

Meissner Corpuscles and Somatosensory Acuity: The Prehensile Appendages of Primates and Elephants

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ABSTRACT

Meissner corpuscles (MCs) are specialized mechanoreceptors located exclusively in the papillae of glabrous skin. They are confined largely to cutaneous pads of the extremities and respond to transient, phasic, or vibratory stimuli. Though absent in most eutherian taxa, MCs are reported in all primates studied, being most developed in modern humans. The location of MCs between the internal ridges of the epidermis indicates they are well situated to detect friction or deformation at the external surface. Accordingly, MCs are hypothesized to provide primates generally with an enhanced tactile perception. However, the selective pressures favoring greater somatosensory acuity in primates are seldom considered. Interestingly, primate digital dexterity varies greatly. In general, dexterity improves with the extent to which foraging requires food manipulation or textural evaluation. This observation implies that MC density could vary accordingly. Here we report on the density of MCs in five anthropoid taxa selected to represent diverse dietary regimes. Results show that greater MC density correlates with the extent to which primates are frugivorous; however, locomotor and/or phylogenetic effects cannot be discounted.

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Key words: Pongo; Ptilocolobus; Hylobates; Theropithecus

Cartmill (1974, 1992) hypothesized that basal primates were visually directed predators of fauna on slender branches, a milieu that favored a wide field of stereopsis and clawless prehensile hands for visually tracking and grasping prey. The fine-branch niche model for primate origins has since enjoyed wide acceptance, although competing views have emphasized the importance of foraging on fruits, nectar, and/or cryptic prey (Rasmussen, 2002). Recently, reports on the grasping skill of tree shrews and an extinct plesiadapiform, *Carpolestes simpsoni*, indicate that prehension preceded orbital convergence, that is, fruit-foraging predated fauna capture during primate evolution (Sargis, 2001; Bloch and Boyer, 2002). However, a clawless opposable hallux is not a uniquely derived character trait (Kirk et al., 2003). Nevertheless, it is generally deduced that fruits have long been included in the primate diet to some extent (Ravosa and Savakova, 2004). In short, grasping food and small-diameter supports were probably

key factors in the development of primate manual prehension (Lemelin, 1999).

A distinctive aspect of primate grasping is the degree to which manual skills vary (Bishop, 1962, 1964). Strepsirrhines and tarsiers have a single stereotyped pattern of manual prehension characterized as whole-handed flex-

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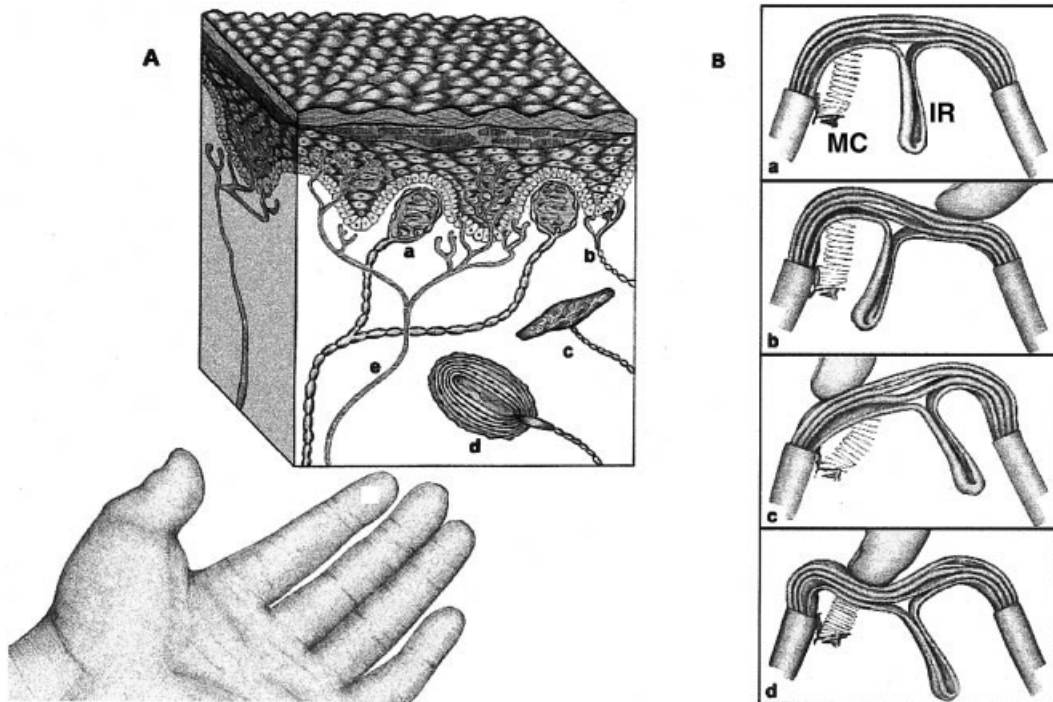


Fig. 1. **A:** Nerve endings of the glabrous digital skin (a) Meissner corpuscles, (b) Merkel disks, (c) Ruffini endings, (d) Pacinian corpuscles, and (e) free nerve endings. Meissner corpuscles connect to and tightly about the basal surface of the epidermis, just below the basement membrane. **B:** Cauna's model of an intermediate ridge (IR) and a Meissner

corpuscle (MC; a). The intermediate ridge may act as a "magnifying lever mechanism" (Cauna, 1954) because its swing transmits oblique stimuli to the Meissner corpuscle (b and c). The spring-like receptor is fully stimulated by pressure coinciding with its axis (d).

ion. The grip is used during locomotion, feeding, and social behavior. In platyrrhines, the pattern is similar: digit I flexes with the other digits in a uniform plane. However, platyrrhines enjoy some degree of interdigital dexterity; objects can be held in a scissors grip between two digits or grasped with a single curling digit. Interestingly, prehension is not restricted by the presence of claws in *Saguinus* (Lemelin and Grafton, 1998) or, notably, the tree kangaroo, *Dendrolagus matschiei* (Iwaniuk et al., 1998). Among platyrrhines, only *Cebus apella* and, to a lesser extent, *Cacajao* (Bishop, 1964) appear to possess a characteristic precision grip (Costello and Frigaszy, 1988).

Among cercopithecoids, there are two forms of prehension: a grip between the thumb and some part of the hand and/or digit II; and a grip involving independent control of digits I and II. This latter grip is used for grooming, feeding, and fine manipulations. Bishop (1964) noted that the precision grip of baboons, macaques, and mangabeys is similar to that of *Homo*, which has been described as having "the ultimate refinement in prehensibility" (Napier, 1962: p. 59). Baboons may control each digit separately, but thumb-index prehension is best developed in the Hominoidea (Bishop, 1964). Interestingly, the digital proportions of humans are most similar to that of baboons (Jolly, 1970). Accordingly, the singular evolution of interdigital control is usually linked to a terrestrial context in which animals engaged in complex manipulations of small food objects (Straus, 1942; Bishop, 1964; Welles, 1976).

Meissner Corpuscles

The tactile properties of such objects are processed by the somatosensory system, which uses information from receptors that respond to touch and vibration, body movement, temperature, and pain (Kaas, 1993). Object identification arises from two types of mechanoreceptors (Srinivasan and LaMotte, 1987): slowly adapting (SA) receptors that signal light maintained pressure, and rapidly adapting (RA) receptors that signal the onsets and offsets of skin indentations (Coleman et al., 2001). Meissner corpuscles (MCs) are RA receptors that respond to transient or phasic stimuli. MCs are located in the dermal papillae of glabrous skin, where they connect to and tightly about the basal surface of the epidermis (Fig. 1A). They are innervated by one or two myelinated fibers from the subepidermal nerve plexus (Cauna, 1956; Castano et al., 1995; Nolano et al., 2003). The fibers lose their myelination before entering the corpuscle, an ovoid capsule of perineural cells (Munger and Ide, 1988). Therein, the nerve endings branch repeatedly, adopting a ribbon-like shape with bulbous expansions (Guinard et al., 2000; Nolano et al., 2003). Collagen fibers and fibrocytes bond the spiraling nerve endings to stacks of lamellar Schwann cells and attach the capsule to the epidermis (Halata, 1975). The tortuous and circumscribed expansion of unmyelinated nerve endings into lamellar disks is a distinctive feature of MCs. Although this complex innervation has led to speculation that MCs could have a nociceptive function (Paré

et al., 2001), aspects of the disciform expansion suggest a primary role in mechanoreception.

Recently, Takahashi-Iwanaga and Shimoda (2003) reported that the disk margins are serrated with fine projections of lamellar Schwann cells that tightly hold the collagen trabeculae to the inner aspect of the pericorpuscular capsule. They concluded that the disks are susceptible to mechanical deformations of surrounding tissues and, furthermore, that the distortion of axonal endings during the dynamic phase of tissue deformation is sufficient to generate RA receptor potentials. Similarly, Castano et al. (1985: p. 296) observed that "even the minutest deformation of the skin [can be] immediately transmitted to the capsule and, via the cross-beam system linking it to the framework, to the transducer elements of the corpuscle." The disciform expansion is thus well suited to mechano-electrical transduction. Accordingly, MCs are hypothesized to play a key role in modulating the perception of elastic texture (Lindblom, 1965; Halata, 1975; Munger and Ide, 1988; Bensmaïa, 2002).

Distribution and Adaptive Significance of Meissner Corpuscles

MCs are reported from the lips and extremities of primates and marsupials, e.g., *Didelphis virginiana* (Winkelmann, 1964). Murine and sciurid corpuscles are similar in shape, but smaller and less elaborate (Brenowitz, 1980; Munger and Ide, 1988). Given the importance of haptic senses to humans, especially during food evaluation (Szczeniak and Bourne, 1969), it is surprising that relatively little quantitative data have been published on the distribution and comparative morphology of primate MCs (Winkelmann, 1962; Grzycki, 1970; Castano et al., 1985, 1991; Bolanowski and Pawson, 2003; Güçlü et al., 2003). This lack of comparative data is problematic when modeling the origins and evolutionary ecology of primate somatosensory adaptations.

Martin (1990: p. 502–503) noted the alignment of MCs beneath epidermal ridges and suggested that the structures serve a dual function, frictional and tactile, that aids the perception and prevention of slippage (the "friction hypothesis"): "The ventral surfaces of [primate] extremities bear tactile pads with cutaneous ridges (dermatoglyphs) that reduce slippage on arboreal support in association with dermal Meissner corpuscles" (p. 639).

Enhanced tactile sensitivity on slender substrates probably conferred strong selective advantages to euprimate ancestors (Cartmill, 1979; Hamrick, 1998). Supporting this hypothesis is the fact that atelines possess MCs on the ventrodorsal aspect of their tails, where a patch of dermatoglyphic skin is present (Biegert, 1961; Garber and Rehg, 1999). The prehensile tail aids suspension from small branches during feeding and locomotion (Grand, 1984). However, a linkage between MCs and epidermal ridging is not universal. MCs are absent in *Urogale everetti* (Winkelmann, 1963), a terrestrial tree shrew that shares pedal ridging in common with other tupaiids, e.g., *Tupaia* and *Ptilocercus* (Wu, 1988; Martin, 1990; Lemelin, 2000).

Although the selective advantages of preventing arboreal slippage are clear, the dispersion of MCs raises the possibility of a more specialized function in anthropoids. In humans, RA receptors are concentrated at the distal ends of digits I–III (Johansson, 1978; Johansson and Vallbo, 1979), where tactile acuity is greatest (Caruso et

al., 1994). MC densities range from 5.4 mm^{-2} in the thenar eminence to 33 ± 13 and $24 \pm 10 \text{ mm}^{-2}$ in the pads of digits III and V, respectively (Bolton et al., 1966; Nolano et al., 2003). Such a dispersion may serve an acute sensory function analogous to the tactile fovea of dolphins and star-nosed moles (Pettigrew and Frost, 1985; Catania and Kaas, 1997; Catania and Remple, 2004). The concept of a tactile fovea is based on the primate visual system (Polyak, 1957). In haplorrhines, the fovea centralis is a dense concentration of specialized retinal photoreceptors represented by a disproportionately large cortical region. Sophisticated ocular motor control directs the fovea toward a stimulus of interest. Recently, the notion of a fovea has been extended to other sensory modalities, e.g., the electrosensory fovea of gymnotid fish (Castelló et al., 2000) and the auditory fovea of echolocating bats (Neuweiler, 2003).

The motor control and magnified cortical representation of digits I–III (Woolsey et al., 1942; Sur et al., 1980; Rizzolatti and Luppino, 2001; Blake et al., 2002) are consistent with the notion that monkey digits may function as a tactile eye, having a small behavioral focus, or fovea at the center. For anthropoids, a tactile fovea may permit detailed evaluation of objects, such as suitable weight-bearing branches or fruits. The softening texture of ripening fruits is a salient sensory cue (Brady, 1987; Dominy, 2004), and digits I–III are crucial for precision grasping (Napier, 1960) and the perception of elastic texture (Peleg, 1980). Such observations raise the possibility that high MC density in anthropoid digits could have evolved to facilitate the rapid assessment of fruit edibility (the fruit texture hypothesis).

Compellingly, epidermal ridging may improve somatosensory acuity because papillary ridges transmit elastic energy to intermediate ridges, which in turn act as "magnifying levers" to MCs (Fig. 1B) (Cauna, 1954). However, the digits of raccoons are richly innervated by mechanoreceptors but feature poorly developed papillary ridges (Munger and Pubols, 1972). Furthermore, the functional significance of intermediate ridges is equivocal; they are not unique to primates or always associated with MCs (Lemelin, 2000). Indeed, among Asian elephants (*Elephas maximus*), the hirsute skin on the projecting flange (or finger) of the trunk possesses intermediate ridges, but not MCs (Winckler, 1973; Verdan, 1979; Rasmussen and Munger, 1996). Interestingly, proboscis morphology and prehensile skill differ between Asian and African elephants (Fig. 2). Because *Loxodonta africana* uses its trunk to grasp objects precisely, including fruits, it is compelling to examine it for MCs. If they exist, the finding would be consistent with a role in assessing texture, not friction.

The goal of this analysis is to provide a preliminary and quantitative description of MC density in a comparative sample of anthropoid primates. Predictions were tested on the assumption that receptor density parallels sensitivity (Meisami, 1989; Catania, 1999; Ruth et al., 2002; Martin et al., 2004). Predictions were derived from the above hypotheses regarding the functional similarities between the prehensile appendages of anthropoids and one African elephant. The specific questions addressed include the following: Does the distal trunk tip, or finger, of the African elephant possess MCs? Do systematic differences in MC density vary as a positive function of a frugivorous diet (as predicted by our fruit texture hypothesis), or does

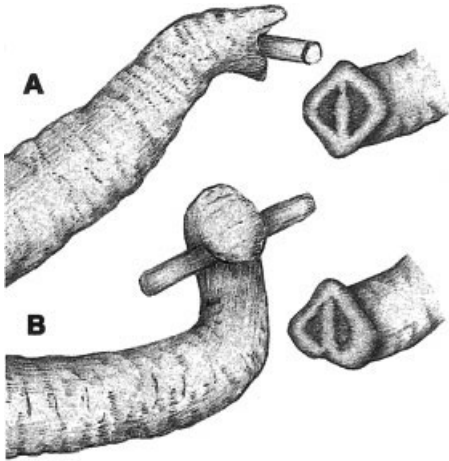


Fig. 2. **A:** The trapezoidal morphology of the trunk in the African elephant (*Loxodonta africana*) permits opposition between the ventral and dorsal tips or fingers. Reportedly, such prehension permits the grasping of a single coin from a concrete floor (Shoshani, 1997). **B:** The prehensile skill among Asian elephants (*Elephas maximus*) is less refined and involves curling of the trunk around an object.

MC density not vary at all, or vary as a function body size and/or locomotor pattern?

MATERIALS AND METHODS

Subjects and Tissue Collection

Tissues were obtained from the cadavers of five anthropoid primates housed in the Department of Anthropology, University of Chicago. Each adult cadaver was fixed and preserved in ethyl alcohol in the 1960s. Provenances are unknown. For each specimen, the manual integumentary tissue was excised from the cutaneous pad between the interphalangeal crease and distal tip of digits I and II. Tissues were immersed in 10% neutral buffered formalin and processed for paraffin embedding. Taxa were chosen on the basis of dietary diversity and state of preservation: a gelada (*Theropithecus gelada*), a red colobus (*Piliocolobus badius*), a silvered langur (*Trachypithecus cristatus*), an orangutan (*Pongo pygmaeus*), and a white-handed gibbon (*Hylobates lar*). The University of Chicago Institutional Animal Care and Use Committee approved this protocol under Animal Care and Use Procedure number 71305.

A female African elephant (*Loxodonta africana*) was captured near Ngorongoro, Tanzania, and brought to the Brookfield Zoo, Chicago, on 7 June 1972, at the estimated age of 1 year (ISIS no. 22301). She died at the zoo on 16 June 2003. During necropsy, zoo staff removed and froze the distal 30 cm of the trunk. Axial sections of this segment were cut and small 10 mm pieces of tissue were excised for analysis. Tissues were immersed in 10% neutral buffered formalin and processed for paraffin embedding. The Biological Research Steering Committee of the Chicago Zoological Society approved this protocol.

Histochemical Preparations

A Leica 2135 rotary microtome was used to cut 4 μm sections in the sagittal or transverse plane of the digit. Sections were mounted and stained with Masson's

trichrome (Sheehan and Hrapchak, 1982). The technique is a sequence procedure employing a plasma and collagen fiber stain. Staining was done at an acidic pH to increase collagen selectivity. Sections were deparaffinized and hydrated in 95% alcohol, flooded with Bouins Fixative (EK Industries, Joliet, IL) for 3 min, and washed in running water for 3 min. Sections were placed in Harris hematoxylin 130 (Surgipath Medical Industries, Richmond, IL) for 3 min and washed in running water. Next, sections were flooded with 1% Biebrich Scarlet in 1% acetic acid for 2 min, washed in running water, and flooded with phosphomolybdic and phosphotungstic acid solution for 1 min. Next, sections were flooded with 2.5% aniline blue in 2.5% acetic acid for 2 min, washed in distilled H_2O , and flooded with 1% acetic acid for 1 min. Finally, sections were rinsed once in 95% alcohol and twice in absolute alcohol before two changes of xylene and mounting in synthetic resin.

Light Microscopy

MCs were identified and quantified using a Leitz Diaplan stereo light microscope. Single- and double-blind counts of whole and partial MCs were determined at 2.5 \times or 6.3 \times magnification. The plane for MC counts ran through the depth of the viewing field. Density was determined by computing the volar area of 4–5 tissue sections. Area was calculated from the length of each section, as measured with an ocular micrometer, and the known thickness (4 μm). Images were captured with an Olympus IX81 microscope equipped with a Retiga EXi camera (Q-Imaging, Burnaby, Canada).

Data Analysis

To investigate the relationship between frugivory and MC density, nonphylogenetic and phylogenetic approaches were used. For nonphylogenetic analysis, a reduced major axis (RMA) regression was computed on the basis that both variables are assumed to have an associated error. RMA is least sensitive to assumptions on the error structure of the data and is the least-biased estimate of the underlying functional relationship (LaBarbera, 1989). A phylogenetic approach was also used on the basis that continuous biological data potentially violate standard statistical assumptions of independence due to phylogenetic relatedness (Felsenstein, 1985). Data were adjusted for phylogenetic similarity with the method of comparative analysis by independent contrasts (CAIC) using version 2.6.9 (Purvis and Rambaut, 1995). The primate phylogeny was derived from Purvis (1995).

RESULTS

Preservational artifacts limited the range of our study. Shrinkage and separation of the stratum corneum from the germinal layers occurred in most specimens (Fig. 3). Accordingly, not every digit that was sampled yielded identifiable MCs. Compellingly, however, the results were consistent with previous reports despite differing methodologies (Table 1). In a study of serial sections, Güçlü et al. (2003) reported a density of 7.2 MCs $^{-2}$ in digit I of a male baboon (*Papio* sp.). Herein, a density of 10.2 MCs $^{-2}$ was found in digit II of a male gelada (*Theropithecus gelada*), a closely related species.

The positive relationship between MC density and the proportion of time spent feeding on fruits is illustrated in Figure 4A. Examination of the plot identifies an outlier,

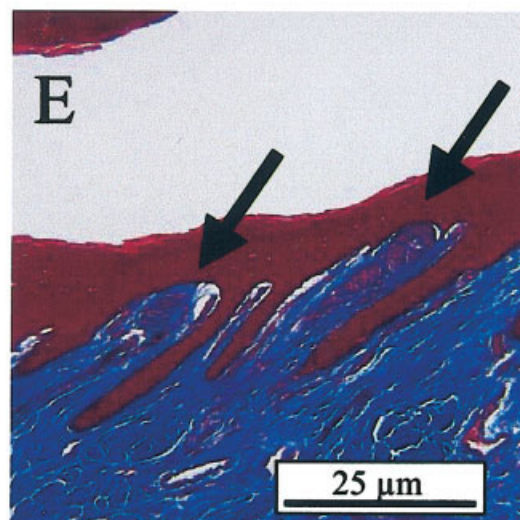
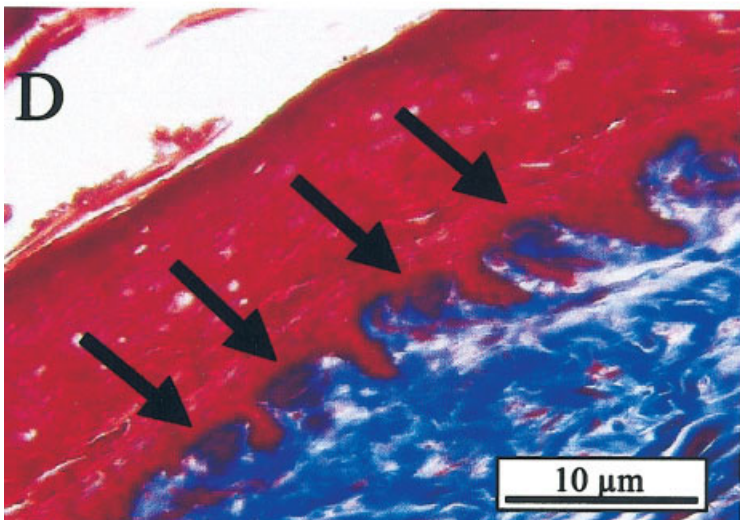
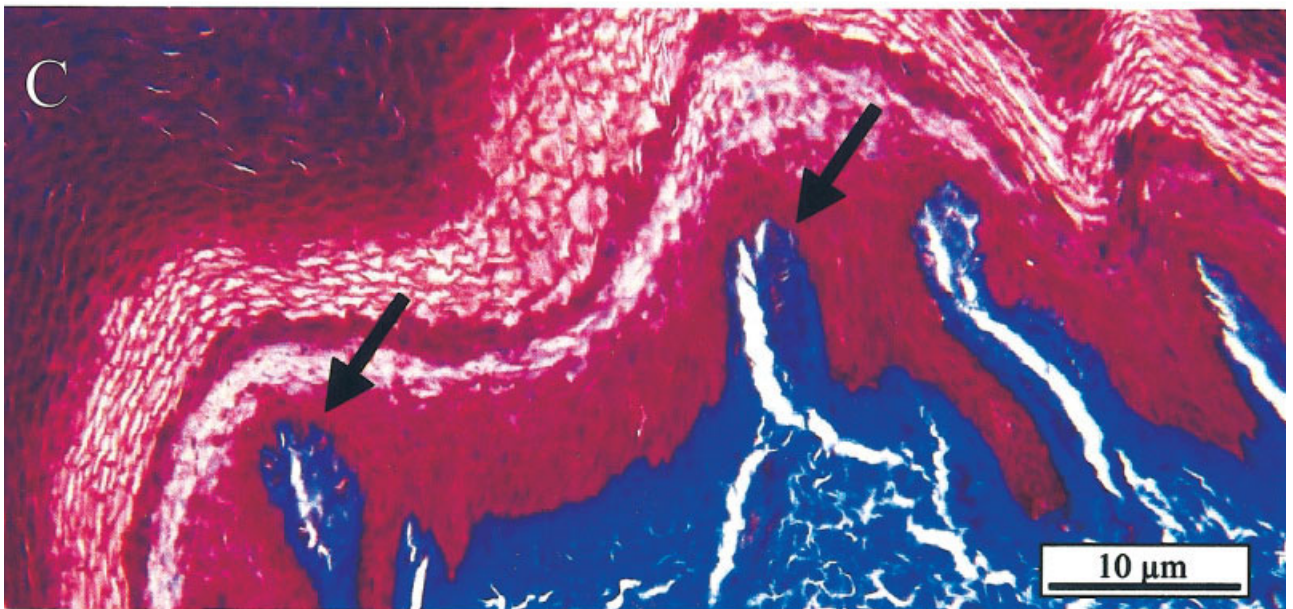
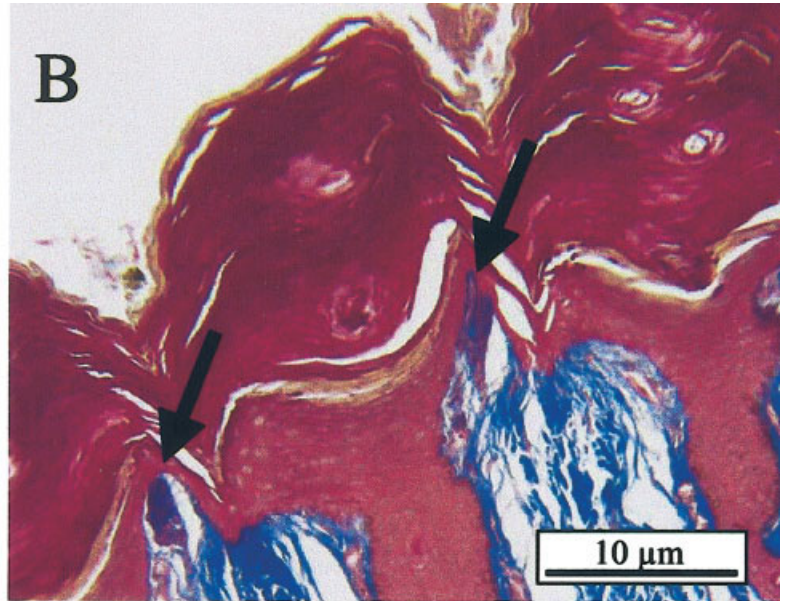


Fig. 3. **A:** Detail of an orangutan Meissner corpuscle. Collagen and mucus appear blue and muscle fibers and cytoplasm appear red. Arrows indicate MCs in **(B)** *Ptilocolobus badius*, **(C)** *Theropithecus gelada*, **(D)** *Hylobates lar*, and **(E)** *Pongo pygmaeus*. Specimens were poorly preserved. Note the disassociation between the keratinized layer and the remaining deeper levels of the epidermis in A, D, and E.

TABLE 1. Density of Meissner corpuscles in the digits of nonhuman primates

Primate taxon	Sex	Age	Digit	MCs/mm ²	Diet		
This study^a							
<i>Hylobates lar</i> (white-handed gibbon)	M	Adult	II	45.8	Fruit (50%), foliage, insects, flowers (Rowe, 1996)		
<i>Pongo pygmaeus</i> (orangutan)	F	Adult	I	14.3	Fruit (61%), foliage, insects, honey (Galdikas, 1988)		
<i>Ptilocolobus badius</i> (red colobus)	F	Adult	II	16.7	Fruits and seeds (6%), foliage (73%), flowers (Struhsaker, 1975)		
<i>Theropithecus gelada</i> (gelada)	M	Adult	II	10.2	Fruits and seeds (6%), grass (90%) (Dunbar, 1977)		
<i>Trachypithecus cristatus</i> (silvered langur)	F	Adult	I	11.7	Fruit (10%), foliage (80–90%), seeds (Rowe, 1996)		
Güçlü et al. (2003)^b							
<i>Aotus</i> sp. (night monkey)	F	?	II	43.0	Fruits (50–80%), insects, leaves, flowers (Wright, 1989)		
			III	44.4			
			V	46.2			
<i>Macaca mulatta</i> (rhesus macaque)	F	6	I	34.4	Fruits (65–70%), leaves, insects, small vertebrates, fungi (Lindburg, 1977)		
			M	?		II	32.2
			III	33.2			
			V	21.0			
<i>M. radiata</i> (bonnet macaque)	F	12	I	31.2	Fruits (47–53%), seeds, leaves, flowers, small vertebrates (Rowe, 1996)		
			II	28.9			
			V	27.5			
<i>Papio</i> sp. (baboon)	M	?	I	7.2	Fruits (14%), foliage, storage organs (Barton et al., 1993)		

^aMC density from 4–5 transverse sections.

^bMC density from one serial section; only distal sections are reported here.

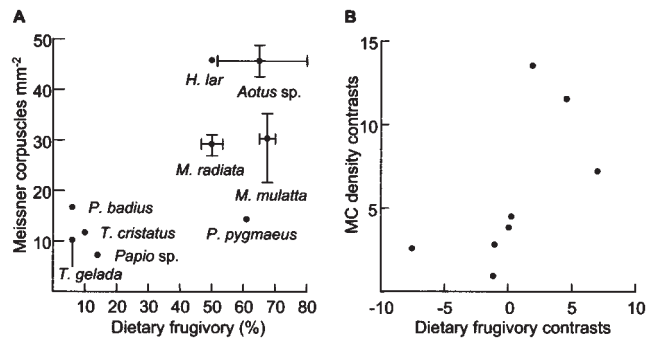


Fig. 4. **A:** Relationship between MC density and the proportion of time spent feeding on fruits. The slope of the reduced major axis regression is 0.55 ± 0.33 ($P < 0.01$). Whiskers represent the range of MC densities in the digits of a single individual (Table 1). **B:** Independent contrasts in MC density and dietary frugivory. Regressions of contrasts on contrasts must pass through the origin; the slope is 0.26 ($P = 0.22$).

the orangutan (*Pongo pygmaeus*), which has a lower density of MCs (14.3 mm^{-2}) than expected based on its diet. As a point of reference, this value is similar to mean densities reported for digit I in humans, e.g., 16 mm^{-2} (Bolton et al., 1966) and 17 mm^{-2} (Güçlü et al., 2003). An analysis of the data that adjusts for potential phylogenetic bias reveals no significant relationship; however, a positive trend is apparent and the sample size is low (Fig. 4B). Lastly, despite the partially glabrous nature of the trunk ventral tip of *Loxodonta africana* (Fig. 5A), no clearly identifiable MCs were found (Fig. 5B–E). This result is consistent with reports on the trunk tips of *Elephas maxi-*

mus (Winckler, 1973; Verdan, 1979; Rasmussen and Munger, 1996).

DISCUSSION

Evidence suggests that the elephant trunk evolved to facilitate snorkel breathing in an aquatic ancestor (Gaeth et al., 1999; West, 2001). Innervation of the trunk resembles the mystacial skin of rodents or lip tissue of orangutans (Vij et al. 1973; Rasmussen and Munger, 1996). Rasmussen and Munger (1996) correlated the innervation with the tactile ability to grasp small objects. Interestingly, distinctive aspects of the visual system appear to support this function. The retinal ganglion cells of *Loxodonta africana* are concentrated in the upper temporal region. Stone and Halasz (1989) suggested that this pattern evolved to monitor the actions of the trunk. Orbital convergence and the lower visual field of primates may function similarly, that is, to support manual grasping (Previc, 1990). On the basis of these seemingly homologous specializations, we examined the trunk of *Loxodonta africana* for MCs. Here we report their absence.

We also report on the digital density of anthropoid MCs. A positive correlation was found between MC density and frugivory. While this finding is consistent with the fruit texture hypothesis, a variety of confounding factors must be considered. First, MCs are generally fully developed at birth but lost with age (Cauna, 1964; Renehan and Munger, 1990). For example, Bolton et al. (1966) reported that MC density in digit V can decline from 24.0 ± 9.9 (in subjects aged 11–30 years) to $8.4 \pm 3.3 \text{ mm}^{-2}$ (in subjects aged 71–84 years). Second, an inverse relationship between MC density and digital surface area indicates that digit size is an important variable (Bolton et al., 1966;

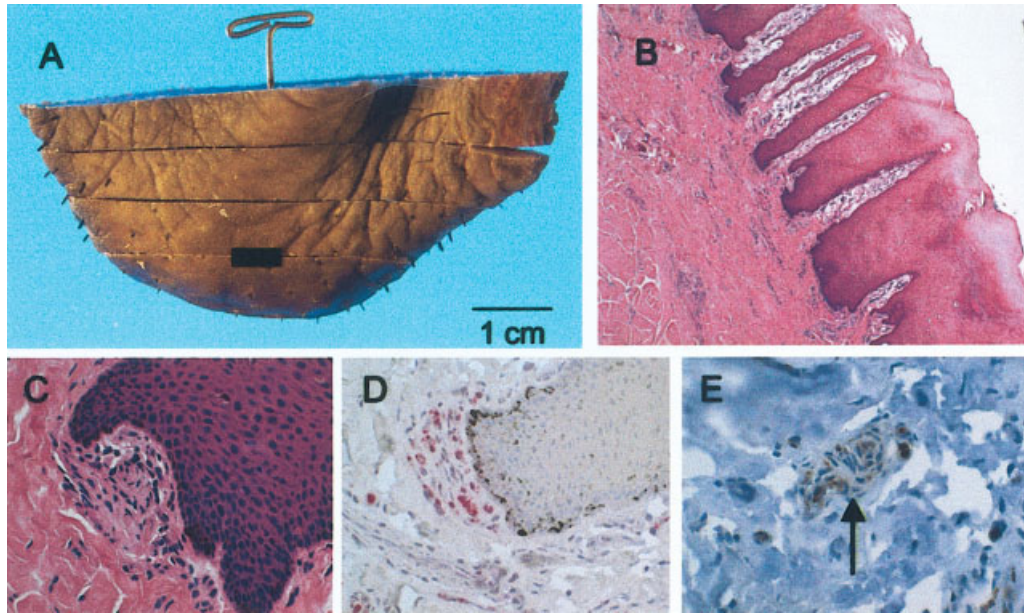


Fig. 5. **A:** The distal trunk tip, or finger, of *Loxodonta africana* is characterized by a central glabrous region with dermal ridges. The black rectangle represents the region of excised tissue. **B:** Rete pegs and papillary dermis (hematoxylin and eosin stain, 40 \times). **C:** Clusters of

peripheral nerves at base of rete peg (hematoxylin and eosin stain, 400 \times). **D:** Clusters of peripheral nerves highlighted by S100 stain (200 \times). **E:** Peripheral Meissner-like nerve ending in papillary dermis (S100 stain, 100 \times).

Dillon et al., 2001). Third, Cauna (1964) observed that MC density declines with frequent manual labor, but he presented no data. Accordingly, incisive and definitive statements regarding our results cannot be made; factors apart from a frugivorous diet can influence the density of MCs. Regardless, it is interesting to speculate on the advantages of a digital fovea in anthropoids.

Fruit Texture Hypothesis: A Tactile Fovea in Primates?

Inferring process from pattern must be a cautious endeavor, and our fruit texture hypothesis cannot be supported from our limited data. However, a paucity of data provides little evidence for any one particular model of MC evolution. In his review of the primate somatosensory cortex, Kaas (1993: p. 509) observed: "Higher primates have [several] specializations, first in the peripheral input where there is an unusual emphasis on the use of the hand as a tactile organ, and then in the thalamus and cortex where more subdivisions of the brain are devoted to the somatosensory system. The elaborations and specializations seen in higher primates appear to relate largely to being able to identify and recognize objects and surfaces by touch. The specializations start in the skin of the hand, where large numbers of receptors are concentrated in the finger tips, which are used for active exploration. The process of object identification is aided by fine motor control of the hand and digits, and modifications in [the] motor cortex."

Mechanosensory adaptations that enhance active exploration and object recognition tend to facilitate foraging (Pettigrew et al., 1998; Catania, 1999; Hamrick, 2001). For anthropoids, evaluating fruits haptically may provide a rapid means of discerning fruit edibility (Dominy, 2004).

For example, van Roosmalen (1985: p. 87) described the tendency of spider monkeys to inspect fruits on the basis of smell and texture because "external properties (like colour) do not give a decisive answer on the stage of maturity." Similarly, Wrangham (1977: p. 510) observed that "[chimpanzees] often inspect individual food items by sight, touch, or smell." Unfortunately, the use of haptic cues during fruit selection is seldom studied.

However, palpation of a fruit in order to assess texture requires interdigital dexterity, a skill that is not associated with frugivory or MC density. Although the latter two parameters are correlated with each other, we believe the relationship reflects a generalized pattern associated with complex foraging. In field studies, dexterity is important for constructing tools or foraging on physically defended foods, such as thistles, abrasive leaves, and protected fruits (Byrne et al., 2001; Corp and Byrne, 2002a, 2002b). In this regard, complex exploratory foraging may have been the selective regime favoring interdigital dexterity (MacNeilage, 1990). Terborgh (1983: p. 98) described such foraging in *Cebus apella*, the platyrrhine with the greatest manipulative skill: "It bites open bamboo canes, hollow dead twigs, and dead palm rachides; it is particularly attracted to palm crowns, where it rummages through the debris that accumulates in the funnel-like apical regions. It often rummages through matted vine tangles, sending down showers of dead stems and leaves. Another common pursuit is the stripping of bark from dead trunks and limbs."

Although this food-exposing behavior involves much whole-handed grasping, MacNeilage (1990) suggested that the variable nature and presentation of such food products favored a precise grip. In this regard, interdigital dexterity also facilitates food preparation. Cant and Te-

merin (1984: p. 330) noted that “many [primate food] items include edible and inedible (or undesirable) parts . . . there may be soil adhering to the bases of grass stems, tough husks on fruit, large seeds or dense hairs on caterpillars.” Digital dexterity “endows [the] consumer with the capacity to extract the portions it wishes to eat and [to] discard the rest.” Compellingly, the tactile fovea of dunlins and star-nosed moles functions similarly. It processes tactile information during probing and exploratory foraging. If digits I–III of catarrhines are homologous sensory structures, their dexterity and tactile acumen may have evolved in the context of opportunistic manual foraging.

Regrettably, the nature of our data set cannot support or refute this notion. Relevant to our study is the observation that “[*Aotus trivirgatus*] seems to have very little independent control of [its hand]. It reaches with fingertips leading, whether for branches or insects or fruit, and it is adept at catching insects with its hands.” Furthermore, “it probably has far more tactile sensitivity [than prosimians have]. A pet [*Aotus*] will feel over one’s face with its touchpads. Lemuriformes and Lorisiformes often grab and hold one with their hands, but never explore a surface with their fingertips” (Bishop, 1964: p. 213–214). This lack of interdigital dexterity coupled with a high density of digital MCs appears to represent a specialized locomotor adaptation instead of a dietary one. Evaluating suitable substrates on the basis of texture may be emphasized during nocturnal foraging. Such a possibility is consistent with the friction hypothesis (Martin, 1990) and the fact that opossums also possess MCs but seldom forage with their hands (Winkelmann, 1964). Similarly, the high density of MCs in the digits of *Hylobates lar* may be an adaptation to sensing friction during ricochet arm swinging. However, gibbons do engage in a variety of complex manipulations during feeding (Tuttle, 1972). In this regard, the relatively low MC densities in the digits of *Pongo pygmaeus* and *Theropithecus gelada*, two taxa that forage opportunistically and enjoy a high degree of interdigital dexterity, may simply reflect the relatively large surface area of their digits.

Accordingly, we cannot soundly argue to have teased apart the influences of diet, locomotion, and phylogeny in the evolution of the primate somatosensory perception. Nevertheless, the notion of tactile foveation in anthropoids is intriguing. If the concept is warranted, we suggest that the tactile fovea developed to permit greater somatic information during digital probing and exploratory foraging. In this regard, we favor the view that invasive and complex foraging selected for increased interdigital dexterity (MacNeilage, 1990).

Future insights may result from examining the primate corticospinal tract (CST) (Heffner and Masterton, 1983; Iwaniuk and Whishaw, 2000). Although CST length corresponds with forelimb dexterity in mammals, there is no relationship between CST length and a variety of behavioral traits, such as diet or arboreality (Iwaniuk et al., 1999). However, CST distribution in the neocortex may be more closely related to such adaptations (Nudo and Masterton, 1990). In the end, our analysis may be viewed as an exploratory tool for evaluating and generating hypotheses regarding the evolution of primate special senses. Such hypotheses must eventually be tested by careful direct observation in the field or laboratory.

NOTE ADDED IN PROOF

Addendum

After this article went to press we examined the digital tissue of an adult male western gorilla (*Gorilla gorilla gorilla*). The tissue was obtained from a cadaver kept in the Department of Anthropology, University of California - Santa Cruz. The diet of *G.g. gorilla* is composed of fruit, 67%; seeds, leaves, stems, pith, 17%; and animal prey (including termites, caterpillars, and insect larvae), 3% (Rowe, 1996). The density of MCs in digit I was 11.3/mm². Adding this datum to Figure 4A produces an RMA slope of 0.53 ± 0.36 ($P < 0.01$). Adding this datum to Figure 4B does not change the slope (0.26) or P-value ($P = 0.22$) of the regression of independent contrasts. The authors thank A. L. Zihlman for access to this tissue.

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LITERATURE CITED

- Barton RA, Whiten A, Byrne RW, English M. 1993. Chemical composition of baboon plant foods: implications for the interpretation of intra- and interspecific differences in diet. *Folia Primatol* 61:1–20.
- Bensaïma S. 2002. A transduction model of the Meissner corpuscle. *Math Biosci* 176:203–217.
- Biegert J. 1961. Volarhaut der Hände und Füße: Handbuck der Primatenkunde. In: Hofer H, Schultz AH, Starck D, editors. *Primatologia*, vol. 2. Basel: Karger. p 1–326.
- Bishop A. 1962. Hand control in lower primates. *Ann NY Acad Sci* 102:316–337.
- Bishop A. 1964. Use of the hand in lower primates. In: Buettner-Janusch, J, editor. *Evolutionary and genetic biology of primates*, vol. 2. New York: Academic Press. p 133–225.
- Blake DT, Byl NN, Merzenich MM. 2002. Representation of the hand in the cerebral cortex. *Behav Brain Res* 135:179–184.
- Bloch JI, Boyer DM. 2002. Grasping primate origins. *Science* 298:1606–1610.
- Bolanowski SJ, Pawson L. 2003. Organization of Meissner corpuscles in the glabrous skin of the monkey and cat. *Somatosens Mot Res* 20:223–231.
- Bolton CF, Winkelmann RK, Dyck PJ. 1966. A quantitative study of Meissner’s corpuscles in man. *Neurology* 16:1–9.
- Brady CJ. 1987. Fruit ripening. *Annu Rev Plant Physiol* 38:155–178.
- Brenowitz GL. 1980. Cutaneous mechanoreceptor distribution and its relationship to behavioral specializations in squirrels. *Brain Behav Evol* 17:432–453.
- Byrne RW, Corp N, Byrne JME. 2001. Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. *Anim Cogn* 3:347–361.
- Cant JGH, Temerin LA. 1984. A conceptual approach to foraging adaptations in primates. In: Rodman PS, Cant JGH, editors. *Adaptations for foraging in nonhuman primates: contributions to an organismal biology of prosimians, monkeys, and apes*. New York: Columbia University Press. p. 304–342.
- Cartmill M. 1974. Rethinking primate origins. *Science* 184:436–443.
- Cartmill M. 1979. The volar skin of Primates: its frictional characteristics and their functional significance. *Am J Phys Anthropol* 50:497–510.

- Cartmill M. 1992. New views on primate origins. *Evol Anthropol* 1:105–111.
- Caruso G, Nolano M, Lullo F, Crisci C, Nilsson J, Massini R. 1994. Median nerve sensory responses evoked by tactile stimulation of the finger proximal and distal phalanx in normal subjects. *Muscle Nerve* 17:269–275.
- Castano P, Ventura RG, Maddaloni M. 1985. Notes on morpho-functional differences between the Meissner's corpuscles of man and the green monkey (*Cercopithecus aethiops* L.). *Folia Morphol* 33:294–298.
- Castano P, Ventura RG, Pizzini G, Marcucci A, Morini M. 1991. Unmyelinated nerve fibers associated with Meissner's corpuscle in the green monkey (*Cercopithecus aethiops* L.). *Funct Dev Morphol* 1:51–54.
- Castano P, Rumio C, Morini M, Miani A Jr, Castano SM. 1995. Three-dimensional reconstruction of the Meissner's corpuscle of man after silver impregnation and immunofluorescence with PGP 9.5 antibodies using confocal scanning laser microscopy. *J Anat* 186:261–270.
- Castelló ME, Aguilera PA, Trujillo-Cenóz O, Caputi AA. 2000. Electoreception in *Gymnotus carapo*: pre-receptor processing and the distribution of electoreceptor types. *J Exp Biol* 203:3279–3287.
- Catania KC, Kaas JH. 1997. Somatosensory fovea in the star-nosed mole: behavioral use of the star in relation to innervation patterns and cortical representation. *J Comp Neurol* 387:215–233.
- Catania KC. 1999. A nose that looks like a hand and acts like an eye: the unusual mechanosensory system of the star-nosed mole. *J Comp Physiol A* 185:367–372.
- Catania KC, Remple FE. 2004. Tactile foveation in the star-nosed mole. *Brain Behav Evol* 63:1–12.
- Cauna N. 1954. Nature and function of the papillary ridges of the digital skin. *Anat Rec* 119:449–468.
- Cauna N. 1956. Nerve supply and nerve endings in Meissner's corpuscles. *Am J Anat* 99:315–350.
- Cauna N. 1964. The effects of aging on the receptor organs of the human dermis. In: Montagna W, editor. *Advances in the biology of skin*, vol. 6, aging. Oxford: Pergamon Press. p 63–96.
- Coleman GT, Bahramali H, Zhang HQ, Rowe MJ. 2001. Characterization of tactile afferent fibers in the hand of the marmoset monkey. *J Neurophysiol* 85:1793–1804.
- Corp N, Byrne RW. 2002a. The ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of *Saba florida*. *Behaviour* 139:147–168.
- Corp N, Byrne RW. 2002b. Leaf processing by wild chimpanzees: physically defended leaves reveal complex manual skills. *Ethology* 108:673–696.
- Costello MB, Fragaszy DM. 1988. Prehension in *Cebus* and *Saimiri*: I, grip type and hand preference. *Am J Primatol* 15:235–245.
- Dillon YK, Haynes J, Henneberg MJ. 2001. The relationship of the number of Meissner's corpuscles to dermatoglyphic characters and finger size. *J Anat* 199:577–584.
- Dominy NJ. 2004. Fruits, fingers, and fermentation: the sensory cues available to foraging primates. *Integr Comp Biol* 44:29–37.
- Dunbar RIM. 1977. Feeding ecology of gelada baboons. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes*. New York: Academic Press. p 251–273.
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am Nat* 125:1–15.
- Gaeth AP, Short RV, Renfree MB. 1999. The developing renal, reproductive, and respiratory systems of the African elephant suggest an aquatic ancestry. *Proc Natl Acad Sci USA* 96:5555–5558.
- Galdikas BMF. 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *Int J Primatol* 9:1–35.
- Garber PA, Reh JA. 1999. The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *Am J Phys Anthropol* 110:325–339.
- Grand TI. 1984. Motion economy within the canopy: four strategies for mobility. In: Rodman PS, Cant JGH, editors. *Adaptations for foraging in nonhuman primates: contributions to an organismal biology of prosimians, monkeys, and apes*. New York: Columbia University Press. p 54–72.
- Grzycki S. 1970. Variability and differences in the structure of digital tactile corpuscles of *Cercopithecus aethiops*. *Z Mikrosk Anat Forsch* 82:29–41.
- Güçlü B, Bolanowski SJ, Pawson L. 2003. End-to-end linkage (EEL) clustering algorithm: a study on the distribution of Meissner corpuscles in the skin. *J Comput Neurosci* 15:19–28.
- Guinard D, Usson Y, Guillermet C, Saxod R. 2000. PS-100 and NF 70-200 double immunolabeling for human digital skin Meissner corpuscle 3D imaging. *J Histochem Cytochem* 48:295–302.
- Halata Z. 1975. The mechanoreceptors of the mammalian skin: ultrastructure and morphological classification. *Adv Anat Embryol Cell Biol* 50:5–75.
- Hamrick MW. 1998. Functional and adaptive significance of primate pads and claws: evidence from New World anthropoids. *Am J Phys Anthropol* 106:113–127.
- Hamrick MW. 2001. Morphological diversity in digital skin microstructure of didelphid marsupials. *J Anat* 198:683–688.
- Heffner RS, Masterton RB. 1983. The role of the corticospinal tract in the evolution of human digital dexterity. *Brain Behav Evol* 23:165–183.
- Iwaniuk AN, Nelson JE, Ivanko TL, Pellis SM, Whishaw IQ. 1998. Reaching, grasping and manipulation of food objects by two tree kangaroo species, *Dendrolagus lumholtzi* and *Dendrolagus matschiei*. *Aust J Zool* 46:235–248.
- Iwaniuk AN, Pellis SM, Whishaw IQ. 1999. Is digital dexterity really related to corticospinal projections? a re-analysis of the Heffner and Masterton data set using modern comparative statistics. *Behav Brain Res* 101:173–187.
- Iwaniuk AN, Whishaw IQ. 2000. On the origin of skilled forelimb movements. *Trends Neurosci* 23:372–376.
- Johansson RS. 1978. Tactile sensibility in the human hand: receptive field characteristics of mechanoreceptivity units in the glabrous skin area. *J Physiol* 281:101–123.
- Johansson RS, Vallbo AB. 1979. Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptor units in glabrous skin. *J Physiol* 286:283–300.
- Jolly CI. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5:5–26.
- Kaas JH. 1993. The functional organization of somatosensory cortex in primates. *Ann Anat* 175:509–518.
- Kirk EC, Cartmill M, Kay RF, Lemelin P. 2003. Comment on “grasping primate origins.” *Science* 300:741B.
- LaBarbera M. 1989. Analyzing body size as a factor in ecology and evolution. *Annu Rev Ecol Syst* 20:97–117.
- Lemelin P, Grafton BW. 1998. Grasping performance in *Saguinus midas* and the evolution of hand prehensibility in primates. In: Strasser E, Fleagle JF, Rosenberger A, McHenry H, editors. *Primate locomotion: recent advances*. New York: Plenum Press. p 131–144.
- Lemelin P. 1999. Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *J Zool* 247:165–175.
- Lemelin P. 2000. Micro-anatomy of the volar skin and interordinal relationships of primates. *J Hum Evol* 38:257–267.
- Lindburg DG. 1977. Feeding behavior and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik Forest in North India. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London: Academic. p 223–249.
- Lindblom U. 1965. Properties of touch receptors in distal glabrous skin of the monkey. *J Neurophysiol* 28:966–985.
- MacNeilage PF. 1990. Grasping in modern primates: the evolutionary context. In: Goodale MA, editor. *Vision and action: the control of grasping*. Norwood: Ablex. p 1–13.
- Martin G, Rojas LM, Ramirez Y, McNeil R. 2004. The eyes of oilbirds (*Steatornis caripensis*): pushing at the limits of sensitivity. *Naturwissenschaften* 91:26–29.
- Martin RD. 1990. *Primate origins and evolution: a phylogenetic reconstruction*. Princeton: Princeton University Press.
- Meisami E. 1989. A proposed relationship between increases in the number of olfactory receptor neurons, convergence ratio and sensitivity in the developing rat. *Brain Res Dev Brain Res* 46:9–19.

- Munger BL, Ide C. 1988. The structure and function of cutaneous sensory receptors. *Arch Histol Cytol* 51:1–34.
- Munger BL, Pubols LM. 1972. The sensorineural organization of the digital skin of the raccoon. *Brain Behav Evol* 5:367–393.
- Napier JR. 1960. Studies of the hands of living primates. *Proc Zool Soc Lond* 134:647–657.
- Napier JR. 1962. The evolution of the hand. *Sci Am* 207:56–62.
- Neuweiler G. 2003. Evolutionary aspects of bat echolocation. *J Comp Physiol A* 189:245–256.
- Nolano M, Provitera V, Crisci C, Stancanelli A, Wendelschafer-Crabb G, Kennedy WR, Santoro L. 2003. Quantification of myelinated endings and mechanoreceptors in human digital skin. *Ann Neurol* 54:197–205.
- Nudo RJ, Masterton RB. 1990. Descending pathways to the spinal cord: IV, some factors related to the amount of cortex devoted to the corticospinal tract. *J Comp Neurol* 296:584–597.
- Paré M, Elde R, Mazurkiewicz JE, Smith AM, Rice FL. 2001. The Meissner corpuscle revisited: a multiafferented mechanoreceptor with nociceptor immunochemical properties. *J Neurosci* 21:7236–7246.
- Peleg M. 1980. A note on the sensitivity of fingers, tongue and jaws as mechanical testing instruments. *J Text Studies* 10:245–251.
- Pettigrew JD, Frost BJ. 1985. A tactile fovea in the Scolopacidae? *Brain Behav Evol* 26:185–195.
- Pettigrew JD, Manger PR, Fine SLB. 1998. The sensory world of the platypus. *Phil Trans R Soc Lond B* 353:1199–1210.
- Polyak SL. 1957. The vertebrate visual system. Chicago: University of Chicago Press.
- Previc FH. 1990. Functional specialization in the lower and upper visual fields in humans: its ecological origins and neurophysiological implications. *Behav Brain Sci* 13:519–575.
- Purvis A. 1995. A composite estimate of primate phylogeny. *Philos Trans R Soc Lond B* 348:405–421.
- Purvis A, Rambaut A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput Appl Biosci* 11:247–251.
- Rasmussen LEL, Munger BL. 1996. The sensorineural specializations of the trunk tip (finger) of the Asian elephant, *Elephas maximus*. *Anat Rec* 246:127–134.
- Rasmussen DT. 2002. The origin of primates. In: Hartwig WC, editor. *The primate fossil record*. Cambridge: Cambridge University Press. p 5–9.
- Ravosa MJ, Savakova DG. 2004. Euprimate origins: the eyes have it. *J Hum Evol* 46:355–362.
- Renehan WE, Munger BL. 1990. The development of Meissner corpuscles in primate digital skin. *Brain Res Dev Brain Res* 51:35–44.
- Rizzolatti G, Luppino G. 2001. The cortical motor system. *Neuron* 31:889–901.
- Rowe N. 1996. *The pictorial guide to living primates*. East Hampton: Pagonias.
- Ruth P, Schmidtberg H, Westermann B, Schipp R. 2002. The sensory epithelium of the tentacles and the rhinophore of *Nautilus pompilius* L. (Cephalopoda, Nautiloidea). *J Morphol* 251:239–255.
- Sargis EJ. 2001. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). *J Zool* 253:485–490.
- Sheehan DC, Hrapchak BB. 1982. *Theory and practice of histotechnology*, 2nd ed. Columbus, OH: Battelle.
- Shoshani J. 1997. What can make a four-ton mammal a most sensitive beast? it's a nose! it's a hand! it's an elephant's trunk! *Nat Hist* 106:36–44.
- Srinivasan MA, LaMotte RH. 1987. Tactile discrimination of shape: responses of slowly and rapidly adapting mechanoreceptive afferents to a step indented into the monkey fingerpad. *J Neurosci* 7:1682–1697.
- Stone J, Halasz P. 1989. Topography of the retina in the elephant *Loxodonta africana*. *Brain Behav Evol* 34:84–95.
- Straus WL Jr. 1942. Rudimentary digits in primates. *Quart Rev Biol* 17:228–243.
- Struhsaker TT. 1975. *The red colobus monkey*. Chicago: University of Chicago Press.
- Sur M, Merzenich MM, Kaas JH. 1980. Magnification, receptive-field area, and “hypercolumn” size in areas 3b and 1 of somatosensory cortex in owl monkeys. *J Neurophysiol* 44:295–311.
- Szczesniak AS, Bourne MC. 1969. Sensory evaluation of firmness. *J Text Studies* 1:52–64.
- Takahashi-Iwanaga H, Shimoda H. 2003. The three-dimensional microanatomy of Meissner corpuscles in monkey palmar skin. *J Neurocytol* 32:363–371.
- Terborgh J. 1983. *Five New World primates: a study in comparative ecology*. Princeton: Princeton University Press.
- Tuttle RH. 1972. Functional and evolutionary biology of hylobatid hands and feet. In: Rumbaugh D, editor. *Gibbon and Siamang*, vol. 1. Basel: Karger. p 136–206.
- Verdan C. 1979. La trompe, main de l'éléphant: étude de ses terminaisons préhensives et tactiles. *Ann Chir Plast* 24:392–396.
- van Roosmalen MGM. 1985. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazonica* 15 (suppl. 3/4):1–238.
- Vij S, Kanagasuntheram R, Krishnamurti A. 1973. Sensory nerve terminations in the oral tissues of some pongidae. *Folia Primatol* 20:312–320.
- Welles JF. 1976. A comparative study of manual prehension in anthropoids. *Saugetierkundl Mitt* 24:26–38.
- West JB. 2001. Snorkel breathing in the elephant explains the unique anatomy of its pleura. *Respir Physiol* 126:1–8.
- Winkelmann RK. 1962. Cutaneous sensory end organs of some anthropoid apes. *Science* 136:384–386.
- Winkelmann RK. 1963. Nerve endings in the skin of primates. In: Buettner-Janusch J, editor. *Evolutionary and genetic biology of primates*, vol. 1. New York: Academic Press. p 229–259.
- Winkelmann RK. 1964. Nerve endings of the North American opossum (*Didelphis virginiana*): a comparison with nerve endings of primates. *Am J Phys Anthropol* 22:253–258.
- Winckler G. 1973. Particularités de la structure de la trompe de l'éléphant récepteurs capsules et anastomoses arterio-veineuses. *Bull Ass Anat* 57:955–962.
- Woolsey CN, Marshall WH, Bard P. 1942. Representation of cutaneous tactile sensibility in the cerebral cortex of the monkey as indicated by evoked potentials. *Bull Johns Hopkins Hosp* 70:399–441.
- Wright PC. 1989. The nocturnal niche in the New World. *J Hum Evol* 18:635–658.
- Wrangham RW. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London: Academic. p 503–538.
- Wu JY. 1988. An observation on the dermatoglyph and dental pattern of tree shrew (*Tupaia belangeri chinensis*). *Chinese J Zool* 23:29–32.