

Reaching and grasping behavior in *Macaca fascicularis*: a kinematic study

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Abstract The prehensile hand is one of the major traits distinguishing primates from other mammal species. All primates, in fact, are able to grasp an object and hold it in part or entirely using a single hand. Although there is a wealth of behavioral data regarding grasping movements in humans and apes, there is relatively little material on macaques, the animal model often used to investigate neuronal mechanisms responsible for grip control in humans. To date, evidence regarding free-ranging macaques is confined to observational data, while quantitative reports describe studies carried out in laboratory settings or in captivity. The purpose of the present study was to provide the first kinematic descriptions of basic grip behavior with regard to precision and power grips in free-ranging macaque monkeys. Video footage of those animals grasping objects was analyzed frame-by-frame using digitalization techniques. The results revealed that the two types of grips considered are each characterized by specific kinematic signatures. It was also found that hand kinematics was scaled depending on the type of grasp needing to be adopted and the intrinsic properties of the object to be grasped. In accordance with data concerning humans, these findings indicate that the intrinsic features of an object affect the planning and control of reach-to-grasp movements even in free-ranging macaques. The data presented here take research in the field of comparative reach-to-grasp kinematics in human and non-human primates another step forward as they are based on precise

measurements of spontaneous grasping movements by animals living/acting in their natural environment.

Keywords Reach-to-grasp · *Macaca fascicularis* · Kinematics · Primatology

Introduction

One of the hallmarks of humankind is the ability to perform a complex repertoire of manual grips (Marzke 1994). Grasping in humans and apes was first described in Napier's landmark work concerning precision and power grips (Napier 1956, 1961): Precision grips mainly involve the tips of the forefingers and thumbs to hold small objects. Power grips, instead, involve wrapping all four fingers and the palm around an object to hold larger objects.

A number of studies have addressed a variety of grasping behaviors in monkeys and apes (e.g., Christel 1993; Pouydebat et al. 2006; Spinozzi et al. 2004), but only a few have focused on the macaque species (Pouydebat et al. 2006; Macfarlane and Graziano 2009), an animal model that is often used to study the neuronal mechanisms underlying the control of grip in humans (for review see Castiello 2005).

Some comparative kinematic studies on grasping behavior in the human species and in macaques living in captive, non-natural conditions have been carried out to investigate the similarities and differences existing across the two species (Fogassi et al. 1991; Christel and Billard 2002; Roy et al. 2000, 2002, 2006; Pouydebat et al. 2009; Sacrey et al. 2009; Jindrich et al. 2011).

A large part of the data from these studies indicates similarities in hand shaping across species (Fogassi et al. 1991; Christel and Billard 2002; Roy et al. 2000, 2002,

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2006; Sacrey et al. 2009). More specifically, hand aperture appears to be scaled depending on the object's size (e.g., Fogassi et al. 1991; Roy et al. 2000). Total movement time is affected by the size of the object to be grasped as reaching to grasp a small object takes longer than reaching to grasp a larger one (e.g., Fogassi et al. 1991; Roy et al. 2000). When differences across types of grasping (i.e., precision vs. power grips) are considered (Fogassi et al. 1991), peak wrist velocity is lower and the moment when the animal's fingers start to close around an object is anticipated, just as in humans, during precision (i.e., small objects) compared to power grip movements (e.g., Gentilucci et al. 1991; Castiello 1996).

As far as differences are concerned, not all general features characterizing human action were also noted in the animals. Roy et al. (2000) reported that in monkeys the amplitude of arm peak velocity and the time of maximum grip aperture appeared to be similar regardless of the size of the object to be grasped. In humans, the amplitude of peak velocity is higher, and the time of maximum grip aperture occurs later for larger compared to smaller objects (e.g., Gentilucci et al. 1991; Jakobson and Goodale 1991). Other authors noted relevant kinematic irregularities in the velocity and acceleration profiles of arm movements with a greater instability of posture and joint kinematics in macaques compared to humans (Christel and Billard 2002).

Although these studies seem to favor the hypothesis that macaques and humans share a number of kinematic features, important differences have been noted and the debate continues to unfold. Some investigators have distinguished between different types of grips but have studied only a single exemplar (Fogassi et al. 1991). Working with only a limited number of subjects, others did not distinguish between the types of grips being used by the animals even if the objects being handled clearly required different types of grips (Roy et al. 2000, 2002, 2006). Other investigators focused exclusively on precision grip movements (e.g., Christel and Billard 2002) or pincer grasps (Sacrey et al. 2009).

In view of the limited number of animal exemplars studied, the constrained conditions in which these were tested, the fact that the objects used in those experiments were so very different (i.e., food, perspex cylinders), the data available are insufficient to draw any definite conclusions. This work, which studies the kinematics of reach-to-grasp movements by free-ranging macaque monkeys handling small and/or large objects requiring, respectively, precision and power grips, attempts to answer some of these questions. Although many grips carried out by the macaques during filming did not fit into the simple power and precision grip categories, our analysis was nevertheless confined to those two grips in order to render our data

comparable with previous laboratory findings and literature on human subjects.

Materials and methods

Study species

Twenty adult *Fascicularis* macaques (*Macaca fascicularis*), all belonging to a single free-ranging troop made up of 65 animals living in Pulau Besar, Langawi, Malesia, were studied.

Data collection

A total of 10 h of video footage was filmed between 10.00 a.m. and 14.00 p.m. daily from November 2 to 27, 2008. The video was filmed ad libitum using a digital camcorder. In view of the difficulty in filming any particular monkey grasping an object for any length of time before it moved away or turned its back, ad libitum rather than all-occurrence sampling was considered the most appropriate method to assess this behavior in natural conditions (Altmann 1974). The monkeys were all filmed standing or sitting on the ground as they grasped objects during normal daily behavior. Every effort was made to avoid contact with them, and the video footage was consequently filmed from a distance. In particular, a zoom lens was used as to maintain the focal length constant for the entire recording session. Only reaching and grasping movements performed on a plane perpendicular to the camera axis and with the animal lying in the central part of the image were selected for further processing. As it is well documented in the literature concerning both humans (e.g., Gentilucci et al. 1991) and macaques (e.g., Roy et al. 2000) that a large part of reaching and grasping movements take place in the sagittal plane, this methodology was followed to avoid the presence of motion artifacts. All the objects that were gripped/grasped were naturally found in the environment and were not introduced by the experimenters.

Grip classification

The data included in our analysis exclusively regarded grasping that could be unambiguously identified and classified according to the skin surface areas that contacted the object. It was possible to determine the surface areas contacting the object by analyzing the video frame sequences. As explained above, although all grasping movements were analyzed, our study focused on precision and power grips (Fig. 1). As already outlined, precision and pinch grips refer to all types of grips used for fine manipulation involving the thumb and the index finger.

Used to manipulate small objects such as seeds, soil fragments, or blades of grass, the distal pad of the thumb is opposed to the radial side of the index finger during pinch grip tasks. Used to manipulate large objects such as stones or pieces of fruit, all four fingers and the palm are wrapped around an object in one direction while the thumb is wrapped around it in the opposite one during a power grip task. In natural environments, spontaneous movements do not necessarily fit into the classical power and precision grip categories: At times three fingers are involved, and at others various finger combinations are utilized often changing fluidly from one configuration to another. For the sake of comparison, the movements most closely resembling those studied in laboratory experiments were selected and further analyzed (Fogassi et al. 1991). The video sample was analyzed frame-by-frame (frame duration: 20 ms) using an in-house software developed to perform post hoc kinematical analysis (Castiello et al. 2010; see “Data analysis” section).

Data analysis

The video footage was transferred to an in-house software developed to perform two-dimensional (2D) kinematic analysis. Care was taken to compare only those movements that were carried out while the animals were in a sitting position (i.e., with the elbow flexed and the torso bent forward) and that were characterized by similar hand–object distances (20 ± 0.3 cm). That position (Fig. 1) was chosen because it facilitated comparison across kinematic studies on humans (e.g., Gentilucci et al. 1991) and macaques (e.g., Fogassi et al. 1991; Christel and Billard 2002; Roy et al. 2000). To avoid any skewing effect, only reaching and grasping movements performed along a plane

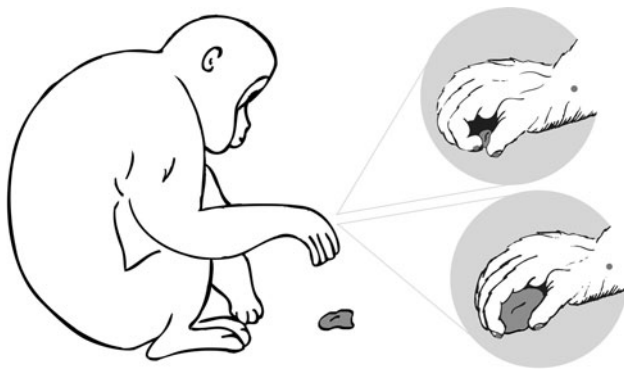


Fig. 1 Schematic drawing representing the posture adopted by the animal during the reach-to-grasp movement and the positioning of the markers upon the digits for the purpose of digitalization. Markers were located (post hoc) on the wrist, and the distal phalanx of the thumb and index finger. In the *upper panel* a precision grip involving the tip of the forefinger and thumb to hold small objects is represented. In the *lower panel* a power grip involving wrapping all four fingers opposite to the thumb to hold larger objects is represented

perpendicular to the camera axis were analyzed. A frame of reference identifying X and Y axes as horizontal (ground) and vertical directions was manually set by an operator. A known length, selected case by case, in the camera’s field of view and in the same plane as the movement was used as the measurement reference unit. As shown in Fig. 1, markers were then made on each subject’s wrist to indicate the reaching component and on the nails of the index fingers and the thumbs to indicate the grip aperture as a function of time. The starting position was defined as the right hand resting on the ground in between the legs. The hand starting area for the selected movements was similar across subjects (± 0.3 cm²). Initiation of movement was defined as zero wrist velocity. The end of the movement was defined as the moment when the hand grasped the object. The analysis procedures were performed manually and post hoc by a single analyst. Movement tracking procedures were then performed in order to extract a number of kinematic parameters based on spatial and temporal indexes. In accordance with the previous grasping kinematical studies in monkeys and humans (e.g., Roy et al. 2000; Gentilucci et al. 1991; Jakobson and Goodale 1991), the following dependent measures were considered: (1) the total movement duration from the time the subject started the action to the time its hand grasped the object; (2) the time from wrist peak velocity to the end of the movement (deceleration time); (3) the time when the maximum grip aperture occurred (the maximum distance between the thumb and the index finger); and (4) the maximum grip aperture amplitude (the maximum distance between the thumb and the index finger). In accordance with the observation protocol, the laterality quotient (LQ) was 75 (± 12) with a LQ of 100 reflecting a full right-hand preference. In order to facilitate comparison with human data, only right-hand grasping movements made to pick up one of two kinds of objects—small balls of clay ~ 1 cm for precision grips and round stones ~ 4 cm for power grips—were analyzed. These particular objects were chosen because they resembled those used in the previous studies on humans and macaques (i.e., spherical objects). All of the objects that were assessed were indigenous to that area and were not introduced into the environment by the experimenters. Food items were not considered because monkeys typically do not pause to grasp those objects but carry out continuous joint movements as they grasp and take food to their mouths. Fifty movements for each of the two types of grasping movements (precision and power grips) studied were selected and analyzed for each of the subjects studied. A repeated-measures analysis of variance (ANOVA) was carried out to compare the type of movement (precision grip; power grip) for each dependent measure. Temporal measures were considered in both absolute and relative terms (i.e., as a percentage of total movement duration).

Results

Literature findings in humans consistently indicate that, with respect to whole hand (power) grips (e.g., Castiello 1996; Gentilucci et al. 1991), precision ones are characterized by a longer movement duration, a prolonged wrist deceleration time, a lower wrist peak velocity amplitude, and an anticipated and lowered amplitude of maximum grip aperture. No differences in the times to peak wrist velocity regardless of the type of grasp are usually found. In the same way, in macaques, the reaching component was characterized by a bell-shaped wrist velocity profile with single peaks occurring at 52 and at 53 % of the total movement times for precision and power grips, respectively ($F(1, 19) = 1.41, P > 0.05$). Nor were peak latencies for the two grip types significantly different when the absolute time was considered (202 vs. 207 ms; $F(1, 19) = 2.05, P > 0.05$). The total duration of reach-to-grasp movements did vary when the two types of grasping were compared (precision grip = 412 ms; power grip = 388 ms; $F(1, 19) = 10.22, P < 0.01$). The deceleration time was longer for the precision than for the power grip movements ($F(1, 19) = 12.23, P < 0.01$; 205 vs. 186 ms; Fig. 2a). The peak velocity amplitude was higher for the power than for the precision grip movements ($F(1, 19) = 35.27, P < 0.001$; 1,112 vs. 876 mm/s; Fig. 2a). The grasping component was characterized by a maximum grip aperture, which occurred at 71 and 75 % of the total movement time for the precision and power grips, respectively ($F(1, 19) = 42.18, P < 0.0001$). The latency of this peak varied across grip types also in absolute terms (precision grip = 275 ms; power grip = 302 ms; $F(1, 19) = 12.11, P < 0.01$; Fig. 2b). The maximum grip aperture amplitude was affected by the type of grasping ($F(1, 19) = 38.23, P < 0.0001$; Fig. 2b). On average, the animals adopted a smaller grip aperture amplitude when they grasped a small object using a precision grip compared with movements in which they grasped a larger object using a power grip (2.8 vs. 5.5 cm, respectively; Fig. 2b).

Discussion

The aim of this study was to investigate the kinematic parameterization of unconstrained reach-to-grasp movements in macaque monkeys. It differs from previous kinematic studies on macaques because it focuses on spontaneous grasping movements during free-ranging daily activities in the animals' natural environment. Most previous studies have, instead, focused on animals in controlled settings manipulating a limited number of foreign objects introduced by the investigators themselves (Fogassi

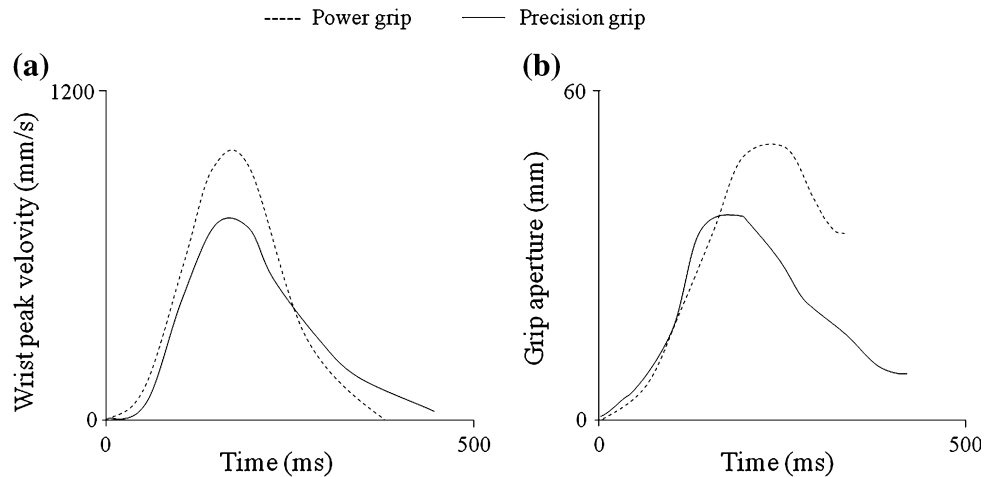
et al. 1991; Christel and Billard 2002; Roy et al. 2000, 2002, 2006; Pouydebat et al. 2009; Jindrich et al. 2011).

Important neurophysiological data concerning prehensile movements can be gathered from studies on cortical representations of hand movements in the inferior parietal lobe and in the ventral premotor cortex (for review see Rizzolatti and Luppino 2001). In experiments outlined in those studies, functional properties of F5 neurons (area F5 is connected with the hand field of the primary motor cortex) were assessed using a series of single-unit recordings in macaque monkeys. Those experiments showed that the activity of F5 neurons is correlated with specific distal motor acts and not the execution of individual movements, with grasping-with-the-hand neurons forming the largest class of F5 neurons. As F5 neurons become active only if a particular type of action (e.g., grasping) is executed to achieve a particular kind of goal (e.g., to take possession of food), the hypothesis of a "motor vocabulary" according to which each "word" corresponds to a category of motor neurons that represents the way in which an action or one of its temporal segments is executed was formulated in order to conceptualize the function of those neurons (Rizzolatti et al. 1988). There also seems to be a strict relationship between the type of prehension coded by a neuron and the physical characteristics of the stimulus triggering a visual response (Rizzolatti et al. 1988; Gallese et al. 1994; Fogassi et al. 2001).

The data outlined here seem to indicate that when an animal accesses its "motor vocabulary" to execute prehensile actions in a situation without constraints, its kinematics reflects a natural matching between the type of grip to be adopted and the physical characteristics of the object to be grasped. A lower wrist peak velocity amplitude, a longer movement and deceleration time, an anticipated peak in the maximum grip aperture, and a smaller grip aperture amplitude during precision as compared to power grips were noted in the free-range macaques observed. Like humans, macaques seem to be able to alter their movement patterning depending on the grip needing to be adopted.

Our findings on a large sample of subjects mirror those described by Fogassi et al. (1991) in a single exemplar whose grasping movements were similar to human ones (e.g., Gentilucci et al. 1991), but they differ from a laboratory study in which the authors did not find differences in the amplitude of peak velocity and the time of maximum grip aperture depending on object size (e.g., Roy et al. 2000). These differences might have been due to the types of stimuli adopted. Fogassi et al. (1991), in fact, had the animal interact with different-sized objects eliciting different types of grasping (i.e., precision grip and whole hand grasp), just as occurs in natural contexts. In other studies (e.g., Roy et al. 2000, 2002), instead, the size of the objects to be grasped may not have determined differences in the

Fig. 2 Panel **a** shows wrist peak velocity for power and precision grip movements in a representative subject ($N = 6$). Panel **b** shows grip aperture for power and precision grip movements in a representative subject ($N = 6$)



prehensile action, and to date, how animals grasp objects has not been clearly delineated.

Due to the difficulty in carrying out systematic studies in unconstrained conditions, little is known about how non-human primates organize natural grasping actions. Using the experimental protocol outlined here, it was possible to examine the animals' natural behavior in their normal habitat utilizing an experimental paradigm (post hoc digitalization) to investigate freely performed movements by a large number of exemplars handling indigenous objects.

In view of the similarities in the kinematic patterns of reaching and grasping in humans and in macaque monkeys in their natural ambience, that species could be a useful model for understanding human motor control (Rizzolatti and Luppino 2001). In this respect, the neural organization for object prehension in non-human primates appears to result from a complex and intricate interaction between spinal and cortical neural mechanisms which are not yet completely understood. It is possible that other ecological paradigms could unveil how those neural interactions compare across different species.

This could be a relevant issue given that some findings indicate that the macaque species may have potential clinical utility in cell therapy and tissue engineering. The macaque is, moreover, the animal model used to evaluate the potential of selected therapies for neuromotor disorders such as spinal cord injuries (Courtine et al. 2007) or to develop brain machine interfaces for arm control (Hochberg et al. 2006; Jackson et al. 2006; Kim et al. 2007). Comprehending the similarities in human and macaque movement behavior is vital if the animal model is to be exploited for human benefit.

It should also be remembered that most studies concerning the planning and control of hand orientation in grasping movements tend to focus on the use of a single hand in relation to a single object to grasp or to manipulate.

However, as outlined in the literature (Macfarlane and Graziano 2009), macaque monkeys utilize a diversity of grasping behavior, and not only with a single hand. Some involve both hands, others the mouth, the foot, or arm opposition between the forearm and chest.

Gripping, moreover, is not limited to picking up, grasping, or manipulating objects; climbing grips, for instance, are substantially different from manipulative grips in the sense that they present fewer variants and are more stereotyped. The present study could be considered a preliminary step toward characterizing diverse modes of unconstrained grasping behavior in macaque monkeys.

This study presents some limitations. The first is that it utilized two- rather than three-dimensional kinematics, but a two-dimensional approach is the only way to film movements in totally natural, unconstrained conditions. A great amount of energy was dedicated to establishing the experimental criteria of the movements to be analyzed. High sampling frequency, a state-of-the-art digital technique for tracking specific movements, and an appropriate action framing system helped to prevent motion artifacts and to guarantee high-fidelity parameterization (see "Materials and methods" section).

The second limitation is that the work does not present a full report on homologies across species. Our analyses were confined to differences in the kinematics between precision and power grips in macaques and possible parallels with humans grasping actions. Debating whether reach-to-grasp behavior (and its kinematics) is task-constrained and therefore shared by many animals who perform similar actions (e.g., Iwaniuk and Whishaw 2000; Sacrey et al. 2009) fell outside the scope of the present study.

The third limitation is that our analysis focused exclusively on grips used to handle clay balls and rocks and did not consider a wider range of behaviors, objects (e.g.,

grasping grass, fruit, and flowers), and postures. The study design, in fact, gave priority to gathering a quantitative pool of data for kinematic analysis of movements by free-ranging macaques that could be compared with those carried out by laboratory exemplars and humans. Further research will reveal whether object types/sizes and/or postures affect reach-to-grasp kinematic parameterization and how the kinematics of these movements compares with those in humans.

To conclude, despite the difficulties encountered in conducting this research project, these findings provide new information delineating how macaques' grasping behavior has naturally evolved. The novelty of our approach lies in the experimental protocol (post hoc) used to study reach-to-grasp movements performed in totally natural conditions. The study, in fact, fills an important gap in the literature by delineating a controlled experimental protocol that imposed no constraints on the animals studied.

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