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RESEARCH ARTICLE

Diversity of grip in *Macaca mulatta*

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Abstract Much of the research on the neuronal basis of prehension focuses on macaque monkeys. Yet most of the behavioral description of grip types pertains to humans and apes. The purpose of the present study was to provide a catalogue and description of basic grip behavior in macaque monkeys. The observational study explored the diversity of grasping behavior in 157 semi-free ranging rhesus macaques. Video footage of monkeys grasping objects ad libitum was analyzed frame-by-frame, and grips were classified based on the skin surface areas that contacted the object. When monkeys held objects for manipulation, 15 distinct grip categories were observed. When monkeys held support points during climbing, two grip categories were observed. Not all grips were performed with the hand. Some involved the mouth, the foot, or an opposition between the forearm and chest. Grip in macaque monkeys is more diverse than the narrow range of grip that is typically studied.

Keywords Prehension · Grasp · Primatology · Rhesus · Ethology

Introduction

Grasping is one of the most important behaviors in primates. The grasping of objects in humans and apes was first systematically described by Napier (1956, 1961) who distinguished two general classes of grip: the precision grip for holding small objects, often performed between the tip of the forefinger and the tip of thumb, and the power grip for holding larger objects, often performed by wrapping all four fingers and the palm around an object in one direction and wrapping the thumb around the object in the opposing direction. This dichotomy of grip formed the basis of almost all subsequent studies of grip.

In humans, Napier's original two grip types were subdivided into many finer gradations. For example, Cutkosky (1989) categorized at least nine grips used by machinists. Patkin (1981) categorized the grips used in microsurgery. Kamakura et al. (1980) and Kroemer (1986) categorized grips based on photographs of the static postures of the human hand holding introduced objects. Wong and Whishaw (2004) categorized precision grips in children and adults who were asked to pick up small beads. Skerik et al. (1971) developed a taxonomy based on the evaluation of congenitally anomalous hands. Kapandji (1982) focused on the operations needed to restore hand function during reconstructive surgery. Several groups used an analysis of forces to categorize grip (Arbib et al. 1985; Cooney and Chao 1977; Santello and Soechting 2000). Elliott and Connolly (1984) suggested a functional categorization of grip into those that immobilize objects and those that manipulate objects.

Studies also addressed the range of grips in non-human primates. Christel (1993) studied captive chimpanzees, bonobos, gorillas, orang-utans, silvery gibbons, and lar gibbons. The animals were given small pieces of food, and subtypes of precision grip were classified based on surface areas of contact on the fingers. The greatest variety of grips was observed in orang-utans (15 types) followed by gorillas (12 types), chimpanzees (9 types), bonobos (4 types), silvery gibbons (4 types), and lar gibbons (2 types). Testing the same set on humans, the authors reported 13 different grip types, less than found for orang-utans.

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Pouydebat et al. (2006) used a different set of introduced objects to test precision grip in captive chimpanzees, gorillas, orang-utans, baboons, capuchins, macaques, and humans, and confirmed that precision grip can be divided into a variety of subtypes. Spinozzi et al. (2004) tested grip in capuchin monkeys and reported 16 precision grip variants and 4 power grip variants based on surface areas on the hand that contacted the object. Marzke and Wullstein (1996) also proposed a taxonomy of grip in captive chimpanzees manipulating introduced objects.

The neuronal mechanisms responsible for the control of grip have been studied particularly in macaque monkeys (e.g. Murata et al. 2000; Raos et al. 2006; Rizzolatti et al. 1988; Sakata et al. 1995). Yet the behavioral work described above, in which grip types were studied and catalogued, focused mainly on humans and apes. Relatively less work was reported on macaque monkeys. The purpose of the present study was to describe and catalogue common kinds of grips of macaque monkeys in a naturalistic setting, to determine the grip types they normally produce rather than the grip types that they can in principle learn in a laboratory setting. In addition to providing a general description of grip types, we asked three interrelated specific questions.

Diversity of hand grips in macaques

Do macaques rely on a small repertoire of stereotyped grips such as a precision grip and a power grip, or do they use a large assortment of grips?

Diversity of body parts in macaque grip

Almost all studies of grip have focused on the fingers of one hand. Yet grip —if defined as a squeezing force applied to an object in order to hold it or manipulate it—is not at all limited to a single hand. Humans, for example, grip a basketball between two hands, a rolled-up newspaper between the upper arm and the torso, a can of beer between the knees, a piece of laundry between the chin and the upper chest, a pen in the mouth, a telephone between the head and the shoulder, and a stack of books between the forearm and the chest. Grip, in humans, has been generalized to include the opposition of any two body parts to hold an object. Do macaque monkeys grip only with the hand, mouth, and foot, or do they show evidence of a generalized concept of grip that is applied to any body parts that can be opposed?

Compound grips in macaques

Almost all studies of grip cited above focused on how a single object is gripped in the hand. Yet humans have a remarkable ability to grip many objects at the same time. For example, when picking up pennies that have spilled on the floor, we pinch up the pennies between digits 1 and 2, and temporarily store the already-picked-up pennies between the palm and digits 3–5. One hand is performing two grip functions simultaneously. In another example, the one-handed-bottle-opening behavior, we grip the neck of a soda bottle between the palm and digits 3–5, pinch the cap between digits 1 and 2, and then apply a differential force between the two grips, unscrewing the cap. Do macaque monkeys show these compound grips in their natural behavior, or are they limited to a single grip in one hand at one time?

To address these basic questions about grip behavior in macaque monkeys, we collected and analyzed video footage of semi-free-ranging rhesus macaques living unrestricted on the island of Cayo Santiago. We did not introduce specific objects to test grip types; instead we videotaped unobtrusively with a zoom lens to capture the range of grips typical of normal, daily behavior.

Because of our focus on grip behavior, and because of the need of high quality footage from the correct angle to clearly identify the grip, we were unable to collect a large amount of grip data from each individual monkey. Due to natural movement through the environment, monkeys changed position with respect to the camera, occluding their hands, or disappeared into foliage or crowds of other monkeys, or spent long periods of time resting without gripping. We were able to film only an average of 35 clearly identifiable grips per monkey. For this reason, we filmed a large number of monkeys (157) such that the total number of clearly filmed, identifiable grips was 5,554. Because of this method of sampling a small number of grip instances for each monkey over many monkeys, the results provide a description of the natural range of grip in a population, not in an individual. It is possible that individual monkeys had a smaller grip repertoire than we observed in the population.

Methods

Subjects

Video was collected on 157 semi-free-ranging adult rhesus macaques (*Macaca mulatta*) as well as an unspecified number of semi-free ranging infants all living on the island of Cayo Santiago. Because all adults in this population are tattooed, it was possible in post-analysis to determine the identity, sex, age, and number of adults in the video footage. The infants, however, are not tattooed and therefore the identity, sex, and number of infants on the video footage cannot be determined. The video footage included

90 adult females and 67 adult males from six different social groups. Subject ages ranged from less than a year to 22 years old. This research was conducted according to the guidelines set out by the Caribbean Primate Research Center, National Institutes of Health and the University of Puerto Rico Medical Sciences Campus Institutional Animal Care and Use Committee.

Field site

The field site was the 15.2 ha island of Cayo Santiago which lies 1 km off the South-East coast of Puerto Rico (for a comprehensive description of the island see Rawlins and Kessler 1986). Occupied by an introduced population of semi-free-ranging rhesus macaques (*M. mulatta*) since 1938, the island now contains approximately 950 monkeys living in naturally formed social groups. All animals are direct descendants of the original 409 monkeys imported from India (Caribbean Primate Research Center 2007). The animals live in semi-wild conditions. They are fed a diet of monkey chow that they themselves supplement with grass, fruit, flowers, and dirt. Water is available ad libitum from dispensers. There are no predators, and there is no medical intervention by vets, hence the term semi-free-ranging.

Data collection

A total of 15 h of monkey-grasp video footage was collected between 7:00 am and 2:00 pm each day, 17 July to 2 August 2007. This time-period encompassed the end of the breeding season. Video was collected ad libitum (Altmann 1974) using a handheld digital video camcorder (Panasonic PV-GS320). Due to the difficulty filming a particular subject's grasping behavior for any length of time before the subject moved away or turned its back, ad libitum sampling was the most appropriate method for assessing macaque grasp in a large population. Subjects were filmed as they grasped objects during their normal daily behavior. Video footage was recorded from a distance with a zoom lens and all effort was made not to interact with the subjects. No objects were introduced by the experimenters, and except for monkey chow (supplied by island caretakers), all the gripped objects were naturally found in the environment. Subjects were filmed both on the ground and in trees. Every effort was made to film as widely as possible in different parts of the island.

Grip classification

The video sample was analyzed frame-by-frame using Final Cut Pro (Apple Computer Inc.). Every instance of a grip of an object was examined. Grips were classified by areas of skin surface contact (see "Results"). It was usually possible to determine the surface areas of contact by studying the sequence of video frames throughout a grip. However, in some cases, due to occlusion by other objects, the exact surface areas of contact were not determinable. The final data set on grip types included only grips that could be unambiguously identified. Therefore, it is likely that many low frequency grip types were not reported and the actual variety of grasp is probably even greater than described.

For each grip analyzed, a single still frame was stored to represent the best available visual image of that grip. Some of these still frames are provided in the figures throughout the results. It is important to note, however, that these still frames do not contain as much information as the sequence of frames throughout a grip. The still frames may appear ambiguous in cases when the video was not.

Monkeys often performed a series of many mechanically different grips on one object. For example, a piece of food might be picked up in the hand in one type of grip, transferred to the mouth, transferred back to the hand, turned in the hand to a different grip configuration, and so on. As far as was possible given the ambiguities of the video record, we separated the sequence into individual grips performed at different moments in time and classified each grip as a separate instance. In some cases, however, it was not possible to fractionate the video into separate grips at separate moments in time. Sometimes monkeys performed more than one grip at the same time (for example both the hand and the mouth gripping an object). We therefore classified grips into simple (one grip applied to one object at one time) and complex (multiple grips applied to one object or several objects). This classification is described in greater detail in the Results section in the description of the specifics of grip types.

Terminology used to classify grip types

Figure 1 shows a labeled diagram of a macaque hand. Digits are labeled one through five. In the hand, *thumb* is used interchangeably with *digit 1*. *Palmar* and *dorsal* refer to the front and back of the hand, *plantar* and *dorsal* to the front and back of the foot. *Ulnar* and *radial* refer to the two bones of the forearm. The ulnar side of the hand includes the fifth digit. The radial side of the hand includes the first digit. Individual digits each have corresponding ulnar and radial sides. The *phalanges* are the bones of the digits. The first digit is made of two bones, a proximal and distal phalanx. The other digits each consist of three bones, a proximal, middle and distal phalanx. Each digit has a digital pad on its tip. The palm of the hand has a *thenar* pad on the side of the thumb and two *hypothenar* pads on the side of the fifth digit. The digits can move in several ways: they can flex, extend, abduct (move away from an imaginary line drawn through the third digit) and adduct (move

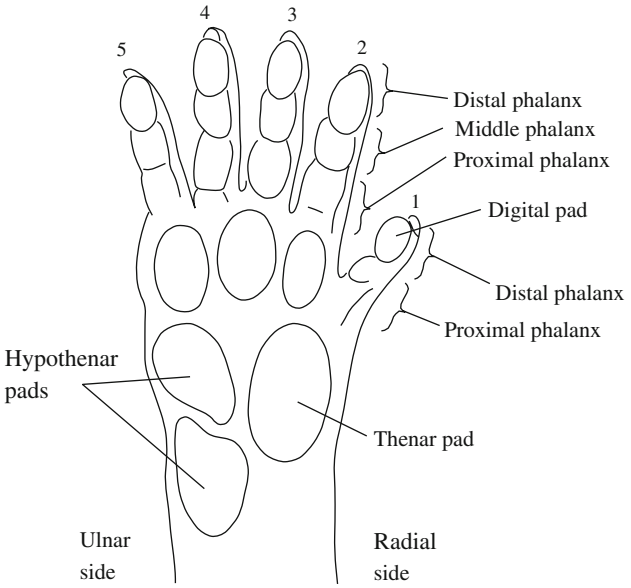


Fig. 1 Drawing of palm-side view of a macaque monkey hand with surfaces labeled. The types of grip were categorized by the hand surfaces that were used to contact the gripped object

towards the same line). The thumb can also rotate so that its palmar side opposes the other digits.

Results

The 5,554 classifiable grips observed in the video record fit into two broad functional categories: manipulation of objects (5,274 instances, 95%) and climbing (280 instances, 5%). This imbalance in number reflects the fact that the monkeys spent most of their time on the ground manipulating objects. The manipulation grips could be further divided into simple grips, in which a single object was held by a single grip (3,441 instances, 62% of total grips), and compound grips, in which multiple grips were applied to an object or several objects at the same time (1,833 instances, 33% of total grips).

Simple grips used for manipulation

Figure 2a shows the categories of simple manipulation grips, based on the area of skin contact on the gripped object. The grip types are shown in order of decreasing frequency. Many low frequency grip types were probably missed and therefore the full repertoire is probably larger.

Pad-to-side grip

The pad-to-side grip (Fig. 3a) was the most common grip we observed, appearing 992 times, or 28.8% of the total number of simple manipulation grips. It involved a precise pinching of an object between digits 1 and 2. In the pad-to-side grip, the distal pad of the thumb opposed the radial side of the second digit. In the prototypical example, the point of contact was at the distal knuckle of the second digit, but some flexibility existed, and the opposition ranged anywhere along the side of the middle and distal phalanges of the second digit. Figure 3a shows a small ball of clay being held, but this grip was used to manipulate many different kinds of small objects including blades of grass, pieces of fruit, and monkey chow.

Pad-to-pad grip

Another high frequency grip, the pad-to-pad grip (Fig. 3b) appeared 921 times, comprising 26.8% of the total of simple manipulation grips. In this grip the distal pads of the first and second digit were perfectly opposed, with a large area of pulp-to-pulp contact. The point of opposition varied, with some instances being held between the very tips of the digits while others covered the entire palmar sides of the distal phalanges. When contact was between the very tips, the digits were partially flexed. As the digits extended, the focus of opposition moved to cover the entire distal pads. Figure 3b shows the grip being used to pull apart hair during grooming. Other commonly held objects were pieces of grass or small bits of dirt.

Thumb-to-second/third grip

In the next grip type (Fig. 3c), the second and third digits worked together in opposition to the thumb. This grip appeared 528 times, comprising 15.3% of the total of simple manipulation grips. In this grip, the palmar side of the thumb opposed the palmar sides of the second and third digits. On the thumb, the point of contact centered over the distal phalanx. On the second and third digits, the point of contact generally included the distal and middle phalanges but sometimes spilled over to the proximal phalanges for larger objects. The thumb could be fully extended (Fig. 3c) or partially flexed. Medium-sized objects, such as pieces of fruit or monkey chow, were frequently held this way.

Hand wrap

Another high frequency grip, the hand wrap (Fig. 3d, e) appeared 421 times, comprising 12.2% of the total of simple manipulation grips. In this grip the four parallel fingers wrapped tightly around an object in a fist shape. The grip involved the palmar side of the entire hand and held the object firmly. Since the hand contoured the object, object circumference created a continuous range of hand wraps. Figure 3d shows one end of the continuum where a larger object was held. The thumb was positioned such that

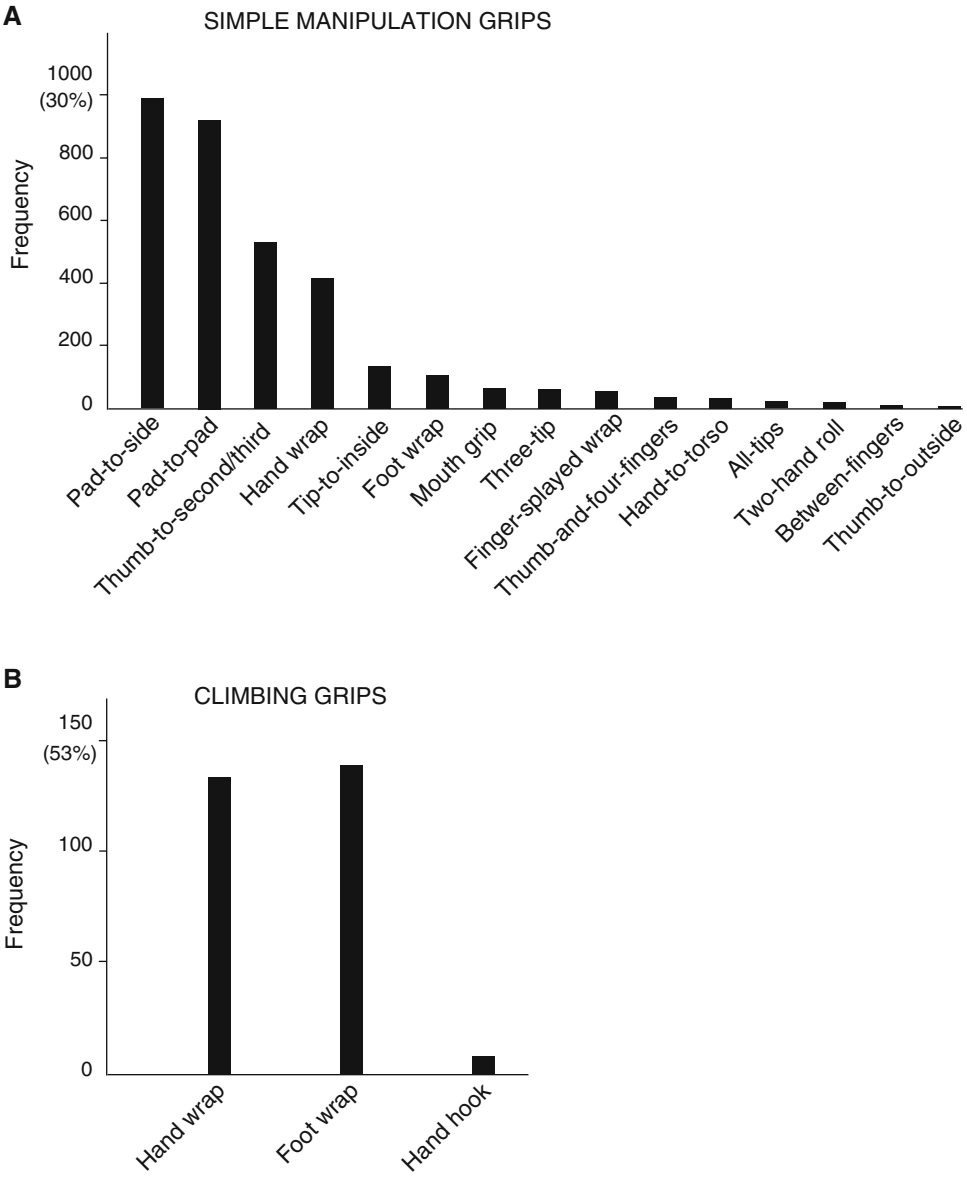


Fig. 2 Categories of grip and their frequency of use. **a** Categories of simple grip (one object in one gripper) used during manipulation of objects. Frequency is shown both as an absolute number and as a percent of the total number of simple manipulation grips. **b** Categories of grip used during climbing. Frequency is shown both as an absolute number and as a percent of the total number of climbing grips

it completely opposed the four parallel fingers. As a result of the object size, the hand could not completely encircle it, and the digits were only slightly flexed.

Figure 3e shows an example from the other end of the continuum with a smaller object. In this case, the twig contacted only the phalanges of digits 2–5, which were fully flexed and rolled-up into a fist shape. The phalanges alone completely encircled the twig. The rest of the hand curled around these phalanges, bracing them. Thus, the distal palm of the hand and the thumb were involved in the grip, but only to provide indirect object contact.

Tip-to-inside grip

The tip-to-inside grip (Fig. 3f) appeared 138 times, comprising 4.0% of the total of simple manipulation grips. In this grip, the tip and distal pad of the thumb opposed the palmar side of the second digit's middle and distal phalanges. In general, the second digit flexed around the object, while the thumb remained extended. The exact extent of the thumb's distal pad that made contact with the object varied somewhat among different instances of this grip. Figure 3f shows an example where a monkey held a small piece of clay. This grip was used for many different small to medium-sized objects.

Foot wrap

The foot wrap appeared 104 times, comprising 3.0% of the total of simple manipulation grips. Figure 3g shows a prototypical foot wrap where the entire plantar side of the first digit opposed the plantar surface of digits 2–5 and the distal sole.

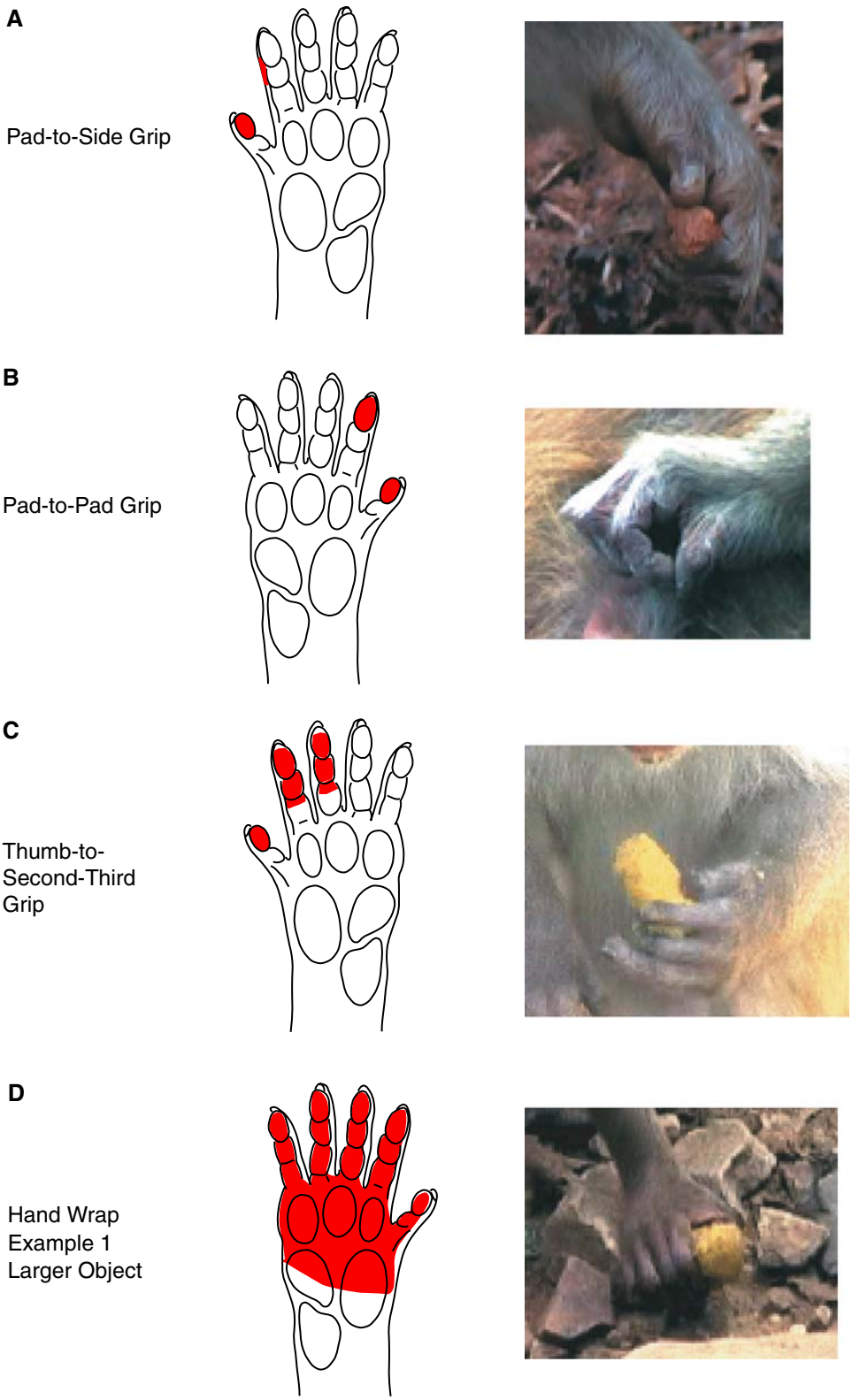
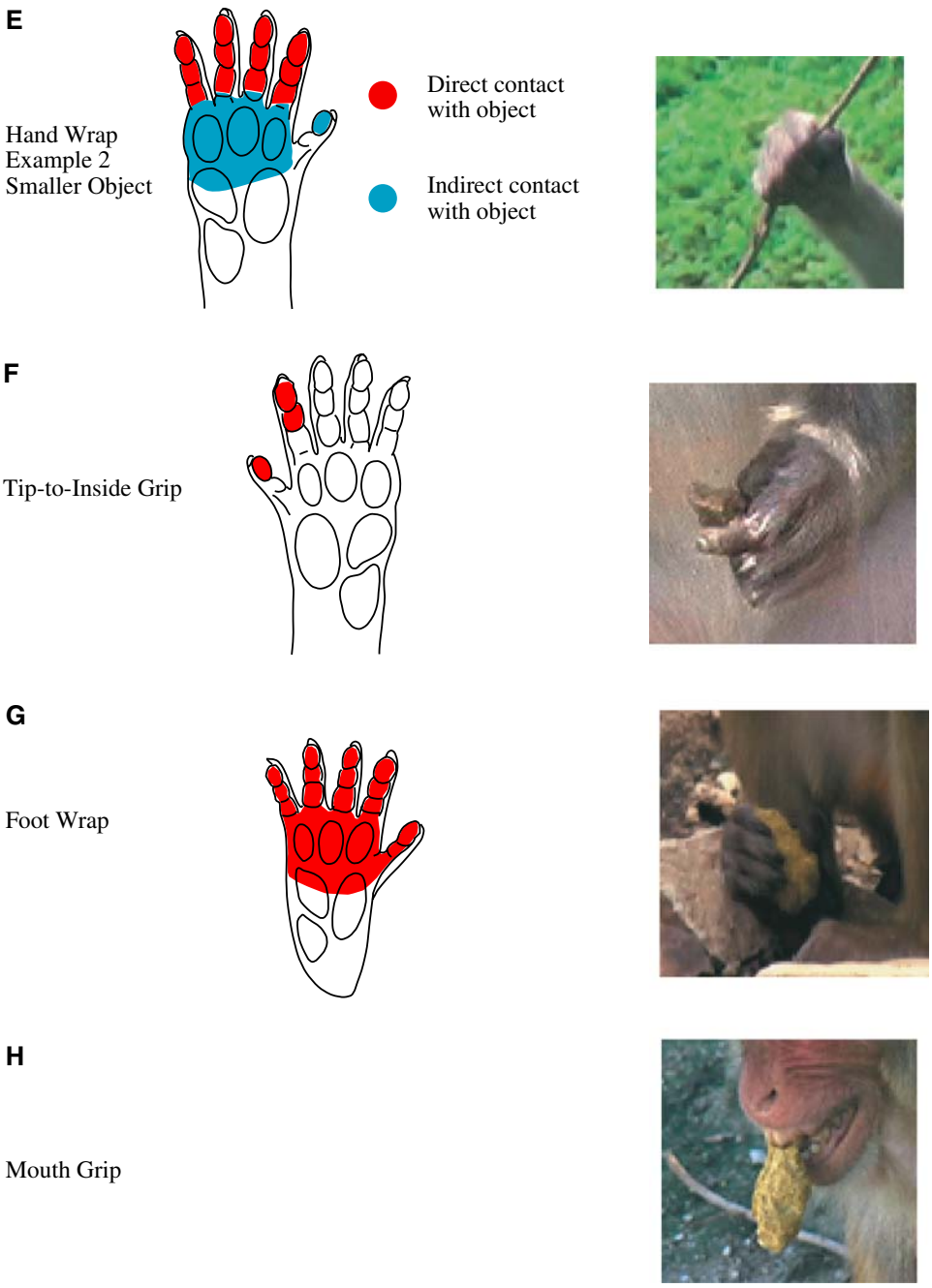


Fig. 3 Simple grips used during manipulation of objects. For each grip type, the surface area of contact is shown in *red* on the hand diagram, and a photo of a typical example is shown

We never observed a monkey manipulating an object with this grip; it was used only for holding. Often a monkey would manipulate an object with its hands, then pass it off to a foot wrap while it manipulated a new object in the hands, then retrieve the first object from the foot to continue manipulating it with the hands. Monkey chow was by far the most common object held in this way.

Fig. 3 continued



Mouth grip

The mouth grip (Fig. 3h) occurred 68 times, comprising 2.0% of the total of simple manipulation grips. In this grip, the monkey held an object in its mouth either between the teeth or loosely between the lips. This was not an instance of the teeth biting down in order to chew or break a piece of food. Rather objects were held in the mouth while the monkey moved around or if its hands and feet were otherwise occupied. Objects held in a mouth grip ranged in size from a small piece of chow (Fig. 3h) to a coconut held by the husk.

Three-tip grip

The three-tip grip (Fig. 3i) occurred 64 times, comprising 1.9% of the total of simple manipulation grips. In this grip, the tip of the thumb opposed the tips of the second and third digits. In the prototypical example shown in Fig. 3i,

Fig. 3 continued

I

Three-Tip Grip

J

Finger-Splayed Wrap

K

Thumb-and-Four-Fingers Grip

L

Hand-to-Torso Grip

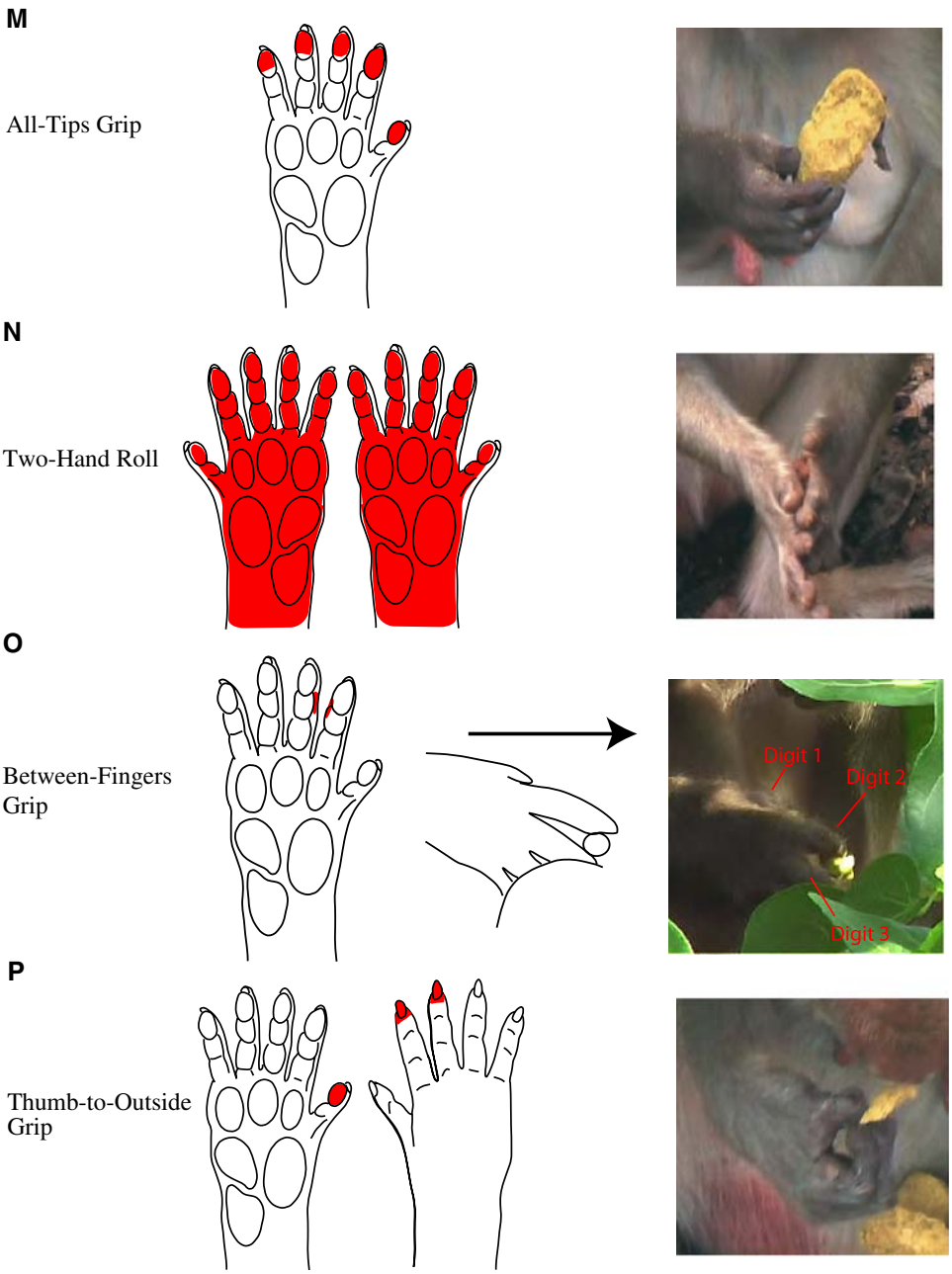


Fig. 3 continued

the monkey held a small rock. Objects of that size were by far the most common ones held this way.

Finger-splayed wrap

The finger-splayed wrap (Fig. 3j) appeared 62 times in our sample, comprising 1.8% of the total of simple manipulation grips. Like the hand wrap, this grip involved the entire palmar surfaces of the five digits and hand. In the hand wrap, digits 2–5 were pressed against each other, acting as a single unit, and the object was held by means of an opposition between the fingers as a whole and the palm, or between the fingers as a whole and the thumb. In the finger-splayed wrap, in contrast, the fingers were separated and spread around the object, and therefore the object was held by means of a five-way opposition among all the fingers. Figure 3j shows an example where a monkey held a large rock with a finger-splayed wrap.

Thumb-and-four-fingers grip

The thumb-and-four-fingers grip (Fig. 3k) appeared 42 times in our sample, comprising 1.2% of the total of simple manipulation grips. In this grip, the thumb was positioned

to oppose the four fingers. The object was held between the palmar sides of the five digits without touching the palm of the hand. The main distinction between this grip and the hand wrap is that the palm did not contact the object. Contact with the thumb centered on the distal phalanx, with the focus closer to the tip. Digits 2–4 generally contacted the object completely, from the tips all the way down to the middle of the proximal phalanges. Given its smaller size, digit 5 generally had a smaller range, only touching the object between its tip and middle phalanx. Figure 3k shows an example where all five digits were lightly flexed in order to contour the object. This grip was commonly used to hold pieces of fruit or chow.

Hand-to-torso grip

The hand-to-torso grip (Fig. 3l) occurred 35 times in our video sample, comprising 1.0% of the total of simple manipulation grips. In this grip, the palm supinated, the digits spread, and a basket shape was made where the ulnar side of the hand and forearm met the torso. Objects were squeezed between the hand or forearm and the torso. Often five to ten objects would be held there at once, some only contacting the body indirectly via another object. The hand-to-torso grip was most common with pieces of monkey chow; however, we observed instances in which an adult female used the grip to hold an infant monkey. Despite the fact that multiple objects were sometimes held, the hand-to-torso grip was not classified as a compound grip because the collection of objects was effectively treated as a single continuous object held using a single opposition between two body parts. In this sense it was a single grip performed on something that acted mechanically as (and often was) a single object.

All-tips grip

The all-tips grip (Fig. 3m) occurred 27 times in our video sample, comprising 0.8% of the total of simple manipulation grips. In this grip, the monkey held the object between the tips of all five digits. The thumb opposed the other digits. Opposition focused on the digit tips but could also involve the pads of the distal phalanges. Digits 2–5 were adjacent to each other or slightly spread, and the degree to which the thumb rotated into complete opposition varied slightly. Figure 3m shows an example in which a monkey used the all-tips grip to hold a piece of chow.

Two-hand roll

The two-hand roll (Fig. 3n) appeared 23 times, comprising 0.7% of the total of simple manipulation grips. It involved the object being rolled back and forth between the facing palmar sides of both hands. The range of object contact extended from the tips of the parallel digits down the entire length of the hand and even included the distal forearm. The hands were always moved in opposite directions. The movements were not necessarily only along the long axis of the hand, but sometimes side to side as well. Objects manipulated in this way varied in size from a small piece of dirt (Fig. 3n) to a large coconut. This behavior seemed mostly to be used for cleaning or sloughing the sides off an object. Even though the two-hand roll involved both hands, it was classified as a simple grip because it included a single opposition between two body parts. It was mechanically a single clamp placed on an object.

Between-fingers grip

The low frequency between-fingers grip (Fig. 3o) appeared 12 times in our video sample, comprising 0.3% of the total of simple manipulation grips. The photograph in Fig. 3o is partially occluded and shadowed, but the hand can be distinguished (an outline of the hand is also shown) and the sequence of adjacent video frames further clarified the grip. Unfortunately, with so few instances of the between-fingers grip, we were not able to find a better still frame for it. In the between-fingers grip the object was pinched between the adjoining sides of two parallel digits, most often the second and third (like a cigarette grip in a person). Figure 3o shows a monkey holding a small piece of fruit. Other small diameter objects, such as twigs, were also held in a between-fingers grip.

Thumb-to-outside grip

The thumb-to-outside grip (Fig. 3p) occurred only four times in our video sample, comprising 0.1% of the total of simple manipulation grips. In this grip, the palmar pad of the thumb's distal phalanx opposed the dorsal side of the second and third digits' distal phalanges, on top of the nails. All three digits were almost fully flexed. This grip was observed with small objects including slivers of chow and pieces of clay.

Compound grips

In addition to the simple grips described above where a hand held a single object, we also observed what we termed compound grips (1,833 instances), much more complex grips in which a monkey held an object with many grips simultaneously, or held many separately controlled objects in one hand.

For example, a coconut might be gripped by both hands, both feet, and the mouth simultaneously as the monkey tore

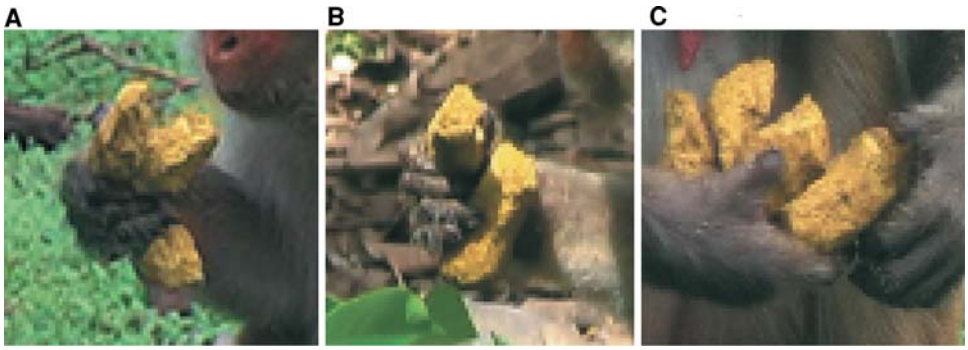


Fig. 4 Compound grips in which several objects were stored in one part of the hand while another object was manipulated in a different part of the hand

at the husk. A smaller piece of fruit might be gripped by both hands and the mouth simultaneously. In these cases of many grippers on one object, the compound grip could be described as a simultaneous use of several of the simple grips. Categorizing these complex grips more precisely was difficult because of occlusion by the many body parts and the object being gripped. Thus whether the grip involved a specific subset of, or all of, the right and left hands, right and left feet, and mouth was often not possible to determine. Furthermore, these grips had a constantly shifting quality. For example, in manipulating a coconut, a monkey might tear violently at the husk, its different grippers coming into play and then disengaging in rapid changes. With these caveats in mind, we obtained the following breakdown of complex grips.

Grips that simultaneously used the mouth and both hands accounted for 1,024 instances (56% of complex grips).

Grips that simultaneously used the two hands, but no other gripper, accounted for 500 instances (27.3% of complex grips). These compound grips were different from the two-hand roll (described above as a simple grip) in the following manner. A two-hand roll involved a single opposition between two body parts, with one object squeezed between. A compound grip involving the two hands, in contrast, included two distinct grips on the object. For example, one hand might apply a hand-wrap grip to hold an object, while the other hand might apply a pad-to-pad grip to pinch off a part of the object. The main functional advantage of applying two grips to an object, one grip in each hand, was that it allowed the animal to apply a differential force between the two grips, thereby twisting or breaking the object. In contrast, a single grip allows only for holding, squeezing, or carrying an object.

Grips that simultaneously used many grippers, often in a manner difficult to assess, sometimes involving simultaneous use of all hands, feet and mouth, accounted for 145 instances (7.9% of complex grips).

Grips in which many separate objects were held in a single hand (the one-handed storage grip) accounted for 164 instances (8.9% of complex grips). This type of compound grip was distinctive and easily identified in the video record. Some examples are shown in Fig. 4. The monkeys would hold one or more objects in a storage grip using the palm and digits 4 and 5, while at the same time manipulating another object with digits 1–3. The one-handed storage hold was functionally two grips in one hand, a storage grip and a manipulation grip that operated independently of each other.

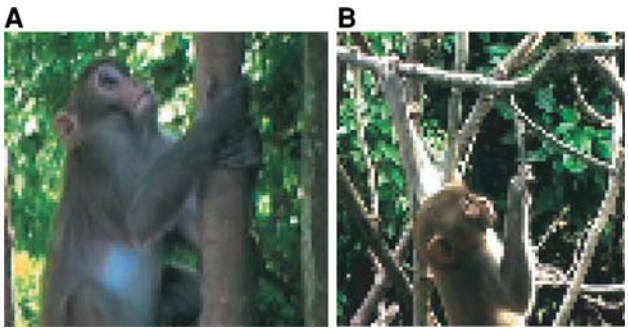


Fig. 5 Climbing grips. **a** The climbing wrap could be used for the hand or the foot. **b** The climbing hook was observed only in the hand

Climbing grips

The monkeys spent most of their time manipulating objects on the ground, and therefore only 5% of our footage included monkeys climbing. Unlike manipulation, during climbing only two different kinds of grips were observed: the climbing wrap (involving the hand or foot) and the climbing hook (involving the hand only). Figure 2b shows the relative distribution of these grip types.

Climbing wrap

Figure 5a shows the climbing wrap, by far the most common of the two functional categories, appearing a total of 273 times, 134 times in the hands and 139 times in the feet. For simplicity's sake, we will describe the grip in the hand, but it was the same regardless of whether it was a hand or foot grip. Like the power wrap, this grip

used the entire palmar surface of the hand. The thumb abducted and rotated until it partially or entirely opposed the other four parallel digits. All digits modulated their flexion and extension in order to follow the contour of the object being grasped. Thus, the subtleties of the grip depended on object size. For a large branch the hand was almost flat, but for smaller branches the hand was flexed into a fist.

Climbing hook

The climbing hook (Fig. 5b) was rare, appearing only seven times in our video sample. Unlike the climbing wrap, the climbing hook appeared only in the hand, not the foot. In this grip, digits 2–5 were held together and were flexed at the distal or middle knuckle, forming a hook from which the monkey briefly hung. In contrast to the hand wrap, the thumb did not play an active role.

Discussion

The present study cataloged the grasp behavior of macaque monkeys. The study differed from previous studies of grip in primates in three main ways. First, although grasp has been described in macaques, it has not been described or catalogued in the same detail as in humans and apes (e.g. Christel 1993; Cutkosky 1989; Kamakura et al. 1980; Kroemer 1986; Marzke and Wullstein 1996; Patkin 1981; Pouydebat et al. 2006; Spinozzi et al. 2004; Wong and Whishaw 2004).

Second, in the present study, we described spontaneous grip throughout the course of normal daily activity. In this way, the results revealed the relative proportions of grip types in the natural repertoire. In contrast, most previous studies focused on grips that primates used in a controlled setting on a limited number of introduced objects (e.g. Christel 1993; Marzke and Wullstein 1996; Pouydebat et al. 2006).

Third, the present study differed from previous studies in analyzing a larger range of grip behavior. The studies cited above examined grip of a single object in a single hand for the purpose of manipulating the object. In our sample, this type of grip comprised 58% of the total grips observed. We also considered grips between the two hands, in the mouth, in the foot, between the hand and the torso, compound grips of multiple objects, and grips used during climbing rather than during manipulation of objects. Our study therefore examined a greater range of behavior. We examined all behavior that could be considered a grip of an object.

Three specific questions were raised in the introduction and are addressed below.

Diversity of hand grips

Do macaque monkeys rely on a small repertoire of canonical hand grips, or do they use a large assortment of grips that are flexibly adapted to specific circumstances?

Classically, Napier (1956) described two canonical grip types: a precision grip for manipulation of small objects and a power grip for manipulation of larger objects. Napier pointed out that each of these two types consisted of many variants. Of the manipulation grip types that we observed, three of them involved the first and second digits coming together to pinch a small object. These grips were the pad-to-pad grip, the pad-to-side grip, and the tip-to-inside grip. These three variants are similar to the canonical precision grip. The pad-to-pad grip in particular exactly matches the classical precision grip. Together, the three variants comprised 60% of all simple manipulation grips and 44% of all grips observed.

We also observed two grip types that involved the palm and all five digits wrapping around an object: the hand wrap and the finger-splayed wrap. These two grips are similar to the canonical power grip. Together they comprised 14.0% of all simple manipulation grips and 9% of all grips observed.

These results show that the most common grips were indeed several variants of the classical precision grip and power grip. However, the monkeys had a large repertoire of less common grips involving many configurations of the fingers and many different surfaces of skin contact with the object, as well as grips that transcended a single hand. The results suggest that monkeys can flexibly produce a great range of grip types for different purposes, but that a small number of types are more common or more useful than others.

The grips during climbing seemed to have exactly the opposite character. They were stereotyped rather than flexible. We observed only two types of climbing grips: a simple climbing wrap and a hand hook. Different instances of the climbing wrap were virtually identical in hand conformation, the variance apparently caused mechanically by the size of the branch that the animal was gripping rather than by any differences in grip technique. The hand hooks were much less common, but within the small sample, they were also virtually identical.

A previous study directly comparable to the present study is Christel (1993) in which small food objects were given to primates and grips were categorized by the surfaces on the hand that contacted the object. Although macaque monkeys were not studied, a range of other primates were, and in each case a diversity of grips was reported. For example, orang-utans were reported to have 15 distinct grip types. The grip types were not described in as much detail as in the present study, but the diversity of primate grip described in Christel (1993) is consistent with the diversity reported here.

Diversity of body parts in macaque grip

Do macaque monkeys grip only with body parts that are specifically adapted for gripping (the hand, foot, and mouth), or do they show evidence of a generalized concept of grip that applies to any two body parts that can be opposed? We observed monkeys to grip objects in one hand, between the two hands, in the mouth, in the foot, and between the hand/forearm and the chest. Of these different grips, only the grip between the hand/forearm and chest suggests any real generalizing. We did not observe any monkeys gripping in the armpit, between the knees, between the chin and the chest, or between the side of the head and the shoulder. The results suggest a limited flexibility. Grip in monkeys, at least in their natural repertoire, appears to involve mainly those body parts that are mechanically adapted for gripping. It may be that monkeys lack the cognitive sophistication to invent novel ways of gripping.

Compound grips in macaques

Are macaque monkeys limited to gripping a single object in the hand at a time? We observed 164 instances of compound grips in which more that one object was gripped in the same hand. For example, a monkey might store a piece of food by gripping it between the palm and digits 4 and 5, and at the same time, in the same hand, hold and manipulate a piece of food by gripping it between digits 1, 2, and 3.

It is not surprising that a monkey holds several small objects together in one grasp. In principle, whether the object is one continuous piece, or made of several smaller pieces, the grasp could be the same. For example, the hand-to-torso grip sometimes involved one larger object (such as a baby monkey) or many small objects (such as a collection of chow). The compound grips described here, however, are different from a single grasp of many pieces. They are surprising in that more than one mechanical grasp was used in one hand at the same time. One grasp focused on the ulnar side of the hand and the second grasp focused on the radial side of the hand. These two grasps were apparently independent in the sense that, while one or several object were stored in the ulnar grip, objects could be picked up, put down, and manipulated in the radial grip. Essentially, the hand was acting like two hands, a storage hand and a manipulation hand.

The functional importance of compound grips

Monkeys sometimes grip objects for the purpose of storing them or examining them, in which case a single grip is sufficient. But examining an object is a limited advantage. It is useful to act on the object. Ideally the animal needs two grips, at two different locations on the object, such that a differential force can be applied that will alter the object.

Arguably the simplest action on an object is biting it and tearing off a piece. The mouth can be said to be the original gripper. Consider a predator such as a dog eating a carcass. If the carcass is large enough then gravity does the job of stabilizing the carcass while the dog grips and tears with its mouth. A small carcass, however, is not easily manageable in this manner and the dog resorts to a double grip. One grip is between a forepaw and the ground, pinning and stabilizing the object. The other grip is between the teeth. A predator such as a dog or lion therefore can be said to have a two-grip manipulation of objects that involves an interaction between the forepaw and the mouth.

Animals that sit on their hindquarters can achieve a more controlled grip by opposing the two forepaws. Squirrels for example sit on their haunches and hold a seed (or French fry) between the pads of their forepaws while chewing it. Here again is a two-grip action on an object. The differential force introduced between the mouth grip and the two-paw grip allows pieces of the food to be bitten off. Furthermore, the object can be rotated or adjusted in the two-paw grip to aim different parts of it at the mouth. Manipulation of objects in this framework is still focused on the mouth and interactions between the forepaws and the mouth.

In primates grip becomes more complex yet. Opposability is possible not only between the two forepaws, but between separate elements on a single forepaw. This advance is major because it allows a two-grip manipulation that does not include the mouth. Each hand can independently grip an object. A differential force can then be applied between the two hands, twisting the object, tearing it, or breaking it. The manipulation of objects can become dissociated from the mouth.

As found in the present study, monkeys (and certainly humans) are capable of even more flexibility by apply two grips within a single hand. In essence it is possible to hold an object with one grip and twist it with a second grip, all within the digits of one hand.

Range of grasp in natural behavior

There is a certain tendency in the neuroscience literature on the control of grip to focus on the grip of one hand on one object for the purpose of acquiring the object. If there is a fundamental message of the present study, it is that grip in macaque monkeys is more diverse. Simple hand grips of single objects did actually comprise 58% of all grips that we observed. However, a range of other grips was also observed. It is worth remembering that the mouth and foot are also used as grippers. The foot is different from the

hand in that it is used for storage but apparently not for manipulation. Grip can involve other body parts such as the forearm against the torso. It can involve multiple grips at the same time, even multiple grips in the same hand at the same time. It is also worth remembering that grip is not limited to the acquisition or manipulation of objects; it is also used for climbing. Climbing grips are fundamentally different from manipulation grips, in that they are more stereotyped and repeated with fewer variants. There is no previously published account of this full range of grasp in the natural behavior of macaque monkeys. The purpose of the present study was to provide this basic description.

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