130.4	371.1	—
<i>p</i>	NS	NS	NS	NS	NS	NS	NS	—
AVG Ss	98.0	10.4	30.2	108.8	27.0	155.6	430.0	—
AVG Mm	7.8	3.3	21.6	5.2	23.2	54.0	115.1	—
<i>p</i>	0.008**	NS	NS	0.005**	NS	0.033*	0.020*	—
Percentage correct on size ALLS task								
Ss1a	100.0	100.0	97.4	85.9	85.9	59.5	—	88.1
Ss2a	100.0	100.0	98.9	96.7	87.0	68.1	—	91.8
Ss3a	86.7	95.0	75.0	78.7	77.4	58.3	—	78.5
Ss4a	100.0	100.0	84.0	82.7	67.3	56.4	—	81.5
Ss5a	100.0	100.0	83.3	94.0	95.9	78.0	—	91.8
AVG Ss	97.3	99.0	87.7	87.6	82.7	64.1	—	86.4
AVG Gc	98.6	97.8	92.5	93.5	87.2	57.0	—	87.7
<i>p</i>	NS	NS	NS	0.075	NS	0.037*	—	NS
AVG Ss	97.3	99.0	87.7	87.6	82.7	64.1	—	86.4
AVG Mm	98.5	97.0	93.1	95.5	89.1	72.4	—	90.5
<i>p</i>	NS	NS	NS	NS	NS	NS	—	NS

*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

true for *Saimiri*). However, *Cebus* made more errors than *Galago* before reaching criterion for all but one of the texture comparisons (Fig. 15B). As a result, *Cebus* made 36% more errors overall before mastering all comparisons. There were few statistical differences between *Cebus* and *Macaca* in the efficiency of learning the different texture comparisons (Fig. 16B). Although *Cebus* made more errors on all individual comparisons before reaching criterion than *Macaca*, only one significant difference was found (320–80 gr/in) and two approached significance (320–40 and 120–40 gr/in). On the total number of errors made across all six comparisons *Cebus* showed significantly higher errors scores than *Macaca* (Table 8, top; Fig. 16B).

Texture ALLS. Following acquisition training the two *Cebus* were tested on the texture ALLS task. With the exceptions of the 320–40 and 320–80 gr/in comparisons, performance for both animals was below 80% correct (Table 8, bottom). *Cebus* performed less well than *Galago* on all six comparisons and on two comparisons (120–40 and 80–40 gr/in) *Cebus* performed significantly below *Galago* (Table 8, bottom; Fig. 15B). The species difference in average performance on all six tasks approached significance. On average and on all but the two most difficult comparisons, *Cebus* performed strikingly below *Macaca* ($p = 0.057$; Fig. 16B), but even for these two difficult comparisons, the percentage correct made by *Cebus* was at least 12% lower than for *Macaca* (Table 8, bottom; Fig. 16B).

Texture discrimination, *Cebus*–area 1

Texture acquisition. After the single unilateral lesion in the left hemisphere, Cb1 was retested with its right hand on all six

texture comparisons (Cb1b). It mastered all comparisons more quickly and made substantially fewer errors than preoperatively (Cb1a; Table 8, top; Fig. 14). Likewise, Cb2, after a similar sized lesion of area 1 in its left hemisphere (Cb2b), mastered all comparisons with its previously trained right hand more efficiently than before the lesion. Following an area 1 lesion in the right hemisphere (Cb2c), Cb2 was tested on its left hand. It mastered all six comparisons even more rapidly and with fewer errors although it had never been tested on this hand before (Table 8, top; Fig. 14).

The remarkable postoperative improvement in efficiency of acquisition of the difficult 320–120 gr/in led us to present a more difficult comparison, 320–180 gr/in to further explore the apparent improvement in texture discrimination capacity. Cb1 mastered the 320–180 gr/in task in 11 sessions with 347 errors, although it never mastered the less discrepant 320–120 gr/in tasks preoperatively after more than 20 sessions. Cb2 also mastered the 320–180 comparison postoperatively, after 16 sessions and 481 errors on the right hand (Cb2b) and only 6 sessions and 219 errors on the untrained hand (Cb2c). These errors are not included in the total errors in Table 8 (top) and Figures 15C and 16C.

Postoperatively, *Cebus*–area 1 made significantly fewer errors than *Galago* while remastering the three first texture comparisons and on the total over all six comparisons (Fig. 15C). The efficiency with which *Cebus*–area 1 remastered the texture comparisons was not significantly different from *Macaca*, except on the initial comparison, which approached significance ($p = 0.052$; Table 8, top; Fig. 16C).

Figure 13. Computer-reconstruction of postcentral gyrus in *Cebus*, showing configuration of one normal (*Cb1 RIGHT*) and three area 1-lesioned hemispheres (*Cb1b LEFT*, *Cb2b LEFT*, *Cb2c RIGHT*) (see Materials and Methods for more details). The brain drawing above each reconstruction shows the relationship of the central sulcus (CS), interparietal sulcus (IP), and lateral sulcus (LS) to the postcentral gyrus. The anterior (A), posterior (P), medial (M), and lateral (L) orientations of the brain drawings, reconstructions, and single cross sections are illustrated on the lower drawings. The relationship of the topographic organization of input from the hand and the cytoarchitectonic areas (3b and 1) to the central sulcus is given in Figure 4. The three-dimensional reconstruction of each hemisphere was based on every 10th section through the lesion, rotated on the x,y,z-axes to obtain a dorsomedial view. The profile of each lesion begins with the most medial section through the lesion, with layer VI drawn throughout the postcentral gyrus and precentral gyrus. The dense layer IV, visible in areas 3a, 3b and 1, is also shown. A second section, through the middle of the lesion, is identified in the profile by an asterisks, and illustrated next to each series of sections. The mediolateral length and three-dimensional volume of the lesion were calculated from digitalized tracings. The illustration at *top right* of the normal hemisphere of *Cb1 RIGHT*, when compared to the three lesioned hemispheres, portrays the reduction of the postcentral gyrus in the anteroposterior plane in the lesioned hemispheres. None of the lesions invaded the white matter, but as shown in the individual cross sections of *Cb1b* and *Cb2c*, the lesion can be seen as restricted to the upper cortical layers.

Texture ALLS. Compared to their own preoperative performance, *Cebus*-area 1 performed better on all comparisons and performed above criterion on the average of the six comparisons. *Cebus* area-1 performed below 80% correct on only two comparisons (80–40 and 320–120 gr/in). *Cb1b* continued to perform below 80% correct on the two difficult comparisons, and *Cb2* showed greater improvement in performance postoperatively than did *Cb1* (Table 8, bottom). For the average performance across the six comparisons, *Cb1b* showed a 7.2% improvement, and *Cb2b* an 11% improvement, on their previously trained right hands. *Cb2c* showed a postoperative per-

formance level on its *untrained* left hand that was 12.7% higher than on its normal right hand (*Cb2a*). In general, *Cebus*-area 1 performed better than *Galago* on all texture comparisons, but only on the difficult 320–120 gr/in comparison did the difference approach significance ($p = 0.058$; Table 8, bottom; Fig. 15C). Although *Macaca* typically scored higher than *Cebus*-area 1 (except for the 320–120 gr/in comparison), there was no significant difference in the performance between them (Fig. 16C). However, the 5% higher performance by *Macaca* (averaged across comparisons) approached statistical significance ($p = 0.068$). Although on average the preoperative performance of *Cebus* was below that of *Saimiri* and *Galago*, postoperative performance levels rose to above *Galago* yet below *Macaca*.

Glabrous hand and foot areas and SI magnification factors for Saimiri and Cebus

The average areas for the glabrous hand and foot (and body weights) are given in Table 9. The areas and weights for *Saimiri* represent the average for two adult males and two adult females. For *Cebus*, skin surface areas and the body weights for the adult female (*Cb1*), subadult male (*Cb2*), and an additional adult male (*Cb3*) and adult female (*Cb4*) are presented. For both species, body weight and skin surface areas appear closely correlated. In *Saimiri*, the skin surface of the glabrous hand was 69% that of the foot but the combined SI hand areas (3b and 1) were only 88% of the SI foot areas, yet the SI/skin magnification factor for the hand in *Saimiri* (14.48×10^{-3}) exceeds that of *Galago* (4.61×10^{-3}) and was similar to that of *Macaca* (15.64×10^{-3}) (Tables 4, 9). The magnification factor for the SI foot area in *Saimiri* was greater than for *Galago* and *Macaca*.

For *Cebus*, the skin area of the hand was only 54% that of the foot whereas the SI hand area was 3.5 times the size of the SI foot area. These remarkable differences in the size of skin surface and SI projection areas (areas 3b and 1) for the hand and foot yielded an extreme difference in magnification factors—hand (29.47×10^{-3}) and foot (4.67×10^{-3}). The cortical magnification factor for *Cebus* hand was twice that for the hand in SI of *Saimiri* and *Macaca*. The similarities and differences between the expansion of the hand and feet areas in SI and SII in these species suggest that the sensory demands of these two glabrous surfaces may be different for these diverse species.

Discussion

The choice of behavioral tasks used in this study was based upon our previous experience with a variety of tactile tasks in normal and SI-lesioned adult *Macaca*. We had expectations as to the behavioral significance of cutaneous input from the glabrous hand to areas 3b and 1, as well as the role of noncutaneous input from the hand to area 2. Our choice of species was based upon the current knowledge available on the structural and functional properties of the somatic sensory system and of taxonomic relations between these different grades (prosimian and anthropoid) and clades (OW and NW lineages) of primates. The results of the behavioral studies will be interpreted in light of information on the structure and function of the tactile system in primates, the use of the hand in natural habitats, and the evolution of the brain in primates of different adaptations and lineages. Finally, we will discuss the structure and function of somatic sensory pathways in different species from a developmental perspective and hypothesize about developmental mechanisms that may underlie the differences in cortical organization that have emerged over the tens of millions of years of evolu-

Table 6. Size discrimination by *Cebus* (in order of difficulty)

	Size comparisons (difference)						Total	Average
	7–18	9–18	12–18	7–12	9–12	7–9		
	mm (11 mm)	mm (9 mm)	mm (6 mm)	mm (5 mm)	mm (3 mm)	mm (2 mm)		
Errors to criterion on size acquisition task								
Cb1a	40	8	29	8	10	194	289	—
Cb2a	23	4	2	12	19	61	121	—
AVG Cb	31.5	6.0	15.5	10.0	14.5	127.5	205.0	—
AVG Gc	87.4	2.0	48.3	77.1	25.9	130.4	371.1	—
<i>p</i>	NS	NS	NS	0.056	NS	NS	NS	—
AVG Cb	31.5	6.0	15.5	10.0	14.5	127.5	205.0	—
AVG Mm	7.8	3.3	21.6	5.2	23.2	54.0	115.1	—
<i>p</i>	NS	NS	NS	NS	NS	NS	NS	—
Cb1b	32	0	6	45	11	74	168	—
Cb2b	5	7	4	10	6	101	133	—
Cb2c	2	0	10	4	9	14	39	—
AVG Cb-1	13.0	2.3	6.7	19.7	8.7	63.0	113.3	—
AVG Gc	87.4	2.0	48.3	77.1	25.9	130.4	371.1	—
<i>p</i>	0.017*	NS	NS	NS	NS	NS	0.008**	—
AVG Cb-1	13.0	2.3	6.7	19.7	8.7	63.0	113.3	—
AVG Mm	7.8	3.3	21.6	5.2	23.2	54.0	115.1	—
<i>p</i>	NS	NS	NS	NS	NS	NS	NS	—
Percentage correct on size ALLS task								
Cb1a	100.0	97.8	91.1	92.3	84.6	65.2	—	88.5
Cb2a	100.0	97.9	92.0	91.9	84.9	65.6	—	88.8
AVG Cb	100.0	97.9	91.6	92.1	84.7	65.4	—	88.7
AVG Gc	98.6	97.8	92.5	93.5	87.2	57.0	—	87.7
<i>p</i>	NS	NS	NS	NS	NS	NS	—	NS
AVG Cb	100.0	97.9	91.6	92.1	84.7	65.4	—	88.7
AVG Mm	98.5	97.0	93.1	95.5	89.1	72.4	—	90.5
<i>p</i>	NS	NS	NS	NS	NS	NS	—	NS
Cb1b	97.8	96.6	83.2	92.1	77.5	58.0	—	84.2
Cb2b	100.0	100.0	90.2	97.7	90.4	61.6	—	89.9
Cb2c	100.0	100.0	97.9	94.8	92.6	79.2	—	94.1
AVG Cb-1	99.3	98.9	90.4	94.9	86.8	66.3	—	89.4
AVG Gc	98.6	97.8	92.5	93.5	87.2	57.0	—	87.7
<i>p</i>	NS	NS	NS	NS	NS	0.058	—	NS
AVG Cb-1	99.3	98.9	90.4	94.9	86.8	66.3	—	89.4
AVG Mm	98.5	97.0	93.1	95.5	89.1	72.4	—	90.5
<i>p</i>	NS	NS	NS	NS	NS	NS	—	NS

*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

tionary history that separate these species. Furthermore, we speculate about how different developmental events may account for the pattern of thalamocortical connections and tactile behavior capacity typical of individual species. Without such a developmental perspective one cannot expect to understand the mechanisms by which species-specific patterns (or individual variation within species) are achieved.

The general and specific contributions of somatic sensory cortex to tactile discrimination capacity in adult Macaca

Our previous behavioral studies in adult *Macaca* demonstrated the selective contribution of area 2 to size and shape discrimination abilities and of area 1 to texture discrimination skill, whereas area 3b was found to be necessary for all tactile discrimination capacity (Randolph and Semmes, 1974; Carlson, 1981). The selective and independent deficits associated with damage to these two SI areas from either area 1 or 2 suggest a

specificity of function referred to as double dissociation of function in the literature on localization of cortical function (Teuber, 1955; Carlson, 1981). Similar to the general contribution of 3b revealed by the selective lesion technique, ablations of area SII in the lateral sulcus (but not area 5 in the posterior parietal region) produce severe and lasting deficits on a variety of tactile discrimination tasks (Ridley and Ettlinger, 1976, 1978; Murray and Mishkin, 1984). Although 3b and SII lesions do not produce the double dissociation of function characterizing areas 1 and 2 lesions, these two areas are necessary for normal levels of tactile function in adult *Macaca*. It is the specific contribution of input from the glabrous hand to area 1 that is of special interest in the present study. By including both size and texture discrimination, it is possible to discuss the modality-specific aspects (cutaneous vs noncutaneous) of the two classes of tasks (texture vs size) from the general sensorimotor and cognitive aspects of the tasks.

TEXTURE ACQUISITION

Figure 14. Individual acquisition profiles for texture tasks by normal *Saimiri* (Ss1–Ss5), normal *Cebus* (Cb1a, Cb2a), and *Cebus*-area 1 (Cb1b, Cb2b/c) are illustrated. See Figure 5 for additional details.

It was not unexpected that *Galago* (a prosimian primate that diverged from the common evolutionary lineage tens of millions of years before anthropoid primates) would make more errors than *Macaca* and require more sessions prior to criterion during the early acquisition sessions due to the nonsensory demands of the tasks alone. General sensorimotor demands of these tasks include such behaviors as reaching, pulling, touching, and comparing both handles in a pair from trial to trial. Cognitive demands include attending to either the size or texture cues and transferring response strategies from one level of difficulty to another and abandoning the previous strategy when shifting from size to texture tasks.

Accounting for some general, nonsensory differences between *Macaca*, *Saimiri* and *Cebus* is more difficult, as they are all classified as anthropoids and as sharing the same grade (or general complexity) of structural organization. *Cebus* are considered to be the most “clever” and inquisitive of the NW primates (e.g., Klüver, 1937; Chevalier-Skolnikoff, 1989). Their manipulative skills and sensorimotor “intelligence” have been examined extensively and are thought to rival that of *Macaca*

(Torigoe, 1985; Gibson, 1986; Chevalier-Skolnikoff, 1989) and to exceed that of *Saimiri* (Costello and Fragasy, 1988). Our predictions were therefore that the efficiency of learning on all tactile tasks by *Cebus* would be more like *Macaca* than *Galago*. Because of the more limited hand use in *Saimiri* (and some parallels between the way *Saimiri* and *Galago* use their hands when grasping objects) it was possible that *Saimiri* would be more like *Galago* than *Macaca*. Differences on size and texture tasks related to nonsensory capacity like “intelligence” were expected to be reflected by greater difficulty with initial comparisons of the size and texture tasks (order of testing) rather than a function of physical differences (order of difficulty).

Size discrimination capacity in *Macaca* and *Galago*

Earlier studies of normal adult *Macaca* showed that they can reliably discriminate a 1–1.5 mm difference from a 12.7 mm standard handle (Semmes and Mishkin, 1965; Randolph and Semmes, 1974). In a later study of infant and juvenile *Macaca* (Carlson, 1984), the standard size handle was reduced to 7 mm, a size more appropriate for younger macaques and for the spe-

Figure 15. Bar graphs show the average number of errors made during texture acquisition and ALLS performance, comparing *Galago* to *Saimiri* (A), *Cebus* (B), and *Cebus-area 1* (C). See Figure 6 for more detail.

cies in the present study. Ablation studies have shown that removal of area 2 in SI of *Macaca* results in a deficit in size discrimination ability, consistent with the predominance of noncutaneous input to this area from receptors associated with joint and muscles (Powell and Mountcastle, 1959; Schwarz et al., 1973). Similarly, in physiological studies of awake *Galago*, we found activity in areas 2–5 and 3a to be activated by noncutaneous input (Carlson and Welt, 1980). The findings of the present studies that *Galago* could master all levels of difficulty of size acquisition tasks and was not significantly different from *Macaca* on five of the six size threshold comparisons are compatible with these physiological findings. However, the significant difference between *Macaca* and *Galago* on the difficult 7–9 mm (2 mm difference) comparison indicates that, although both species have the same sensory capacity over a wide range of size comparisons, *Galago* cannot maintain the same level of performance as *Macaca* on this difficult comparison during the more complex ALLS task.

The ALLS task is more demanding than the acquisition task since the animals are required to make relative judgements across trials, as a handle that was correct on one trial may be incorrect on next trial if paired with a smaller handle. These two species differed significantly on the first two comparisons in order of testing rather than on the most difficult comparisons. *Galago* exhibited more difficulty with the initial size acquisition tasks (ranked by order of testing) than with the three most difficult tasks (ranked by the millimeter differences between handles).

By contrast, the pattern of errors for *Macaca* was related more to the order of difficulty. It was on the third and most difficult comparison (7–9 mm) that both species showed the highest error scores during acquisition and the lowest percentage correct during the ALLS task. It was expected that the error scores of *Galago* and *Macaca* would be more similar on later comparisons and on the size ALLS task, since the differences in general learning capacity became less relevant and sensory demands of the tasks more relevant.

A possible explanation for this finding is that nonsensory abilities, such as the capacity of *Galago* to concentrate consistently on the demands of the task, influence the animal's ability to perform consistently near its sensory threshold for size. Alternatively, it may be that receptors associated with joints and muscles do not project with the same degree of accuracy information about finger position or movement. Furthermore, in *Galago* cortical areas 3a, 2, and 5 (or cuneate or thalamic nuclei) may receive and integrate information from the hand less efficiently or reliably than in *Macaca*, yet *Galago* performed remarkably similar to *Macaca* over a range of size comparisons following initial acquisition, and it was only on the discrimination of the smallest difference that species differences persisted in the ALLS task.

A third possibility (one that we favor) is that the vast difference in hand and finger control in these species limits the capacity of *Galago* to perform the smallest discriminations reliably. *Galago* hand control is characterized as whole hand

Table 7. Texture discrimination by *Saimiri* (in order of difficulty)

	Size comparisons (difference)						Total	Average
	320–40 gr/in. (386 μ m)	120–40 gr/in. (295 μ m)	80–40 gr/in. (243 μ m)	320–80 gr/in. (143 μ m)	320–120 gr/in. (91 μ m)	120–80 gr/in. (52 μ m)		
Errors to criterion on texture acquisition task								
Ss1a	256	7	16	370	1059	10	1718	—
Ss2a	113	3	1	122	1696	14	1949	—
Ss4a	665	4	47	52	2281 ^a	40	3423	—
Ss5a	361	2	164	177	191 ^a	177	1992	—
AVG Ss	349.0	4.0	57.0	180.3	1306.8	60.3	2270.5	—
AVG Gc	227.0	12.0	90.0	65.8	1060.8	103.9	1583.0	—
<i>p</i>	NS	NS	NS	0.022*	NS	NS	NS	—
AVG Ss	349.0	4.0	57.0	180.3	1306.8	60.3	2270.5	—
AVG Mm	77.0	5.2	11.3	26.5	92.2	42.4	321.7	—
<i>p</i>	0.020*	NS	NS	0.009**	0.020*	NS	0.007**	—
Percentage correct on texture ALLS task								
Ss1a	96.9	81.5	65.6	89.1	39.4	75.4	—	74.5
Ss2a	98.3	96.7	83.9	80.3	49.1	79.4	—	81.5
Ss4a	87.0	88.7	81.5	68.5	43.6	69.8	—	73.1
Ss5a	94.6	89.1	58.5	82.1	58.2	69.6	—	75.5
AVG Ss	94.2	89.1	72.4	80.0	47.6	73.6	—	76.2
AVG Gc	93.8	92.5	80.0	83.1	54.7	78.5	—	80.4
<i>p</i>	NS	NS	NS	NS	NS	NS	—	NS
AVG Ss	94.2	89.1	72.4	80.0	47.6	73.6	—	76.2
AVG Mm	96.9	97.8	90.5	94.8	63.7	90.5	—	89.0
<i>p</i>	NS	0.047*	0.073	0.030*	0.030*	0.011*	—	0.018*

^a Animals never reached criterion on this task.*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

Figure 16. Bar graphs show the average number of errors made during texture acquisition and ALLS performance tasks, comparing *Macaca* to *Saimiri* (A), *Cebus* (B), and *Cebus-area 1* (C). See Figure 6 for more detail.

Table 8. Texture discrimination by *Cebus* (in order of difficulty)

	Size comparisons (difference)						Total	Average
	320–40 gr/in. (386 μm)	120–40 gr/in. (295 μm)	80–40 gr/in. (243 μm)	320–80 gr/in. (143 μm)	320–120 gr/in. (91 μm)	120–80 gr/in. (52 μm)		
Errors to criterion on texture acquisition task								
Cb1a	793	37	546	176	1231 ^a	47	3297	—
Cb2a	171	18	11	321	711	453 ^a	1685	—
AVG Cb	482.0	27.5	278.5	248.5	971.0	250.0	2491.0	—
AVG Gc	227.0	12.0	90.0	65.8	1060.8	103.9	1583.0	—
<i>p</i>	NS	NS	NS	0.022*	NS	NS	NS	—
AVG Cb	482.0	27.5	278.5	248.5	971.0	250.0	2491.0	—
AVG Mm	77.0	5.2	11.3	26.5	92.2	42.4	321.7	—
<i>p</i>	0.068	0.068	NS	0.041*	NS	NS	0.045*	—
Cb1b	17	16	446	35	281	145	940	—
Cb2b	10	7	11	12	363	6	409	—
Cb2c	0	3	—	4	51	8	75	—
AVG Cb-1	9.0	8.7	155.0	17.0	231.7	53.0	474.7	—
AVG Gc	227.0	12.0	90.0	65.8	1060.8	103.9	1583.0	—
<i>p</i>	0.006**	NS	NS	0.042*	0.042*	NS	0.012*	—
AVG Cb-1	9.0	8.7	155.0	17.0	231.7	53.0	474.7	—
AVG Mm	77.0	5.2	11.3	26.5	92.2	42.4	321.7	—
<i>p</i>	0.052	NS	NS	NS	NS	NS	NS	—
Percentage correct on texture ALLS task								
Cb1a	91.0	69.0	63.0	80.0	56.0	64.0	—	70.5
Cb2a	86.0	80.2	66.0	80.0	47.0	88.0	—	74.5
AVG Cb	88.5	74.6	64.5	80.0	51.5	76.0	—	72.5
AVG Gc	93.8	92.5	80.0	83.1	54.7	78.5	—	80.4
<i>p</i>	NS	0.028*	0.028*	NS	NS	NS	—	0.056
AVG Cb	88.5	74.6	64.5	80.0	51.5	76.0	—	72.5
AVG Mm	96.9	97.8	90.5	94.8	63.7	90.5	—	89.0
<i>p</i>	0.057	0.057	0.057	0.057	NS	NS	—	0.057
Cb1b	88.0	86.8	63.2	84.2	72.7	71.4	—	77.7
Cb2b	100.0	96.3	90.0	80.8	57.0	88.9	—	85.5
Cb2c	100.0	97.8	81.7	90.9	67.0	86.0	—	87.2
AVG Cb-1	96.0	93.6	78.3	85.3	65.6	82.1	—	83.5
AVG Gc	93.8	92.5	80.0	83.1	54.7	78.5	—	80.4
<i>p</i>	NS	NS	NS	NS	0.058	NS	—	NS
AVG Cb-1	96.0	93.6	78.3	85.3	65.6	82.1	—	83.5
AVG Mm	96.9	97.8	90.5	94.8	63.7	90.5	—	89.0
<i>p</i>	NS	NS	NS	NS	NS	NS	—	0.068

^a Animals did not reach criterion on this task.*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

response, consisting of a rapid, stereotyped five-finger grasp movement (Bishop, 1964). This type of hand control does not appear to have the same potential for information about finger position and movement as the slow, dexterous, and more independent finger movement typical of *Macaca*. Although there has been much speculation about the role of manual dexterity in tactile capacity, studies of adult and infant *Macaca* failed to demonstrate sensory deficits on size or texture discrimination tasks following lesions of the hand area in primary motor cortex (Semmes and Porter, 1972; Carlson, 1984), yet hand movements of *Galago* do not resemble those of an area 4-lesioned *Macaca* but rather reflect the highly stereotypical grasp response of prosimians.

In conclusion, more limited cognitive abilities, less accurate cortical processing of finger movement and position, and less proficient manual dexterity may all contribute to the inferior performance by *Galago* on the most difficult size comparison

in the ALLS tasks. The comparable size discrimination capacity of *Macaca* (with an expanded SI and SII, and a more complex SI topography) compared to that of *Galago* (with a smaller SI and SII, and less complex SI) suggests that the noncutaneous input to areas 2 and 3a in SI, cutaneous input to 3b and SII was sufficient to mediate the level of capacity demanded by the range of size comparisons presented in this study.

Size discrimination capacity in *Saimiri* and *Cebus*

The same characteristic noncutaneous input to area 2 (and 3a) in *Galago* and *Macaca* has been described in *Cebus* and *Saimiri* (Sur et al., 1982; Felleman et al., 1983). Thus, there was no reason to assume that NW anthropoids were deficient in the cortical projection of noncutaneous input shown to be required for size discrimination capacity in *Macaca* (Randolph and Semmes, 1974; Carlson, 1981). Because of this common SI input and the shared anthropoid grade of organization, we expected

Table 9. Cortical magnification factors for SI

<i>Saimiri sciureus</i>					Skin area ^a (mm ²)	SI area ^b (mm ²)	Mag (10 ⁻³)
Ss	Ss1	Ss3	Ss4	Ss5			
G hand	936.3	1095.5	1255.5	855.2	1035.6	15	(14.48)
G foot	1349.63	1552.6	1786	1274.7	1490.73	17	(11.40)
Weight	695	1000	1050	595	835		

<i>Cebus apella</i>					Skin area (mm ²)	SI area ^c (mm ²)	Mag (10 ⁻³)
Cb	Cb1	Cb2	Cb3	Cb4			
G hand	1830.1	1082.5	3188.3	1908.8	2002.4	59	(29.47)
G foot	—	3352.3	4518.3	3197.4	3689.3	17	(4.67)
Weight	2335	1765	4900	1940	2735		

^a Average of Ss1, Ss3, Ss4, Ss5.^b From Sur et al. (1982).^c From Felleman et al. (1983).

Saimiri and *Cebus* to perform as well as *Macaca* and *Galago* on these tasks.

The results from the size discrimination tasks showed that *Saimiri* and *Cebus* differed in learning efficiency from each other and from *Macaca* on the first three size comparisons. *Saimiri* amassed slightly more errors overall than *Galago* and significantly more errors than *Macaca* on size acquisition. Compared to *Galago*, *Cebus* made half the number of errors, while compared to *Macaca* they made twice as many errors. These results suggest that *Saimiri* learned at a rate more similar to *Galago*, whereas the learning rate for *Cebus* was between that of *Galago* and *Macaca*. On the size ALLS, *Saimiri* and *Cebus* (both normal and area 1-lesioned) were significantly better than *Galago* on the difficult size comparisons but insignificantly below the level of *Macaca* on all comparisons. These findings further support the interpretation that area 1 does not contribute to size discrimination capacity, consistent with studies of normal and area 1-lesioned *Macaca* (Randolph and Semmes, 1974; Carlson, 1981). Results from the size tasks also show that all four species have comparable nonsensory capacities necessary to acquire a series of tactile discrimination tasks and to transfer the skill from acquisition training to performance on the more complex ALLS task.

Texture discrimination capacity in *Galago* and *Macaca*

Previous studies of *Macaca* report thresholds, using the same texture comparison in the present study, of between 180 and 150 gr/in when compared to a 320 gr/in standard (Semmes and Mishkin, 1965). When these same comparisons were presented to area 1-lesioned adult *Macaca* tested postoperatively only, thresholds between 120 and 100 gr/in were obtained. Adult *Macaca* with preoperative training on these same texture tasks failed postoperatively to reacquire the 320–180 gr/in comparison (Carlson, 1981).

By the time the present subjects were tested on texture tasks they had considerable exposure to the nonsensory aspects of the testing situation, allowing for sensory capacity to play a clearer role in acquisition and performance than during the size task. During the texture acquisition task, both *Galago* and *Macaca* showed the most errors on the initial (but easy) comparison and the third (difficult, but not the most physically discrepant) texture comparison. This comparison (constituting a 91 μ m dif-

ference) was based on two smooth surfaces, as opposed to the less discrepant 52 μ m difference comparison which was between two rougher surfaces (120–80 gr/in, comprising a smaller relative difference but between two larger grain sizes). The 91 μ m difference comparison was typically the most difficult for all species and individuals tested on this texture series. The greater difficulty of the 91 μ m comparison (320–120 gr/in) was seen both in the errors to criterion in acquisition and in percentage correct on the texture ALLS task (where there is no order effect) suggesting a true sensory-based difference.

On the initial texture comparison both species were less efficient than would be expected by the grain size or grain spacing dimensions of the task. When confronted with the first texture comparisons, many animals (regardless of species) show either random response strategies or fixed position habits. After months of training to detect size differences, subjects were forced to explore other dimensions of the handles to determine that texture cues were the significant feature to discriminate when confronted with handles of the same diameter.

After mastering the first texture comparison, *Galago* was still significantly less efficient than *Macaca* on the second, moderate-level comparison. On the third and most difficult task (320–120 gr/in), *Galago* was vastly inferior to *Macaca* in errors to criterion and in that two of the eight animals failed to master the most difficult task after more than 20 sessions. On texture tasks, *Galago* error scores during acquisition still reflected both “order of testing” and “order of difficulty” effects. On the texture ALLS task *Galago* performed significantly lower than *Macaca* on four of the six (and on all the most difficult) comparisons as well as on the overall average for the ALLS task. The significantly inferior skills of *Galago* on texture comparisons strongly suggest a real sensory deficit on these tasks, known to depend upon cutaneous input to area 1 in *Macaca* (Randolph and Semmes, 1974; Carlson, 1981). These results are consistent with previous research and the theoretical position that the evolution of the second projection from the glabrous hand to area 1 in *Macaca* provides for greater capacity to discriminate textured surfaces.

Texture discrimination capacity in *Saimiri* and *Cebus*

As both NW species have a second projection from the glabrous hand to area 1 as in *Macaca*, it was expected that some similarity would be seen among the three anthropoids and all would be superior to *Galago* on texture tasks. However, the details of SI maps in *Cebus* are more similar to *Macaca* in that the digits project to the entire anterior–posterior expanse of areas 3b and 1 (Fig. 4; Nelson et al., 1980; Felleman et al., 1983). By contrast, in SI hand area of *Saimiri* the digits and palm fields both project to those areas, resulting in a relatively smaller elaboration of the digit surfaces than in *Macaca* and *Cebus* (Fig. 4; Sur et al., 1982).

Saimiri and *Cebus* showed an efficiency and rate of learning on texture tasks that were no different from that of *Galago*. It is clear from the results presented here that both *Saimiri* and *Cebus* had difficulty in learning to discriminate between textured surfaces. This difficulty in learning is best illustrated by the finding that two of the four *Saimiri* and one of the two normal *Cebus* never mastered the 320–120 gr/in comparison mastered by all *Macaca* and six of the eight *Galago*. Both *Saimiri* and *Cebus* had a substantially slower rate of learning on texture tasks and their efficiency was significantly lower than that of *Macaca*. Thus, neither *Saimiri* nor *Cebus* exhibited the behavioral ben-

efits expected from having an expanded and complex glabrous projections to area 1. On the texture ALLS task, *Saimiri* and *Cebus* also behaved similarly to *Galago*, and *Cebus* on average performed strikingly below the level of *Galago*. Compared to *Macaca*, both *Saimiri* and *Cebus* were significantly inferior on texture performance comparisons.

The lack of relevance of the glabrous input to area 1 for texture discrimination capacity in *Cebus* was seen in the inferior performance of normal animals and when the same two *Cebus* were retested following an area 1 lesion. Rather than producing a texture-specific deficit as in *Macaca* after the area 1 lesion, *Cebus* showed a remarkable improvement in performance on texture discrimination tasks. The generality of this improvement is shown in that they mastered a difficult comparison (320–120 gr/in) with fewer errors than they had taken to learn less difficult ones preoperatively. Surprisingly, the animal (Cb1) that had failed to master that comparison during previous training did so after removal of area 1. The other *Cebus* (Cb2) relearned more quickly and efficiently after area 1 lesions in both hemispheres than during original learning. That previous discrimination experience cannot account for the failure to find deficits after area 1 lesion is shown in that the efficiency of acquisition and performance on the ALLS task on the hand that was not previously trained (Cb2c) exceeded that of the previously trained hand following a lesion in contralateral area 1 (Cb2b).

Although our original finding relating deficits on texture tasks to area 1 in *Macaca* was based on animals trained only postoperatively (Semmes and Randolph, 1974), in a subsequent study the same selective deficits for texture tasks following an area 1 removal were demonstrated in animals also trained preoperatively (Carlson, 1981). Those animals failed to reacquire the same 320–180 gr/in that *Cebus*–area 1 mastered in the present study and with the same efficiency as normal *Macaca* on this same comparison (Carlson, 1984). These findings strongly suggest that the expansion and duplication of glabrous input to SI in *Cebus* does not contribute to texture discrimination capacity as it does in *Macaca*. Rather, the processing of glabrous input within area 1 of *Cebus* may compete or interfere with tasks requiring attending to details of surface texture. Area 1 in NW anthropoids may have evolved to process glabrous input for nontexture capacities that would serve to detect tactile features not represented in the type and range of comparisons used in these tasks.

The significance of receptor number and modality in the final SI and SII topography in the size of SI and SII

A comparative issue of major significance for the development, evolution, and behavioral capacity of the somatic sensory system is the nature of sensory receptors in the skin of these species. The dermis of *Galago crassicaudatus* (now *G. garnetti*) is characterized by a dense network of sensory end-organs in the glabrous hand and foot. These resemble the generalized mammalian end-organs more than the specialized Meissner corpuscles, found in digit tips of anthropoids, including apes and humans. The specialized end-organs associated with hairs in *Galago* are also described as primitive, though abundant, in hairy skin (Montagna and Yun, 1961). In *Macaca* numerous Meissner corpuscles are found in the glabrous surface of the hand and foot, with digits having a higher density than palm and sole (Montagna et al., 1964). The greater density of Meissner corpuscles in glabrous skin of *Macaca* than of mammalian end-

organs in the skin of *Galago* is consistent with the overall greater magnification of glabrous skin projections in SI and SII of *Macaca*. It is also expected that this difference in receptor density between these species, between the hand and foot, and between glabrous and hairy skin may contribute to the development of the different topographic patterns seen in SI and SII of these species.

The dermis of *Saimiri* contains Meissner corpuscles as well as another type of papillary nerve end-organ (Machida et al., 1967). The skin of *Cebus* is described to resemble that of *Saimiri*, with Meissner corpuscles common in digits and pacinian corpuscles in the palm and soles but rarely in the digits (Perkins and Ford, 1969). *Saguinus* and *Callithrix* are also found to have Meissner corpuscle in the skin of hand and foot, but (consistent with a single SI areas) the skin of these Callithrichidae is described as “between that of the Prosimii and Anthropoidea” (Perkins, 1968, 1969). To confuse the already muddled picture of primitive and derived features in brain, hand, behavior, and phylogeny of the NW anthropoids, *Aotus* (characterized by two cutaneous SI areas) has some receptors in the glabrous skin that “resemble” Meissner corpuscles but the overall features of the skin led to the conclusion that some NW species (and particularly *Aotus*) might be “considered to be New World Prosimii” (Hanson and Montagna, 1962). Although the NW primates represent an interesting variety of adaptations to arboreal living among primates, the continuing confusion around the phyletics of this infraorder, illustrated here by the inconsistencies in primitive and derived traits of the hand and CNS, makes it difficult to interpret the similarities and differences among NW and OW primates from an evolutionary perspective.

Relevance of natural behaviors to formal tests of tactile capacity

Comments on the natural behavioral repertoires of the four species used in this study seem warranted as a background for evaluation of the apparent sensory differences between species on formal tasks and of differences in brain organization. The prosimian *Galago* is a nocturnal primate that occupies arboreal settings at all levels of the forests. The home ranges of several adult females overlap with that of a single adult male but, except for mother–daughter pairs, adults are found together only during breeding season. The locomotor pattern typical of *G. garnetti* consists primarily of quadrupedal walking and running, less often by leaping, characteristic of the smaller *G. senegalensis*. Their diet consists mainly of tree gums, obtained by using the teeth, but fruits and insects, which require greater use of their manual capacities, are also important food sources (Bearder, 1987). There is limited social use of the hand, as grooming is performed using lower incisors and infants are transported by mouth.

In contrast, *Macaca mulatta* characteristically live in large multimale–multifemale social groups, ranging from 10 to 90 individuals. The total group size in *M. mulatta* appears to vary as a function of availability of resources in a particular habitat. *M. mulatta* are found in a variety of habitats in Asia ranging from urban settings (towns, temples, markets, and train stations) to forested areas. It is a terrestrial species and typically shows a quadrupedal form of locomotion illustrated in Figure 1. The hand is used in a multitude of ways in these diverse habitats as the foraging style of *Macaca* is that of an opportunistic omnivore (Ashmore DeClue, 1992). The social use of hand in *Macaca* is

a prominent part of their natural repertoire as they may spend as much as 25% of their day participating in social grooming. Overall, females spend more time grooming than males, whose grooming rate is strongly correlated with breeding season (Goosen, 1987).

Like *Galago*, *Cebus* and *Saimiri* are arboreal and their hands and feet are adapted for locomotion in trees. *Cebus* spend most of its time in the tree canopy but also frequently come to the ground while foraging or traveling (Fleagle et al., 1981; Robinson and Janson, 1987). *Cebus* uses supports ranging in diameter between 2 and 10 cm, and during locomotion shows prehensile abilities with its hands and feet. *Saimiri* is more often found in the lower canopy and forest understory, typically moving along narrow branches and lianas (<2 cm in diameter). Its locomotor pattern is slightly different from *Cebus* in that it spends a greater amount of time leaping and climbing (Fleagle et al., 1981). Perhaps the acuity to sense size differences is most developed in arboreal primates, but does not become degenerate as species make terrestrial adaptations, like *Macaca mulatta*, whose ancestors are believed to have been arboreal.

Of the two NW species, only *Cebus* uses precision grip, as defined by the capacity to manipulate objects between the thumb and digit tips, or between digit tips, without use of the palm. *Saimiri* uses only a power grip by which objects are held by flexing fingers against the palm (Costello and Frigaszy, 1988). Based on the diversity of prehensile patterns in object manipulation, Torigoe (1985) ranked *Cebus* with the great apes, as showing more diverse abilities than other NW and OW anthropoids. Although 90% of all manipulations were done with the glabrous part of the hand, *Cebus* tended to use its digits less (and palms more) than *Macaca* and apes (Torigoe, 1985). It has been suggested that the manipulative skills of *Cebus* are in part due to its feeding adaptation of extractive foraging (Thorington, 1966; Parker and Gibson, 1977). When foraging they make extensive use of their hands when searching for imbedded food items and hidden insects and require great strength to gain access to pith and nuts (Robinson and Janson, 1987). The diet of *Saimiri* consists mainly of fruits (especially figs) and insects. Insects are usually caught, using power grip (similar to that of *Galago*) while the animal is in motion. Social grooming is uncommon among *Saimiri* (Baldwin and Baldwin, 1981), while the amount of time *Cebus* spends in social grooming (Izawa, 1980; Robinson and Janson, 1987) approaches that of *Macaca mulatta* (Ashmore DeClue, 1992).

If the prominent, and undoubtedly important, glabrous input from the hand to area 1 does not mediate texture discrimination capacity, then to what type of sensory ability might this area contribute in NW anthropoids? Review of the species-typical patterns of hand use of these primates may lead to some predictions about classes of cutaneous processing that might be achieved by these species relative to *Macaca* and *Galago*. By examining their behaviors in the wild, as well as their manipulative capacity under formal tests in captivity, it may be possible to reach an understanding of the extent of their hand use and why texture discrimination capacity may be less important in the natural behavioral repertoire of *Saimiri* and *Cebus* than for *Macaca*. In *Cebus*, but not *Saimiri*, the SI hand area is vastly increased in size relative to the actual skin area and relative to the SI foot area. This finding suggests that these species that occupy the same natural habitats are using their forelimbs differently, but in a manner that might provide clues as to what tactile skills to investigate in captive *Cebus*.

Relevance to the evolution of neocortex to general behavioral capacities

A few remarks about the literature on the general relationship between evolution of neocortex and general behavioral capacity seem warranted, particularly with regard to *Cebus*. A clear evolutionary trend seen in primates is the expansion in brain size beyond the general mammalian scale (Jerison, 1973; Falk, 1980). It is generally believed that diet influences brain size in primates (e.g., Harvey et al., 1987; Milton, 1988). Recently, Sawaguchi (1992) reported that both diet and social structure are significantly correlated with the relative size of neocortex (RSN) over a wide range of primate species. Anthropoids with a predominantly frugivorous (fruit-based) diet had a greater RSN than folivorous (leaf-eating) anthropoids, and polygynous anthropoids had a greater RSN than monogynous anthropoids. However, as Dunbar (1992) points out, it may not be the mating system per se that is associated with elaborated neocortical areas but rather the size of the social group and complexity of the social interactive networks. Determination of the specific role of tactile information and manual dexterity in these general behavioral strategies could benefit from field observations that specifically attend to the sensorimotor functions of the hand in locomotor, feeding, and social behaviors.

It has been suggested that the living members of the Cebidae family, including *Saimiri* and *Cebus*, are the most generalized and therefore most likely reflective of the earliest NW anthropoids (Ford, 1986; Kay, 1990). On the other hand, Hershkovitz (1977) believes that many of the morphological features seen in *Saguinus*, and other callitrichids, are primitive traits. Others suggest that sometime during its evolutionary history the callitrichid family underwent a rapid reduction in body size, suggesting that many of their traits are derived, not primitive (Ford, 1980; Sussman and Kinsey, 1984). However, the brain of *Saguinus* shows very simple sulcal patterns, similar to the brains of prosimians, and compared to other NW primates, its brain shows the most primitive form (Falk, 1980; Carlson et al., 1986). The sulci pattern of the *Cebus* brain is intermediate in complexity to the prosimian-like Callitrichidae and the more complex Atelinae (Falk, 1980) and more complex than *Saimiri*. Stephan (1972) found that the neocortical progression index (calculated from neocortical size in relation to that of a basal insectivore) of *Cebus* was the same as for chimpanzee (60) but higher than *Macaca* (46) and *Saimiri* (43). *Galago* was approximately average for prosimians and had a neocortical progression index of 14.

The present findings suggest that an understanding of the significance of increased neocortical area, and increased cognitive and behavioral capacities, will require studies that focus on specific cortical regions and specific behavioral skills in species of different grades and clades. In fact, the differences in the magnification factor for the glabrous hands and feet even among the closely related NW anthropoids suggest that it may be necessary to consider such regional differences and body parts, as well as cortical projection areas SI or SII. The same caution for the need for greater specificity is seen in the nature of the behavioral tasks in the present experiments. These results show that discrimination of size and texture, and of different levels of difficulty within these tasks, may depend of a different constellation of peripheral receptors and central projection sites. Choosing behavioral tasks that are specific enough to relate to peripheral and central structures, yet that resemble discrimi-

nations made in the natural habitat, is not an easy task. However, if a valid understanding of the relationship between neural organization and behavioral capacity is to be achieved, information about the natural behavioral repertoires of species must be considered.

Relevance of thalamic connections to SI and SII to tactile capacity

New insights into the possible evolutionary mechanisms by which varying patterns of SI and SII input have been achieved, in closely and distantly related species, appear from recent findings on the patterns of thalamocortical in different primates. The original conception of VPL (ventroposterior lateral nucleus; the major source of input to SI) as providing input to both SI and SII in *Macaca* has been modified by recent observations in a variety of species (Jones, 1985). Subsequent studies showed that the VPL projection to SII is less extensive (or lacking) in *Macaca*, and that the projection from inferior VP (VPI) is predominant (Friedman and Murray, 1986; Friedman et al., 1986). The physiological implication of the revised VP–SII connectivity came with the demonstrations that lesions of SI hand area silenced the hand area of SII (Pons et al., 1987), substantiating the notion that SII receives its cutaneous input indirectly via intrahemispheric connections through SI. These findings are consistent with the theory of tactile processing arguing that SII serves as a point in a VP–SI–SII serial pathway to limbic cortex for higher cortical processing of tactile input in *Macaca* (Mishkin, 1979). Yet anatomical studies in adult *Galago* indicate that SII receives its major thalamic projection from ventral zones in the lateral division of VPL and SI receives its input from more dorsal regions of VPL (Burton and Carlson, 1986). Other nuclei, including VPI, also project to SII.

When the pattern of VP–SI and VP–SII connections in *Macaca* and *Galago* are compared to the projection of the glabrous and hairy hand to SI, an interesting coincidence is observed. The direct VPL–SII connections seen in *Galago* are lacking in *Macaca*, while the projection of the glabrous hand to area 1 of *Macaca* is lacking in *Galago*. In *Galago*, the projections of both the glabrous and hairy skin are unambiguously segregated into similarly sized subdivisions in SI (to areas 3b and 1, respectively) and into the ventrodorsal subdivisions in SII. In contrast, the major glabrous input in SI and SII of *Macaca* obscures the minor input from the hairy hand and digits. When comparing the size of the glabrous hand areas in SI and SII, it is important to emphasize that, compared to *Galago*, the glabrous hand areas in SI and SII of *Macaca* have increased relative to the actual skin area, relative to the hairy hand surface, and relative to the cortical projection areas for the glabrous foot. To understand the cortical mechanisms that mediate the more recently evolved tactile capacities of the hand, it is important to consider both the differential cortical projections of the glabrous and hairy surfaces of the hand and the different behavioral demands on these two extremities in the behavioral strategies of *Galago* and *Macaca* in their natural habitat.

Relevance of the development of thalamocortical connections in the evolution of SI and SII organization in primates complexity of SI and SII

The absolute density of receptors in glabrous and hairy skin, as well as the different classes of receptors, can be expected to be important in development, as activity-dependent mechanisms are thought to play a major role in the elimination and main-

tenance of transient connections. In the somatic sensory system the best evidence for such mechanisms operating in the development of thalamocortical projections and SI topography is from developmental studies of the SI barrel fields in rodents. The importance of whisker stimulation in the formation and maintenance of barrel fields has been seen in brainstem and thalamic nuclei as well as cortical projection areas (Van der Loos and Dörfel, 1978; Van der Loos and Welker, 1985).

The expansion and/or duplication of input to SI and SII in different primate species may result from minor variations in the developmental sequences of outgrowth, elimination, and stabilization of thalamocortical and corticocortical connections. The studies of VP–SI–SII relations in adult *Macaca* provide an interesting contrast to those VP projections to SI and SII in adult *Galago*, where we find that VPL projects both to SI and SII (Burton and Carlson, 1986). In adult *Galago*, individual neurons in VPL or VPI project to either SI or SII (but not to both), whereas in the first postnatal weeks many VP neurons extend collaterals to both SI and SII (Carlson et al., 1987). A similar pattern of exuberant thalamic projection to pre- and postcentral gyrus in infant *Macaca* has also been described (Darian-Smith et al., 1990). A developmental mechanism that could transform a single cutaneous SI projection area (and VPL–SI and VPL and VPI–SII pattern) seen in adult *Galago*, to the multiple glabrous SI projection areas (VPL–SI and VPI–SII pattern) of *Macaca* is the robust phenomenon of stabilization of normally transient collaterals (O'Leary, 1989, 1992). If, early in development, the initial outgrowth of VPL axons is specific for neither place (SI or SII) nor submodality (glabrous or hairy), species-typical patterns of elimination and stabilization of collaterals may occur.

Our findings in infant *Galago* that some single VP neurons extend axon collaterals to SI or SII raise the issue of whether the segregated glabrous and hairy hand areas of SI (areas 3b and 1) and SII may come about through selective stabilization based on submodality. If glabrous and hairy inputs initially overlap in SI and SII of the infant, then the processes of elimination and stabilization of collaterals could result in segregation into glabrous–hairy divisions and in selective projection of VPL neurons to SI or SII in adult *Galago*. To achieve the latter pattern all VPI collaterals to SI would be eliminated and those to SII stabilized.

If in *Macaca* the initial outgrowth of thalamic axons also occurs without respect to place (SI or SII) or submodality (glabrous or hairy), a species-typical pattern may result from the elimination of all VPL collaterals to SII, with the maintenance of the remaining VPL collaterals to SI, and the maintenance of all VPI collaterals to SII. A second part of this developmental pattern would be the glabrous input from VPL (predominant in *Macaca*), which would dominate over the sparser hairy input from the hand, with the all VPL-mediated glabrous input projecting to areas 3b and 1, rather than divided between SI and SII as in adult *Galago*.

Primate studies seeking to demonstrate the evolution and development of brain structure and behavioral function need to be as inclusive as the investigations of rodent barrel fields and of SI in carnivores (Welker et al., 1963, 1964) to approach an understanding of brain and behavior relations. The present study raises issues that must be addressed to address the complex brain–behavior relations in this restricted domain of the somatic sensory system as well as for more general behavioral categories. Convergent information is needed from the classical

theoretical debates to current research findings in evolutionary and developmental biology, along with comparative psychology and physical anthropology, to approach these brain-behavior relations in primates.

Differences between the earlier-evolved *Galago* and the more recently evolved *Macaca* must also be considered in a developmental perspective, as it is variation in development of such connections that contribute to the species-typical cortical organization observed in adult animals (deBeer, 1958; Gould, 1977; Carlson, 1990, 1991). In order to account for the behavioral significance of structural and functional features of cerebral cortex, the combined analyses of peripheral receptors, cortical magnification factors, as well as topography and submodality data must be made to begin an understanding of species differences in behavioral capacity. The now classical studies of Welker et al. (1963, 1964) in carnivores set a standard for the level of detail at all levels of a sensory system required to obtain an understanding of the role of cerebral cortex in the evolution of (or in individual differences) in behavioral capacity.

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