

Chapter 12

Functions of the Hand in Primates

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1 Introduction

Nearly 100 years ago, Wood Jones (1920) characterized the hand as a specialized sensory organ and the use of the hands in exploration as a defining characteristic of primates. Thus, from the beginning, researchers have investigated how primates use their hands to touch and handle objects, as well as during locomotion. Understanding how primates use their hands is fundamental to reconstructing and interpreting the evolution of the order to which humans belong to (Napier 1960, 1961, 1980). Primates were present in the Eocene, feeding and moving predominantly on thin and flexible terminal branches (Cartmill 1974; Sussman 1991; Sussman et al. 2013; see Chap. 14). They used both hands and feet to locomote in this environment and the hands to feed. Prehension of small objects (such as insects or fruits) by one hand is considered a primitive characteristic of primates (Washburn 1951; Napier 1961, 1980) and is integral to feeding in all living primates. However, this characteristic is shared with other orders as primates are not alone in using one appendage in prehension. Indeed, Iwaniuk and Whishaw (2000) reported that, of 29 tetrapod orders for which the presence or absence of “skilled forelimb movements” (which includes reaching, grasping, and manipulation with one forelimb) was examined, 13 orders were characterized by such movements. Iwaniuk and Whishaw (2000) showed that skilled movements of the forelimbs in mammals probably share a common origin in early tetrapods, appearing after the divergence of therian mammals (marsupials and placentals) from the monotremes. The prehensile actions of primates must therefore be considered against this ancient backdrop.

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2 Prehension in Primates Compared to Other Therian Mammals

We start this chapter by discussing the primitive physical features of primate hands, described by Wood Jones (1920) nearly 100 years ago. All primates have pentadactyl hands with relatively long and unwebbed digits, a morphology that enables flexion, extension, and rotation of the digits relative to one another and enables the digits of one hand to close around a small object to press it against the palm. All primates have tactile pads on the palmar surface of the terminal phalanges that are richly innervated with sensory receptors, enabling the hand to serve exploratory as well as postural functions. Animals in other orders also possess unwebbed digits, long digits, or a rich supply of sensory receptors on the terminal phalanges (Lemelin and Grafton 1998), but the uniform presence across the order of all three features is characteristic only of primates.

Species lacking some of these characteristics can still use the forelimbs in surprisingly skilled ways. Rodents, for example, with nearly 2000 species inhabiting a vast range of habitats, display skilled movements with the forelimbs (Whishaw et al. 1998). Common skilled forelimb movements in rodents include grasping food using an elbow-in movement and manipulating food with the digits (Whishaw et al. 1998). Beyond these shared features, rodents present a wide variety of specialized skilled forelimb movements across species, in keeping with their ecological diversity, such as unilateral and bilateral grasping (i.e., holding two objects simultaneously). Whishaw (2005) provided an illuminating review of the range of skilled forelimb movements in the common rat (*Rattus norvegicus*). The rat's first digit can move medially toward the palm, so that it can hold an object between the terminal pad of the pollex and the terminal pads of other digits. The fifth digit moves independently, turning medially during grasping, in a thumb-like manner. The two paws can move in parallel and in complementary ways to hold or move an object. Rats make visually guided limb movements, rotate the forearm to aim, and pronate and supinate the limb during reaching. After the digits contact an object, they converge to the palmar pads to hold objects in various orientations. The rich repertoire of skilled forelimb movements in rats reminds us that prehensile skills shared by primates are also found in some members of other orders (see also Ivanco et al. 1996). However, rats, like other rodents, preferentially use olfaction to locate food and pick up food with the mouth when possible, rather than lifting it to the mouth with their paws. Primates, on the other hand, preferentially grasp food with their hands.

Research related to unraveling the evolution of morphology and prehensile skills in primates has looked to procyonid carnivores (such as raccoons and kinkajous) and didelphid marsupials as useful comparative models (Rasmussen 1990; McClearn 1992; Iwaniuk and Whishaw 1999; Lemelin 1999; Lemelin and Schmitt 2007). Kinkajous, for example, grasp objects unimanually while feeding from terminal branches (McClearn 1992). Raccoons grasp objects between

the digits, between the apical and distal palmar pads, or between two paws, rather than in a grasp for which several digits in one hand converge. Raccoons manipulate objects by rolling them between the palms of both paws, with little or no digit movement. Thus, although raccoons use visually guided reaching like primates, they are more similar to other carnivores in how they use their forelimbs (bimanually and without convergent digits during grasping; Iwaniuk and Whishaw 1999).

Didelphid marsupial species exhibit a body mass range that overlaps with cheirogaleid primates (i.e., dwarf and mouse lemurs). Some are primarily terrestrial and others are primarily arboreal (reviewed in Lemelin 1999). The neotropical woolly opossum, *Caluromys*, for example, is almost exclusively arboreal (Charles-Dominique et al. 1981; Rasmussen 1990). Woolly opossums use vision more than other opossums to locate and capture mobile insect prey, collect fruits from terminal branches with their forelimbs, and frequently adopt suspensory postures using the hind limbs, as do cheirogaleid primates (Rasmussen 1990; Lemelin 1999). This is assumed to be the primitive locomotor pattern and feeding niche of early primates (Cartmill 1974; Sussman 1991; Sussman et al. 2013). We know little about skilled prehensive movements during prey capture in these animals, but on ecological grounds one could predict a primate-like pattern of actions, with both forelimbs participating in grabbing flying prey and the palm contacting the prey item first. For example, lorisooids studied by Charles-Dominique (1977) sometimes captured slow-moving invertebrate prey (caterpillars, beetles, ants, etc.) by pressing them against a branch. Ivanco et al. (1996) described prey capture movements in the gray short-tailed opossum (*Monodelphis domestica*), a more terrestrial species than *Caluromys*. The gray short-tailed opossum can capture prey on a solid substrate with one forelimb, although they exhibit less variable and simpler movements compared to rats (*Rattus norvegicus*) in the same situations (Ivanco et al. 1996). Similarly, the pygmy tree shrew (*Tupaia minor*) grasps food items in one hand and moves nimbly on small-diameter supports, whereas the more terrestrial large tree shrew (*Tupaia tana*) does not, suggesting that the former could also be a useful model of prehensive uses of the forelimb in early primates (Sargis 2001).

Additional comparative work on prehensile behavior and the neuromotor system (particularly the corticospinal tracts and their terminations) supporting these movements in rodents, tree shrews, and opossums would be useful for understanding the functional significance of variations in this system across mammals and their relation to inhabiting a small branch environment and their feeding niche. The small branch environment in which early primates lived together with feeding on mobile insect prey probably contributed in a synergistic way to the development of primate-typical use of the hands toprehend food items. Indeed, Toussaint et al. (2013) found that gray mouse lemurs (*Microcebus murinus*) used their hands (rather than the mouth) to grasp food more often while clinging to narrow substrates and used the hands to grasp moving prey regardless of the substrate to which they were clinging.

3 Manual Function in Prosimians as a Window onto Primitive Features of the Primate Hand

Some prosimians, particularly small-bodied cheirogaleids and galagids, are generally thought to be more representative of early primates than the anthropoids and, therefore, are of strong interest for the identification of primitive characters in primates (Charles-Dominique 1972; Martin 1972a). However, one must keep in mind that the extant species of prosimians (i.e., strepsirrhines and tarsiers) reflect their own long evolutionary history and the lemurs in particular have undergone remarkable radiation (Martin 1972b, 1990) and diversification of hand morphology and use (Lemelin and Jungers 2007). The case of the aye-aye (*Daubentonia madagascariensis*) comes to mind and will be discussed further in this chapter.

Bishop (1962, 1964; Jolly 1964; as a point of clarification, Alison Bishop and Alison Jolly are the same person) perceptively described manual function in several species of prosimians with an eye to understanding primitive features that presaged and supported the later elaborations of manual function in anthropoids. Bishop combined experimental studies of orientation of the hand during locomotion with observational studies of spontaneous use of the hands in daily life in unconstrained captive individuals. Thus, she was able to consider manual function in relation to exploration, play, self-care, and social behavior, as well as locomotion and feeding. Despite the variations across lemurs and lorises in hand postures during prehension of substrates during locomotion and while grasping food items, all species studied by Bishop (1964) used the hands in some way during social grooming, to explore novel objects and surfaces, in self-care, and in play. Even lemurs, which often pick up small objects from a surface using the mouth rather than the hands (Bishop 1964; Torigoe 1985), explored novel surfaces with their hands. Schöneich (1993) observed *Lemur catta* using their hands to lift, push, and slide fasteners (chains, pins, hooks, sliding panels) to open a box containing food, replicating Bishop's (1964; Jolly 1964) observations. Ring-tailed lemurs used both left and right hands singly and together and adjusted their hands quickly when the fasteners were presented in novel positions. We can surmise that using the hand for multiple purposes (in social behavior, self-care, play, and exploration, as well as in feeding and locomotion) is a primitive characteristic of primates and that the hands moved and gripped objects and touched surfaces in varied ways in these different situations. In other words, the hands enabled a primate-typical way of life.

4 Functions of the Hand

With the broad functional importance of the hands to primates in mind, we adopt a conceptual framework following Jones and Lederman (2006) that is novel in comparative treatments of manual function. Jones and Lederman (2006) cast hand function into four categories falling along a continuum from sensory functions to

skilled movements that do not involve prehension. These are (a) tactile sensing, (b) active haptic sensing, (c) prehension, and (d) nonprehensile skilled movements. Definitions and examples of common human actions in each category are given in Table 12.1. **Tactile sensing** serves to effect contact between the stationary hand and a surface or an object (which may be moving). This category is likely most employed in nonhuman primates in postural and locomotor activities (e.g., maintaining a secure grip), rather than in prehension of portable objects. The ubiquitous presence of dense sensory receptors in the glabrous skin of the feet as well as the hand (Talbot et al. 1968; Hoffman et al. 2004; see Chaps. 6 and 8) supports this proposal. **Active haptic sensing** serves to effect contact between the hand and a surface as the hand moves voluntarily over a surface or object. It has an exploratory character. This is the usual and preferred activity for identifying objects and extracting information about them. **Prehension** includes reaching to grasp an object and holding it. In humans, the configuration of the hand during prehension is determined by the objective of the task and the properties of the object(s) to be held and so changes dynamically as the task progresses. Most of our treatment in this chapter concerns this category—it is by far the most studied category of manual function in primates. **Nonprehensile skilled movements**

Table 12.1 Explanation of categories of manual functions (following Jones and Lederman 2006)

Category	Function	Characteristic manual action	Common situation in humans
Tactile sensing	Effect contact between the stationary hand and a surface or an object. Affords information about certain properties (e.g., surface texture), especially if the object or surface moves across the skin	The hand is passive. Affords information about certain properties (e.g., surface texture), especially if the object or surface moves across the skin	Climbing a rocky surface using the hands, bracing a hand against a wall, touching a hand lightly on a railing while descending a staircase
Active haptic sensing	Effect contact between the hand and a surface as the hand moves voluntarily over a surface or object	The hand is active	Feeling the texture of a fabric, squeezing an object to evaluate firmness, running fingers around an outer contour to evaluate shape and size of an object
Prehension	Reaching to grasp an object and holding it	The hand is active	Picking up a cup, buttoning a shirt, using a knife and fork, washing dishes
Nonprehensile skilled movements	Pointing and aiming movements, gestures, and actions with instrumental outcomes apparent in humans	The hand is active	Gestures during speech or other symbolic activities (e.g., dancing, conducting music), pressing keys on a keyboard, using a touchscreen, flipping a light switch

include pointing and aiming movements, gestures, and actions with instrumental outcomes. This category is highly apparent in humans. Although most nonhuman primates do not gesture, they still perform a variety of nonprehensile skilled movements as we shall see.

Jones and Lederman (2006) developed this framework to organize a vast literature about normal manual function in healthy humans arising from the disciplines of anatomy, neurophysiology, cognitive science, experimental psychology, developmental psychology and gerontology, kinesiology, hand surgery and rehabilitation medicine, haptic software and robotics, and human factors. We find it useful for our comparative purpose when considering the range of manual function in the primate order, which presents diversity in this domain as in others. This framework has the advantage of treating actions without an anthropomorphic focus; it does not privilege actions particularly valued in humans. It also has the advantage of linking manual function with the sensory systems of the skin, muscles, tendons, and joints. In our treatment of the variations across primate taxa in the given categories of manual function, we consider if the evidence allows us to assign “primitive” and “derived” status to aspects of function. Our assignments in these cases are speculative; we hope that this exercise will prompt others to provide more complete analyses to flesh out these ideas.

4.1 Tactile Sensing

All primates examined to date have rich sensory mechanoreceptors (Meissner corpuscles) in the glabrous skin of the hands and feet (Hoffman et al. 2004; see Chap. 6). These receptors are particularly densely packed beneath epidermal ridges (Martin 1990) and are sensitive to friction (see Chap. 8). Thus, primates are equipped to detect the stability of their grip on the weight-supporting substrate through passive tactile means. Some marsupials have similar receptors, but most other mammal species apparently do not (Winkelmann 1964). These features of tactile sensing shared with marsupials could be linked to movement in an arboreal environment. We are not aware of derived variations among primates in this category of manual function.

4.2 Active Haptic Sensing

In contrast to tactile sensing, in which the hand is passive, active haptic sensing (using the hands to locate, identify, and explore surfaces and objects) is unlikely to be related to locomotor requirements. Exploration is a fundamental aspect of behavior in mobile vertebrates. However, most vertebrates use olfaction, vision, and audition to explore rather than contact with forelimb appendages. Exploring with the hands is a primitive behavior in primates, but derived compared to other mammals in its variety and frequency. Glickman and Sroges (1966), in a classic study comparing

exploratory behavior toward novel objects in zoo animals representing several vertebrate orders, commented that carnivores and primates exhibited more frequent investigatory behavior than rodents or a group of “primitive” mammals. Primates were the only order in which grasping, visual inspection, and manipulation were common. These behaviors are associated with processing and bringing food to the mouth in primates, whereas carnivores mainly use the forelimb when subduing and eating prey (batting, steadying; see also Power 2000 for review of the scanty, more recent literature on this topic concerning animals other than primates). For example, Whishaw (2005) does not describe manual actions that fit investigatory behavior as occurring in rats, although sniffing, rearing, and locomotor exploration are typical of rats (see also Berlyne 1966). In contrast, Bishop (1964) describes lemurs as moving their fingers over the edges of a cut plastic plate, feeling this novel object in an exploratory way, and lemurs, lorises, and galagos as playing with objects. Thus, although mammals from other orders investigate objects using their forelimbs to some extent, primates do so routinely. Within primates, the consensus view is that those species with omnivorous tendencies and that obtain foods via extractive methods (e.g., tearing or pulling items out of the wood or the soil, sifting through leaf debris, and breaking open husked fruits) have the most diverse repertoires of investigatory behaviors (Glickman and Sroges 1966; Parker and Gibson 1977; Torigoe 1985; Fragaszy and Adams-Curtis 1991; Westergaard 1992).

Aye-ayes (*Daubentonia madagascariensis*) present the most specialized actions in primates used for active haptic perception. Their specializations are in accord with the notion that extractive foraging promotes active haptic sensing. Aye-ayes possess an elongated third digit, which they tap extremely rapidly against woody substrates (called tap scanning) while searching for wood-boring larvae (Erickson 1994; Fig. 12.1). Tap scanning produces both active haptic and auditory information about the density of the material, which can then be used to guide and direct aye-ayes’ gnawing and probing with the elongated third digit (Erickson 1991; Erickson et al. 1998). Younger animals tap objects they encounter apparently for general exploratory purposes (Soligo 2005).

Other movements of the aye-aye’s third digit are also specialized. When probing into cavities in search of food, the third digit moves independently from the other digits (Fig. 12.1). Uniquely among primates, the third digit can be moved laterally to enter acute, obtuse, and even right-angled extensions of tunnels because of the ball-and-socket metacarpophalangeal (McP) joint of this digit (Milliken et al. 1991). The terminal phalanx can be hyperextended as much as 30° to allow the finger to follow a tunnel and to move over an encountered object, so that when flexed, the elongated claw on the terminal phalanx acts as a hook to capture what it encounters (Milliken et al. 1991). The fourth digit may also be used for probing, but not tapping, and does not have the special ball-and-socket joint at the MCP joint nor the enhanced flexibility in the terminal phalanx that the third digit possesses (Milliken et al. 1991).

Other primates use a different set of movements for active haptic perception. In humans, species-typical exploratory actions with the hands have been characterized by Lederman and Klatzky (1987, 1990). Exploratory actions include, for



Fig. 12.1 A sequence of images of an aye-aye (*Daubentonia madagascariensis*) retrieving a grub from a hole in a tree trunk. The third digit is inserted (a, b) and then retracted (c), bringing the grub to the mouth (d). Numbers on the lower left refer to frame number (from 30 fps video). Images courtesy of Pierre Lemelin

example, rubbing to detect texture, probing to detect hardness, and contour following to detect shape. Actions of this kind are so commonplace in other species of primates that we are simply likely to overlook them. Researchers have looked for exploratory actions most systematically in tufted capuchin monkeys (*Sapajus apella*, formerly *Cebus apella*¹), which have a reputation for varied and persistent manipulation of objects (reviewed in Fragaszy et al. 2004). For example, Lacreuse and Fragaszy (1997) observed humans and tufted capuchin monkeys reaching through an aperture in an opaque panel to find sunflower seeds deposited on the surface of irregularly shaped clay objects. Monkeys displayed the same classes of exploratory behavior as of humans (probe, pinch, enclosure, contour following, and lateral movement), although humans explored the objects more exhaustively, while monkeys explored them one region at a time. While foraging, capuchin monkeys probe inside holes and crevices, using their whole hands to feel for prey. They use a wide array of digital postures and movements, including movements of the index finger to scrape, pull, and tear (Figs. 12.2 and 12.3). Wild bearded capuchin monkeys (*Sapajus libidinosus*) knock nuts into pits on anvil surfaces as a means of detecting when they are in a stable position prior to cracking

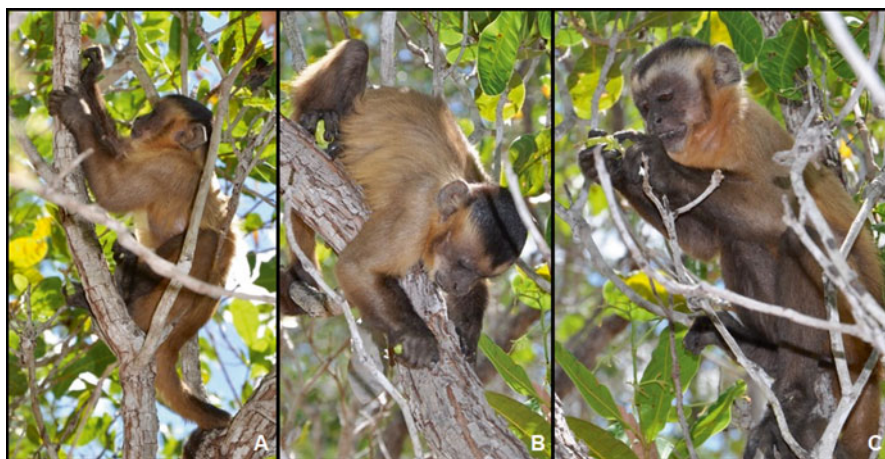


Fig. 12.2 A wild bearded capuchin monkey (*Sapajus libidinosus*) illustrating several grips and independent use of the index finger in a sequence of photos taken while the monkey opened an immature cashew nut pod. (a) The monkey rubs the pod against the rough tree bark with its right hand. The thumb is parallel to the other digits, a common power grip in platyrrhine monkeys. (b) The monkey rubs the same pod in a different direction. The thumb is now at right angles to the other digits. This position of the thumb is not achieved by other platyrrhines as far as is now known. (c) The monkey inserts the index finger of the left hand into the breached pod of the immature nut to extract the kernel. The right hand holds the pod. The thumb on the right hand presses the nut toward the palm and the other digits. This is a second common form of a power grip in platyrrhine monkeys. Photos courtesy of Marino Junior Fonseca de Oliveira

¹See Lynch Alfaro et al. (2012) for reclassification of the robust (tufted) species of the genus *Cebus*, including *apella* and *libidinosus*, into the genus *Sapajus*.

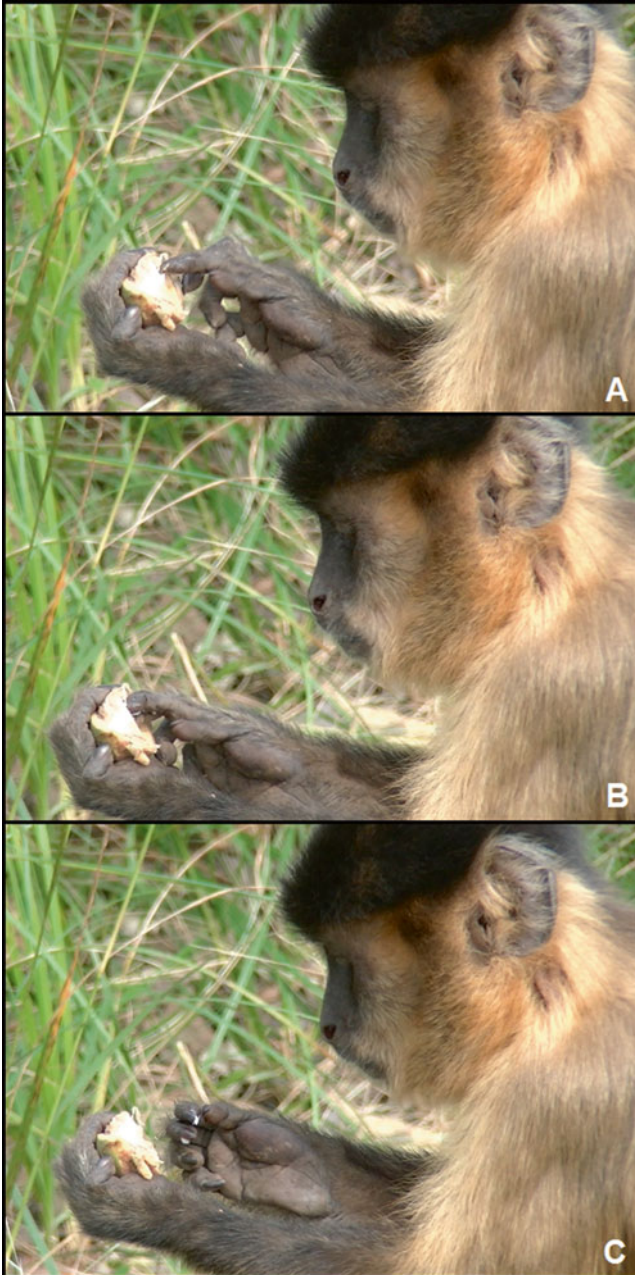


Fig. 12.3 A wild bearded capuchin monkey (*Sapajus libidinosus*) illustrating coordinated bimanual action and the use of the fingers to probe and scrape at a tucum nut that she has cracked open. (a) Scraping with an extended index finger. (b) The terminal phalanx of the index finger is flexed while scraping. (c) Pieces of the nut kernel are held beneath the index and middle fingers. Photos courtesy of Valentina Truppa

them with a stone (Fragaszy et al. 2013). They tap and lift stones in the process of determining which of the two stones is heavier (Visalberghi et al. 2009; Fragaszy et al. 2010). Wild tufted capuchins tap branches with their fingertips or fingernails while searching for invertebrate prey (Gunst et al. 2010). Captive tufted capuchins (*Sapajus* spp.) tap nuts with their fingertips in the course of choosing which ones to open, avoiding empty ones (Visalberghi and Neel 2003; Phillips et al. 2004), and use the index finger to find food in tubes (Spinozzi et al. 2007). Thus, capuchins use their hands to explore their environment in many different ways.

Torigoe's (1985) study remains the most comprehensive direct comparison of exploratory manual activity in many species of nonhuman primates. He presented a length of rope and a wood cube to members of 74 species of primates. These relatively uninteresting, inedible objects elicited exploratory behavior from all the groups he observed. In particular, guenons, mangabeys, and baboons (*Cercopithecus*, *Cercocebus*, and *Papio*, respectively), together with capuchins (*Cebus* and *Sapajus*), and lesser and greater apes (Hylobatidae and Pongidae) exhibited a wide range of exploratory actions.

Some aspects of active haptic perception have been studied in nonhuman primates using psychophysical and physiological methods (e.g., to characterize the function of the various receptors in the skin of the fingers and palm; Talbot et al. 1968). The increased density of Meissner corpuscles (mentioned earlier in relation to passive tactile sensing of friction) in the fingertips suggests that humans and other primates may have "tactile fovea" (regions of enhanced tactile sensitivity that would support active haptic sensing) at the ends of the digits (Hoffman et al. 2004). Hoffman et al. (2004) showed that of nine representative species of nonhuman primates, the more frugivorous species possessed a higher density of Meissner corpuscles in the fingertips, in accord with the hypothesis that these receptors afford perception of elastic texture of fruit (in addition to friction, as noted above), although other plausible relationships could not be disambiguated because of the small data set. However, sensitivity of the hands is largely unstudied in naturalistic tasks. It is plausible, but not confirmed, that anthropoid primates have more sensitive fingertips and engage in more active haptic perception using their fingertips than strepsirrhine primates and nonprimates. The value of active haptic sensing via the fingertips in foraging (e.g., to detect ripeness of fruit via palpation, banging, or tapping) is recognized (e.g., Dominy et al. 2004), but little studied. We lack comparative data on sensitivity to temperature, hardness, and other physical properties. Psychophysical studies of captive individuals could be extremely informative in this area.

4.3 Prehension

Prehension refers to grasping and holding an object in the hand (Napier 1956). Below we describe four types of prehension in nonhuman primates, each differentiated by hand posture and contact points when grasping an object: power grips,

precision grips, in-hand movements, and compound grips. First, however, we describe variation in thumb opposition in primates, as this is the foundation of many forms of prehension.

4.3.1 Thumb Opposition

Napier recognized the importance of thumb opposition in prehension and defined “true” thumb opposition, in which the thumb rotates so that the distal pad is directly opposed to, and/or makes contact with, the distal pads of one or more of the remaining digits (Napier 1961; Napier and Napier 1967; Fig. 12.4). The ability to oppose the thumb to other digits enables a secure purchase on an object, although it is not required to hold an object, as we describe below. Primate taxa vary in the degree of thumb opposition they are able to achieve and, thus, the types of grips and movements they can execute. All Old World monkeys, apes, and humans are able to achieve true pad-to-pad thumb opposition (with the exception of the thumbless colobus monkeys) due to the saddle joint at the first carpometacarpal (CM1) joint (Napier and Napier 1967; Rose 1992). Prosimians and New World monkeys achieve what Napier (1960; Napier and Napier 1967, 1985) referred to as “pseudo-opposition,” as the surface of the CM1 joint is hinge like, therefore limiting rotation of the thumb. Consequently, these primates can press the thumb to the lateral aspect of the second digit (i.e., pad to side), but cannot achieve full pad-to-pad contact. Although Napier did not consider pseudo-opposition to allow for precision handling, functionally both “true” and

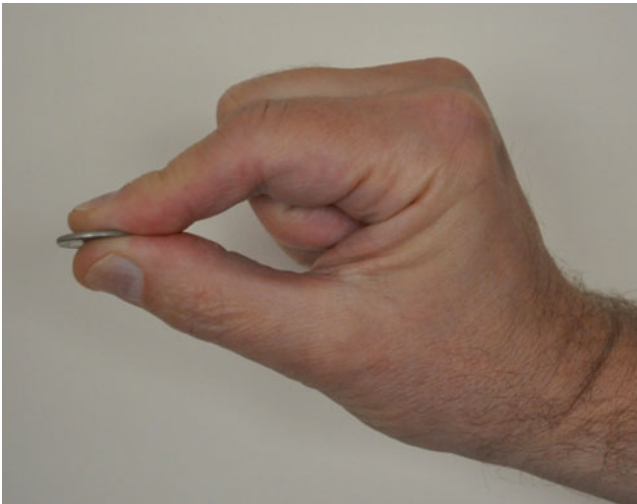


Fig. 12.4 Humans easily make full contact between pads of the thumb and index finger. This posture is what Napier (1961) identified as “true opposition.” Photo by D. Fragaszy

Table 12.2 A sample of terminology used to describe power, precision, hook, and scissor grips among nonhuman primates

Category	Hominoids	Catarrhines	Platyrrhines	Prosimians
Power grip	<ul style="list-style-type: none"> • Power grip^a • Squeeze grip^a • Power grips^b 	<ul style="list-style-type: none"> • Hand wrap^c • Finger-splayed wrap^c • Hand-to-torso grip^c • Climbing wrap^c 	<ul style="list-style-type: none"> • Power grip^d • Enclosed thumb-palm^c • Thumb/index-palm^c • Thumb-thenar^c • Palm-thenar^c 	<ul style="list-style-type: none"> • One hand grasp^f
Hook type	<ul style="list-style-type: none"> • Hook^a • Loose grip^a • Transverse hook grip^g • Diagonal hook grip^g • Extended transverse hook grip^g • Extended diagonal hook grip^g • Ulnar-palmar grasp^h 	<ul style="list-style-type: none"> • Climbing hook^c 		
Precision grip	<ul style="list-style-type: none"> • Pinch grip^a • Pencil grip^a • Tip-to-tip hold^g • Pad-to-tip hold^g • Pad-to-side hold^g • Cup hold^g • Radial-palmar grasp^h • Imprecise grasp^h • Pincer grip^h • Tip-to-tip precision gripⁱ • Lateral precision gripⁱ • Precision grips^b • Thumb-to-finger pad(s)^b • Imprecise^b 	<ul style="list-style-type: none"> • Tip-to-tip precision gripⁱ • Pad-to-pad precision gripⁱ • Lateral precision gripⁱ • Pad-to-side grip^c • Pad-to-pad grip^c • Thumb-to-second-third grip^c • Tip-to-inside grip^c • Three-tip grip^c • Thumb-and-four-finger grip^c • All-tip grip^c • Thumb-to-outside grip^c 	<ul style="list-style-type: none"> • Precision grip^j • Precision grip (types: 1-2; 1-2,3; 1-2,3,4; 1-2,3,4,5)^d • Precision grip (types: I-II distal areas, I-II distal-to-other areas, I-II, III/distal areas, other variants)^e 	
Scissor type	<ul style="list-style-type: none"> • Scissor grip^a • Index and middle finger grip^h • Adduction gripⁱ • Other grips^b 	<ul style="list-style-type: none"> • Between-finger grip^c 	<ul style="list-style-type: none"> • Precision grip (types: 2-3, 3-4, 4-5)^d 	

Note that within each category of movement defined by Napier (1956, 1980), there is a variety in which digits are used in the grasp and the contact points of the object on those digits. This table provides an overview of terms that have been used by researchers to describe various grips that fall within each broad category and highlights the need for a common lexicon that can be used across taxa

(continued)

Table 12.2 (continued)

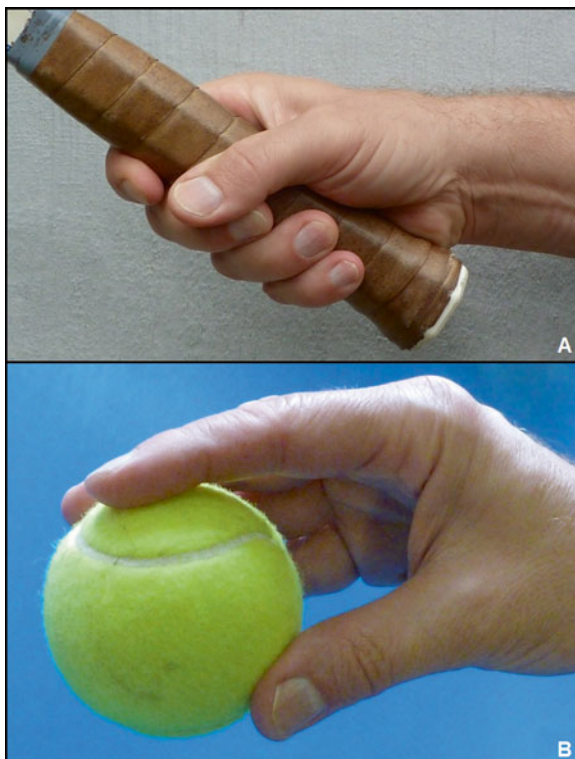
^aByrne and Corp (2001); *Gorilla g. beringei*
^bJones-Engel and Bard (1996); *Pan troglodytes*
^cMacfarlane and Graziano (2009); *Macaca mulatta*
^dCostello and Fragaszy (1988); *Sapajus* spp.
^eSpinozzi et al. (2004); *Sapajus* spp.
^fReghem et al. (2011); *Microcebus murinus*
^gMarzke and Wullstein (1996); *Pan troglodytes*
^hTonooka and Matsuzawa (1995); *Pan troglodytes*
ⁱChristel (1993); *Pan paniscus*, *Pan troglodytes*, *Gorilla g. gorilla*, *Pongo pygmaeus* and *P. abelii*, *Hylobates lar lar* and *H. l. moloch*, *Theropithecus gelada*, *Macaca silenus*, and *Cercocebus aterrimus*
^jChristel and Fragaszy (2000); *Sapajus* spp.

“pseudo-opposition” allow for a multitude of precision grips that have been described in Old World and some New World primates (see Table 12.2). In our view, the categorical distinction between “true” and “pseudo-opposition,” derived from anatomical considerations, does not contribute to our understanding of the array of functional uses of digits opposing each other and the palm that are evident in primates. For example, Pellis and Pellis (2012) described how aye-ayes use their thumb in a distinctive manner to secure food to the palm with no reference to whether they are using “true” or “pseudo-opposition.”

4.3.2 Defining Power and Precision Grips

Napier (1956) coined the terms **power** and **precision** grips to describe the two most basic grasping patterns in humans. Many of the varieties of grips described for humans have also been identified in nonhuman primates (Table 12.2). With the power grip, an object is stabilized against the palm, and the digits converge around the object, as in holding the handle of a hammer or a tennis racket (Fig. 12.5a). Napier identified the **hook** grip as similar to the power grip, but without involvement of the thumb (as in holding the handle of a briefcase; Napier 1956). With the precision grip, an object is held by the digits alone (away from the palm), and in humans the thumb is abducted and rotated to face the palm, thus opposing the other digits, as in holding a tennis ball off the palm (Fig. 12.5b). Napier (1980) also defined the scissor grip, a form of precision grasping that does not involve the thumb (as in holding a pencil between the index and middle fingers). While the properties of the object to be grasped influence whether predominantly a power or precision grip is needed, often a key factor is the intended action (Napier 1956, 1980). For example, a precision grip is used to align the lid of a jar to the threads, but a power grip can be used to tighten the lid (Napier 1980). Due to varying object properties and the varying actions that the objects afford, there is a multitude of forms of power and precision grips that can be adopted (summarized below). In this chapter, we use the term “precision grip(s)”

Fig. 12.5 Human power (a) and precision (b) grips, as described by Napier (1956). Photos by D. Fragaszy



in a general sense to refer to the grasping of an object with the distal aspects of the digits, acknowledging that animals can execute precision grips with different contact points on the digits, all of which can be individually recognized (e.g., Marzke et al. 2009; Pouydebat et al. 2009; Table 12.2).

4.3.3 Power Grips

All primates are able to execute a power grip quite efficiently, although there is considerable variation in the orientation of the digits during closure, depending on the degree of thumb opposition. Usually, a power grip involves contact by all five digits, each flexing and securing an object against the palm. However, a power grip can also be achieved with fewer than five digits, as long as the digits involved are gripping an object against the palm.

Lorisiform and lemuriform species are characterized by a single prehensile pattern, a power grip, with final grips determined by the shape of the object they grasp. Bishop (1964) identified general patterns of prehension in strepsirrhine taxa in terms of posture during reaching and the point of contact of the hand with an object, as well as in terms of the forms of contact of digits with the palm and with

each other. Lorisoids picking up small objects from a flat surface reached with the fingers splayed, contacted the object first with the palmar pads, and then closed all the digits convergently, flexing the interphalangeal (IP) joints and pressing the object between the digital pads and the interdigital pads (Fig. 12.6a). Bishop (1964) described this pattern as precise, although without differentiated control of the digits. The lemuriform pattern differs from the lorisiform pattern in Bishop's (1964) descriptions in that the lemurs reached with roughly parallel (rather than splayed) digits and contacted objects with the digits first, rather than the palm, in common with anthropoid primates. Lemurs flex the fingers at the McP and proximal IP joints, so that an object is held between the digital pads and the proximal palmar pads (Fig. 12.6b). Lemurs also hooked small objects under the two most distal phalanges of digits 2–5 and pulled them toward the palm, with the thumb in line or at about 90° to the palm.

Aye-ayes present a unique variation on the power grip. In this species, the long third digit remains on the dorsal side of the hand when not in use for probing or tapping. During locomotion (in which a power grip is used), especially during head-first descent (which is common in aye-ayes), the third digit is often hyperextended at the McP joint, flexed at the IP joints, and held to one side (Krakauer et al. 2002; Soligo 2005; Kivell et al. 2010). In this position, it does not participate in grasping the substrate. The longer, more robust fourth digit supports a strong grip on the substrate (Soligo 2005). Although aye-ayes cannot achieve a high degree of thumb opposability, they are able to abduct the thumb enough to secure a small object against the palm without assistance from the other digits. This ability, shared only with sifakas among the lemuriforms, suggests that the relative independence of the thumb

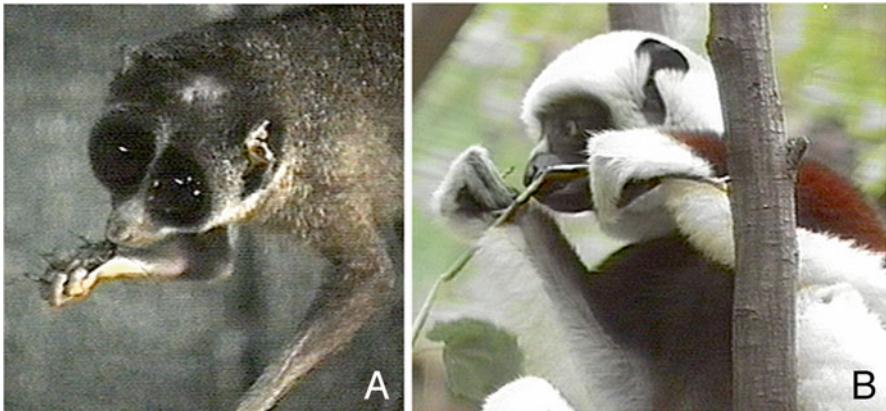


Fig. 12.6 A slender loris (*Loris tardigradus*) and a sifaka (*Propithecus verreauxi*) illustrate the different prehensile patterns described by Bishop (1962, 1964) for lorises and lemurs. (a) The loris holds an insect against the palm with all interphalangeal joints flexed. (b) The sifaka holds plant matter with flexed metacarpophalangeal and proximal interphalangeal joints, pressing it against the proximal palmar pads with the distal pads of the digits. Images courtesy of Pierre Lemelin

Fig. 12.7 Drawing of an aye-aye (*Daubentonia madagascariensis*) holding a food item against the palm with the thumb and with minimal support from the other digits. Reprinted from Pellis and Pellis (2012) with permission of the publisher



is a derived feature that allows the aye-aye to hold the small extracted food items away from its cumbersome, elongated third and fourth digits (Pellis and Pellis 2012; Fig. 12.7).

Tarsiers, nocturnal and small-bodied primates, also present a taxonomically unique pattern of prehension, which can be viewed as a variation on a power grip. They feed on vertebrate and invertebrate prey captured with one or both hands (Niemitz 1984). Niemitz (1984) describes the typical grip of Western tarsiers (*Tarsius* (or *Cephalopachus*) *bancanus*) in which digits 2–4 flex toward the palm, with the pollex flexing more or less parallel to digits 2–4. The fifth digit rotates at the McP joint and flexes to be perpendicular to the other digits, “much like the thumb” (Niemitz 1984, 69; Fig. 12.8). This movement is reminiscent of grasping behavior in rats (see above), which sometimes rotate the fifth digit toward the palm. This hand posture prevents captured mobile prey from escaping. No other primate rotates the fifth digit; this is apparently a derived feature present only in tarsiers. Casual observations of the Philippine tarsier (*Tarsius* (or *Carlito*) *syrichta*) reveal the typical parallel position of the thumb, but do not indicate the rotation of the fifth digit described by Niemitz (1984) (P. Lemelin, personal communication). As the genus *Tarsius* has recently been recognized to be composed of three genera (Groves and Shekelle 2010) and multiple species within each genus, these discrepancies in hand behavior parallel generic variability in tarsiers. In general, we know less about prehensive function in tarsiers than in other primate taxa. Further study of manual function and associated neuromuscular systems in this taxon will be particularly enlightening.

Platyrrhine and catarrhine species use a variety of power grips, and the terminology to describe these grips is likewise varied (Table 12.2). Preshaping of the hand to match the size of the object to be grasped or the features of the surface to be contacted has been described in macaques and tufted capuchin monkeys (Christel and Fragaszy 2000; Roy et al. 2000; Christel and Billard 2002). The precise orientation of the fingers with respect to the object held against the palm varies according to the shape and size of the object relative to the size of the hand and on the degree of radial abduction of the thumb. For example, an individual holding a long, thin

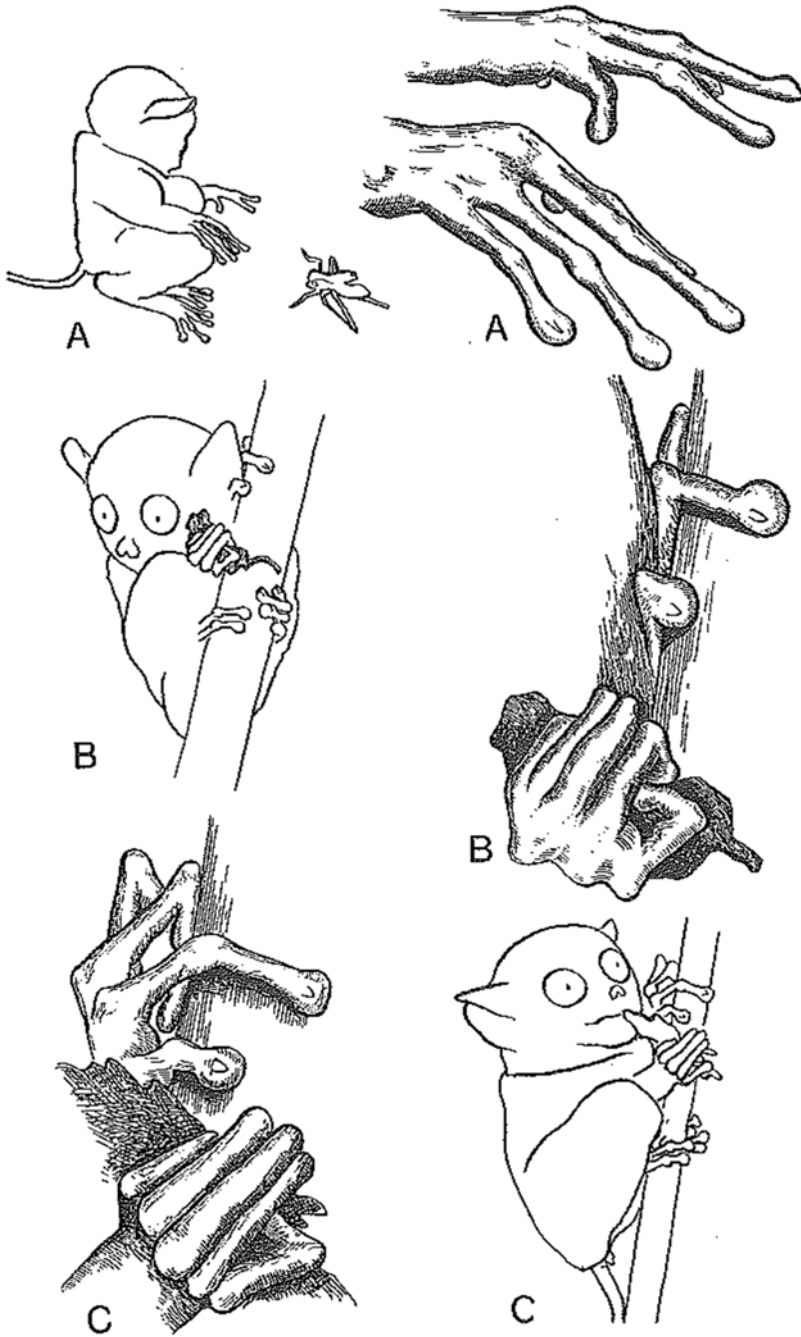


Fig. 12.8 A tarsier (*Cephalopachus bancanus*) just prior to capturing an insect, with fingers splayed (a), holding an insect with the fifth digit rotated to be perpendicular to the other digits (b and c), and eating it (c). The grip posture illustrated in b and c is observed uniquely in tarsiers. Drawn by C. Niemitz and W. von Bischoffshausen, and reproduced from Niemitz (1984) with permission of the author

object commonly abducts the thumb to wrap it over the dorsal side of the other digits. Platyrrhine monkeys can achieve this kind of power grip, although they often keep all the digits parallel during grasping due to their inability to rotate the thumb, as illustrated in the golden-handed tamarin (*Saguinus midas*) by Lemelin and Grafton (1998). Like the aye-aye and sifaka, squirrel monkeys can press the thumb laterally on the sides of an object, and the proximal pollical phalanx can flex 180° to contact the palm, providing a secure grip for small objects (Fragaszy 1983; Costello and Frigaszy 1988; Lemelin and Grafton 1998). Tufted capuchin monkeys preferentially grasp small moving targets using a power grip, but use precision grips on small stationary targets (Costello and Frigaszy 1988). Because they can abduct the thumb with respect to the palm, catarrhine primates probably achieve a greater variety of power grips compared to platyrrhine monkeys. In this regard, Macfarlane and Graziano (2009) provided an extensive description of power grips used by free-ranging rhesus monkeys (*Macaca mulatta*, Table 12.2).

4.3.4 Precision Grips

Precision handling involves the manipulation of objects with the distal surfaces of the digits used in any combination (Landsmeer 1962). The proportional length of the digits and the degree of opposability of the thumb determine the contact points between an object and the digits in a precision grip. Prosimians and many New World monkeys are limited in precision handling due to their inability to rotate the thumb. With the exception of capuchin monkeys (*Cebus* and *Sapajus*), these primates move their digits in unison and parallel to one another and are unable to achieve a precision grip between digits 1 and 2, although many New World monkeys can use a scissor grip between digits 2 and 3 or digits 3 and 4 (*Cacajao*, *Ateles*, and *Lagothrix*, Bishop 1964; *Sapajus*, Costello and Frigaszy 1988; *Saguinus*, Lemelin and Grafton 1998).

Capuchin monkeys (*Cebus* and *Sapajus*) possess some individuated control of the digits, as demonstrated in probing actions with digit 2 and in an array of precision grips executed between the thumb and other digits (Costello and Frigaszy 1988; Christel and Frigaszy 2000; Spinozzi et al. 2004, 2007; Fig. 12.2, Table 12.2). Christel and Frigaszy (2000) noted that tufted capuchin monkeys move single digits independently when the fingers rest on the surface of a board in contrast to a relatively uniform preshaping pattern when fingers are coordinated in space. It appears that contact of the hand with a substrate (a surface or tube) supports better coordination of single digits for diverse grips. Aside from capuchins, Bishop (1964) reported that uakari monkeys (genus *Cacajao*) use the sides of digit 1 against those of digit 2 when manipulating small objects, but her initial observations have not been replicated. Indeed, we are not aware of additional information about prehension in *Cacajao* other than Bishop's (1964) landmark studies; this is clearly a topic deserving further investigation.

Catarrhine primates, particularly cercopithecoids, use a variety of precision grips in foraging and grooming. For example, gelada baboons (*Theropithecus gelada*)

pluck grass between the thumb and index finger while holding a bundle of grass against the palm with the other digits (Maier 1993). Japanese macaques (*Macaca fuscata*) use several variations of a delicate pad-to-pad precision grip between the thumb and index finger to remove louse eggs from the hair follicle while grooming (Tanaka 1998). All catarrhine monkeys routinely use precision grips to pick up small objects. Colobus monkeys (*Colobus*), which have a vestigial thumb, flex the index finger until it touches the pollical nub when picking up small objects (Bishop 1964). Assuming similar function across catarrhine genera, these monkeys exhibit substantial preshaping of the hand when reaching for objects of different sizes (Roy et al. 2000) and kinematic similarities to humans during reaching for prehension (Christel and Billard 2002).

In great apes, digits 2–5 are relatively long and curved, and the thumb is proportionally short compared to other primates, thus limiting pad-to-pad contact in thumb opposition (Napier and Napier 1967; Marzke and Wullstein 1996). Although all great apes are capable of pad-to-pad contact between the thumb and index finger, they have lesser contact area and pressure compared to humans and typically achieve a precision grip between the thumb pad and side of the index finger (Christel 1993; Fig. 12.9). Humans achieve the greatest area of pad-to-pad contact in a precision grip among primates due to a greater ability cup the palm and a relatively long thumb (Marzke 1983; compare Figs. 12.4 and 12.9a). Nevertheless, many different types of precision grips have been documented in apes (e.g., see Jones-Engel and Bard 1996; Marzke and Wullstein 1996; Table 12.2). Christel (1993) documented variations in precision grips in humans, chimpanzees, and bonobos (*Pan troglodytes*

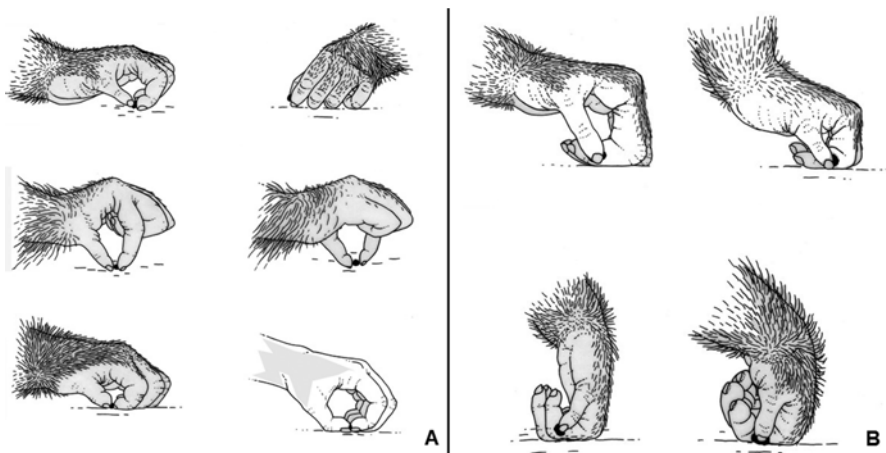


Fig. 12.9 Precision grips in hominids when picking up a small object. (a) Opposition of the thumb to the index finger. *Top row*, chimpanzee (*Pan troglodytes*); *middle row*, orangutan (*Pongo pygmaeus*); and *bottom row*, gorilla (*Gorilla gorilla*) (left) and human (*Homo sapiens*) (right). (b) Lateral opposition of the thumb to the middle phalanx of the index finger. All chimpanzees (*Pan troglodytes*). Drawings by M. Christel and H. Schulze, unpublished and reprinted from Christel (1993) with permission of the publisher and the artists

and *Pan paniscus*), Western gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), and white-handed and moloch gibbons (*Hylobates lar* and *Hylobates moloch*) picking up small pieces of food (Fig. 12.9). Pad-to-pad contact between the thumb and index finger was achieved by chimpanzees, gorillas, and orangutans (see Fig. 12.9). For this task, humans habitually preferred the pad-to-pad precision grip, whereas apes frequently used the lateral side of the index finger in precision grips.

4.3.5 In-Hand Movements

The above discussion highlights the routine use of a variety of grasping patterns in the daily lives of primates. This variety is a hallmark of the order Primates and distinguishes it from other taxonomic groups. Some primates act with objects in skillful ways beyond static grasping. They turn over, rotate, and otherwise move objects held within the hand using **in-hand movements**. An in-hand movement involves manipulation of an object within a single hand using the digits of that hand alone, such as flipping the cap off of a pen (Elliott and Connolly 1984). Human infants exhibit simple forms of in-hand movements within the first year of life, and children are able to perform all documented forms of in-hand movements by the age of 8 years, although with less proficiency than adults (Exner 1992; Manoel and Connolly 1998).

Elliott and Connolly (1984) provided a comprehensive taxonomy of the various forms of in-hand movements used by humans, which was adapted to describe in-hand movements in children (Exner 1992), in-hand movements in chimpanzees (Craet et al. 2009), and in-hand movements in wild mountain gorillas and chimpanzees (Byrne and Corp 2001; Corp and Byrne 2002) (Table 12.3). In-hand movements are categorized as simultaneous, in which an object is moved by the concurrent movement of two or more digits, or as sequential, in which the digits move sequentially to change an object's orientation in the hand (referred to as sequential movements and palmar combinations; see definitions in Table 12.3). Here we discuss which primates are known to use these forms of prehension.

In Elliott and Connolly's (1984) classification of in-hand movements, simultaneous movements are distinguished as simple synergies or reciprocal synergies. A simple synergy involves prehending an object using a static grip and then flexing and extending the digits to move the object through space, without changing the object's orientation (e.g., moving a needle through fabric using only the flexion/extension of the digits). Presumably, any primate that can use a precision grip is able to flex and extend its digits while maintaining a grip on the object (i.e., a simple synergy). This has been documented in adult chimpanzees during a movement called "turnover" (Craet et al. 2009); but even primates using whole-hand control should be able to execute simple synergies by grasping an object with the tips of all five digits and then flexing those digits.

A reciprocal synergy involves the simultaneous movement of two or more digits in opposite directions to turn an object about one of its axes, as in turning a screw. Reciprocal synergies emerge in human children around the age of 2–3 years and are

Table 12.3 Known terminology used to describe in-hand movements among nonhuman primates using Elliott and Connolly's (1984) classification system

In-hand movement	Definition	Hominoids	Catarrhines	Platyrrhines
Simple synergies	Prehending an object using a static grip and then flexing and extending the digits to move the object through space without changing the object's orientation (e.g., moving a needle through fabric using only the flexion/extension of the digits)	<ul style="list-style-type: none"> Combine^a 		
Reciprocal synergies	Movement of the digits after prehension to rotate object about one axis; the thumb moves in the opposite direction of digit(s) simultaneously (e.g., turning a doorknob using only the fingers)	<ul style="list-style-type: none"> Thumb abduction/adduction^b Roll^b 		<ul style="list-style-type: none"> Roll^c
Sequential movements	Concurrent movement of digits in opposing directions allowing for movement of an object about more than one axis (e.g., rotating a pen within the hand)	<ul style="list-style-type: none"> Manipulate^{a,d} Rotation^b Turnover^b 		
Palmar combination	Object is stabilized in the palm, and independent digit movements are used to manipulate part of the object, as in pushing off the cap of a pen	<ul style="list-style-type: none"> Thumb push^b 		
Transfer ^e	Object is grasped in a precision grip with digits 1–2, brought into the palm with a simple synergy and secured with digits 3–5 while the first two digits grasp another object	<ul style="list-style-type: none"> Digit-role differentiation^a Unimanual multitasking^d 	<ul style="list-style-type: none"> Transfer^{f,g} 	

^aByrne and Corp (2001); *Gorilla g. beringei*^bCrast et al. (2009); *Pan troglodytes*^cCrast (2006); *Sapajus* spp.^dCorp and Byrne (2002); *Pan troglodytes*^eThe term “transfer” was not used by Macfarlane and Graziano (2009) or Maier (1993), nor was it a category of movements described by Elliott and Connolly (1984). We include it here because it is a type of in-hand movement that is distinct from sequential movements in some ways. In this regard, Byrne and Corp (2001) considered digit-role differentiation and unimanual multitasking to be forms of sequential movements^fMacfarlane and Graziano (2009); *Macaca mulatta*^gMaier (1993); *Theropithecus gelada*

refined by the age of 7–8 years (Exner 1992; Manoel and Connolly 1998). Similarly, young chimpanzees at age 5 years are fully proficient at using reciprocal synergies to manipulate small objects, as adult chimpanzees do in a variety of ways, routinely and with ease (Craet et al. 2009; Table 12.3). Because capuchins have a relatively high level of individuated control for digits 1 and 2, we investigated whether they can use reciprocal synergies using the same experimental design that elicited these movements in chimpanzees. Two monkeys each used a rudimentary reciprocal synergy once (Craet 2006). They both placed their forelimb against the vertical panel and, while holding the object in a precision grip against the surface of the panel, flexed the index or middle finger toward the palm as the thumb simultaneously extended, thus turning the object about one of its axes. These observations, however, require replication, as the events were rare and the usual means of reorienting the object in the hand was to move it to the other hand or the mouth. This suggests that the neuromuscular anatomy required to execute more complex in-hand movements is less developed in capuchins compared to apes and humans.

Although adult chimpanzees did not execute sequential movements as finely as adult humans, they performed a variety of forms including rotations and turnovers (Craet et al. 2009). To perform a turnover, adult chimpanzees grasped the object between the index and middle fingers and then flexed those digits, bringing the object into the palm (a simple synergy); the object was then rolled over the index finger to be grasped between it and the thumb (Fig. 12.10). When rotating an object within one hand, adult chimpanzees frequently cradled the object in the palm while using the digits to readjust the object's orientation. In contrast, humans are quite capable of moving an object of comparable size without the use of the palm.

4.3.6 Compound Grips and In-Hand Movements

Macfarlane and Graziano (2009) analyzed the rich variety of spontaneous manual actions in rhesus monkeys (*Macaca mulatta*) ranging freely in a natural setting, including gripping an object with two hands concurrently and bracing an object

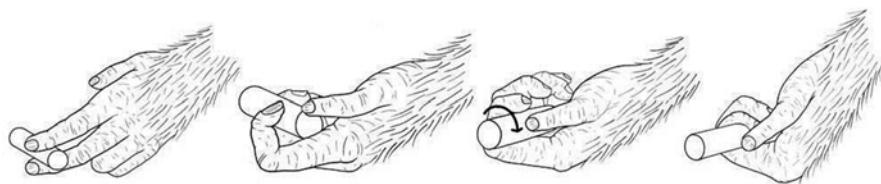


Fig. 12.10 Example of in-hand movements in the chimpanzee (*Pan troglodytes*). The drawings illustrate a “turnover” sequence used by an adult chimpanzee. This sequence was used to pick up an object from the floor and reorient the object within the hand to align it with a correspondingly shaped cutout in a transparent panel. The object is grasped between the second and third digits, which flex and bring the object toward the palm; the object is then rolled over the distal end of the index finger by reciprocal movement of the thumb and index finger; the object is finally grasped in a precision grip between the tip of the thumb and the side of the index finger (drawn by Cheryl Reese)

against the torso. In addition to the typically defined grips of one object held in one hand, these authors defined a variety of compound grips when the monkey held more than one object in one hand. For example, the monkey could hold one or more objects in a “storage grip,” a power grip with the object braced against the palm using digits 4 and 5, and concurrently pick up another object with digits 1–3. Interestingly, Macfarlane and Graziano also observed the macaques shifting objects picked up with the first two digits to digits 3–5 for storage and then picking up an additional object with the first two digits (M. Graziano, personal communication). The transfer of an object within the hand using the digits of that hand alone is by definition an in-hand movement: the monkey used one grip toprehend an object (precision grip with digits 1–2), a simple synergy to bring the object into the palm, and then a second grip to hold the object (power grasp with digits 3–5).

Compound grips and transfer movements have also been identified in other primates, including wild gelada baboons (*Theropithecus gelada*) that continuously pluck grass between the thumb and index finger and transfer the grass to a bundle held against the palm with the other digits (Maier 1993). Wild mountain gorillas (*Gorilla gorilla beringei*) use the same movement with the thistle plant *Carduus nyassanus* (Byrne and Corp 2001), as do chimpanzees (*Pan troglodytes*) with the fruit *Saba florida* (Corp and Byrne 2002). Gorillas’ movements were termed “digit role differentiation” and chimpanzees’ movements “unimanual multitasking” (one hand carries out two actions simultaneously); both were identified as sequential in-hand movements (Byrne and Corp 2001; Corp and Byrne 2002). Transferring an object in this manner may be considered distinct from reciprocal and sequential in-hand movements because concurrent movement of digits in opposite directions is not necessarily present. “Transfer” may qualify as a new category of in-hand movement, as it requires a series of grasps and movements in order to move an object’s location within the hand (Table 12.3).

Both gorillas and chimpanzees in Byrne and Corp’s studies also demonstrated a more sophisticated form of in-hand movement, termed manipulate, in which an object was rearranged within one hand using the digits of that hand alone. As shown in captive chimpanzees (Crast et al. 2009), skill at manipulating and transferring items within the hand increased with age (proficiency develops by age 4–6; Byrne and Corp 2001; Corp and Byrne 2002). Notably, studies have not examined whether catarrhine monkeys use in-hand movements other than the transfer movement. Clearly, however, macaques, gorillas, and chimpanzees make use of compound grips when executing a transfer movement. Chimpanzees probably also utilize a compound grip together with a transfer movement during nutcracking, as they often store one or more nuts in the palm of the hand while preparing another nut to be hammered against an anvil (Boesch and Boesch 1993).

Compound grips and in-hand movements probably rely upon shared neuromotor abilities to activate muscles of the hand and multiple digits independently and in varied coordinative structures. These dynamic aspects of manual function, which are elaborated in humans, require further investigation by primatologists. We know far more about static grip postures than about movements of the hands while manipulating gripped objects. With respect to taxonomic variation, at pres-

ent we can only say that in-hand movements and compound grips are evident in several catarrhine taxa, require validation in capuchin monkeys, and are totally uninvestigated in other groups of primates. Researchers with interests in robotics and prosthetics have developed alternative frameworks to measure movements of the hand (e.g., Bullock and Dollar 2011; Fu and Santello 2011), and we can expect that treatments of this aspect of manual function in nonhuman primates will eventually broaden to include these frameworks as well.

4.4 *Nonprehensile Skilled Movements*

Movements that fall within the last category of manual function in Jones and Lederman's (2006) framework, nonprehensile skilled movements, have received attention from behavioral scientists studying nonhuman primates, but not from functional anatomists or others concerned with the evolution of manual function in primates, to our knowledge. Nonprehensile skilled movements include actions such as the following: (1) urine washing (urinating into the palm of the hand and wiping the urine on the sole of the foot, a common behavior in New World monkeys and prosimians), (2) spreading the hair while grooming (most taxa), (3) sweeping loose debris off a surface (as capuchins do when cracking nuts or digging up roots; D. Fragaszy, personal observation), (4) searching in loose plant debris for animal prey (as some species of lion tamarins, *Leontopithecus*, do; Rylands 1993; Passos and Keuroghlian 1999), (5) positioning the hand to collect ants as they climb onto the hand (slender loris, *Loris*; Kumara, et al. 2005), (6) capturing small objects on the fingertip by pressing them against a hard surface (macaques and chimpanzees; Christel 1993), (7) probing into a narrow opening using a single digit (capuchins, aye-ayes, and chimpanzees), and (8) gesturing communicatively (as in pointing in chimpanzees; Leavens et al. 1996).

Humans produce a far larger variety of these movements than any other species, including manual gestures used in sign language, actions used to modify objects (e.g., molding clay), and actions used to control devices (e.g., keyboards, musical instruments). The same features of movement control that enable compound grips and in-hand movements (i.e., finely controlled and independent movements of the digits, in sequence and concurrently), together with elaborated proprioceptive and kinesthetic sensitivity, also support nonprehensile skilled movements. In this case, it is interesting to note that capuchin monkeys—which may be able to move the thumb in opposite directions from the index finger and move the index finger to the thumb in a precision grip—also move the index finger with partial independence when probing into an opening (Spinozzi et al. 2007; Figs. 12.2c and 12.3a). When they probe with the index finger, the index finger leads and the other digits are initially partially flexed. They flex further toward the palm as downward pressure is applied to the object with the tip of digit 2. That is, the full extension of digit 2 may be passive, while digits 3–5 are flexed (Fig. 12.3b). Thus, the control of digit 2 may be less independent in capuchin monkeys than in chimpanzees, which can point the extended index finger of an unsupported hand (with digits 2–5 flexed) at a distal target (Leavens et al. 1996). The use of the

index finger in probing has not been described for catarrhine monkeys, to our knowledge, but they do scrape with the index finger (e.g., Tanaka 1998). Underlying the ability of capuchins and catarrhines to move the index finger independently, and to oppose the thumb and the index finger, is a relatively elaborated corticospinal tract compared to other primates (for details, see Bortoff and Strick 1993; Lemon 1993; Lemon and Griffiths 2005; see Chap. 6). No doubt this elaboration is also involved in the production of in-hand movements and compound grips.

5 Summary of Major Differences in Manual Function Among Primates

Skilled forelimb movements (aimed reaching, prehension with a single appendage using digital closure) are primitive characteristics in the order Primates that are shared with some other orders of mammals. Some manual functions are apparently derived in primates, and some are derived within certain clades of nonhuman primates. For discussion purposes only (as the data are currently inadequate for proper analysis), a tentative list of these derivations in various phylogenetic groups is given in Table 12.4.

We examined manual function using the four classes of function identified by Jones and Lederman (2006). Tactile sensing is primitive in primates and we are unaware of variations in this function across primates. Active haptic sensing is also probably primitive in primates, but we have few studies of this aspect of manual function in primates and even fewer in other orders. Several derivations have

Table 12.4 Derived characters in manual function observed to date in primates

Taxonomic group	Derived characters
<i>Daubentonia</i>	Specialized use of digit 3 in tapping and extraction, modified joints permitting rotation at McP ^a joint and hyperextension at distal IP ^b joint
Tarsiiformes	Rotation at McP joints of the thumb and digit 5, permitting an oppositional grip; possibly, gains in independent movements of digits (suggested by Niemitz 1984, but not confirmed)
Anthropoidea	Adjacent digits can be used in scissor grip
<i>Cebus</i> and <i>Sapajus</i>	(a) The thumb moves medially to provide functional opposition precision grip with digit 2 and digit 3 (b) Partial independent movement of digit 2, affording probing/extraction (c) Reciprocal movement of the thumb and digit 2 (nascent in-hand movement)
Catarrhini	(a) The thumb “fully” opposes other digits (achieves pulp-to-pulp contact) (b) Compound grips and transfer in-hand movements
Hominoidea	Full independent movement of digit 2 (extension and flexion)
Hominae	Reciprocal and sequential in-hand movements

^aMcP metacarpophalangeal

^bIP interphalangeal

occurred in prehensile function. Principal among these are the following: (1) the ability to press digits together to hold objects between the lateral sides of adjacent digits in a scissor grip, which apparently evolved after anthropoids diverged from prosimians; (2) the ability to oppose the thumb and other digits and individuated control of the thumb and digit 2, which evolved early in the radiation of catarrhine primates and independently and to a lesser extent in cebids; (3) the ability to move objects held within one hand and to perform concurrently more than one manipulative action with some digits and another manipulative action with the remaining digits of the same hand (in-hand movements and compound grips), which evolved early in the radiation of catarrhine primates; (4) the ability to rotate digit 5 toward the palm, reported only for tarsiers; and (5) the independent movement of digit 3 for tapping and probing and the placement to one side of this digit during some locomotor circumstances, both present only in aye-ayes. Nonprehensile skilled actions are probably derived in primates compared to other mammals, specialized across taxa, and vastly elaborated in humans. The independent use of the index finger in probing and scraping actions is the most commonly described nonprehensile behavior in nonhuman primates; this ability evolved in catarrhine primates and independently, and to a lesser extent, in cebids.

6 Future Directions

We see four topics as high priority for attention in future research. First, there is the problem of a common vocabulary to identify hand postures and movements that applies across primate taxa. Table 12.2 is intended to highlight the overlap in prehensile abilities across primates and the problem of having multiple taxonomies to describe them. We need to develop a standard terminology to describe grips involving specific contact points on the hand and sequences of movements.

Second, active haptic perception requires attention because uses of the hand in exploration are mostly unknown outside of humans. It is telling that our most comprehensive comparative studies in this area were published decades ago and were meant as initial explorations of this topic. They relied upon presentations of large and simple objects, such as wooden blocks and rope (Glickman and Sroges 1966; Torigoe 1985), and did not address the precise manner in which individuals use the body to investigate and handle objects. Bishop (1962, 1964; Jolly 1964) set the standard for more detailed studies in the early 1960s, and we have yet to approach that standard again.

Third, although much of the discussion concerning the evolution of manual function in primates has centered around grips, we suggest that in-hand movements and nonprehensile movements contribute as much or more than grips per se to the differentiation of manual function across primates. These movements underlie many species-typical skilled actions in humans, including exploratory functions of the hand. We know almost nothing about the extent to which Old World monkeys and lesser apes use these movements in their daily lives and very little about how great

apes use them. The comparative approach can reveal much more about the evolution of complex and intricate manual dexterity, which is so natural and routine for humans that it goes completely unappreciated in our day-to-day activities. We see this dimension of manual function as an important target for comparative research.

Fourth, we need to assess manual actions in natural circumstances, to develop an integrated comparative understanding of manual function in daily life of various species across the order. At present we know variations exist across taxa in the details of manual function, but we do not have a systematic basis for comparing either the quality or quantity of variation (see Leca et al. 2010 for a detailed description of stone-handling patterns in Japanese macaques and Macfarlane and Graziano 2009 for an equally detailed but independent treatment of manual function in rhesus macaques). One promising direction for understanding ecological and behavioral factors associated with different types of hand movements is to explore evolutionary convergence in the forms and the kinematics of these actions (e.g., Reghem et al. 2013) in New and Old World primates. This effort will be possible once a systematic taxonomy of manual function in primates is in hand (pun intended). If we can achieve this at the centennial of the publication of Wood Jones' (1920) insightful volume, we will be able to answer more of his and John Napier's fundamental queries about this appendage that is so central to human activity and human identity.

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