RESEARCH ARTICLE

How posture affects macaques' reach-to-grasp movements

**Luisa Sartori · Andrea Camperio-Ciani ·
Maria Bulgheroni · Umberto Castiello**

Abstract Although there is a wealth of behavioral data regarding grasping movements in non-human primates, how posture influences the kinematics of prehensile behavior is not yet clearly understood. The purpose of this study was to examine and compare kinematic descriptions of grip behaviors while primates (macaque monkeys) were in a sitting posture or when stopping after quadrupedal locomotion (i.e., tripedal stance). Video footage taken while macaques grasped objects was analyzed frame-by-frame using digitalization techniques. Each of the two grip types considered (power and precision grips) was found to be characterized by specific, distinct kinematic signatures for both the reaching and the grasping components when those actions were performed in a sitting position. The grasping component did not differentiate in relation to the type of grip that was needed when, instead, the prehensile action took place in a tripedal stance. Quadrupedal locomotion affected the concomitant organization of prehensile activities determining in fact a similar kinematic patterning for the two grips regardless of the size of the object to be grasped. It is suggested that using a single kinematic grip patterning for all prehensile activities might be both the by-product of planning a grasping action while walking and a way to simplify motor programming during unstable tripedal stance.

Keywords Grasping · Kinematics · Macaques · Evolution · Primatology

L. Sartori · A. Camperio-Ciani · M. Bulgheroni · U. Castiello (✉)
Department of General Psychology, University of Padua,
Via Venezia 8, 35131 Padua, Italy
e-mail: umberto.castiello@unipd.it

Introduction

Providing them with the ability to grasp and/or hold objects using a single hand, the prehensile hand with curling fingers is one of the most distinctive traits of primates (Napier 1956, 1961; Bishop 1964; Costello and Fragaszy 1988; Christel 1993; Marzke 1994; MacFarlane and Graziano 2009; Reghem et al. 2011; Toussaint et al. 2013; see also Sustaita et al. 2013). In view of their ecological and evolutionary implications, some investigators have reported on a variety of reaching and grasping behaviors in monkeys and apes (e.g., Christel 1993; Hopkins et al. 2002; Spinozzi et al. 2004; Pouydebat et al. 2006, 2008, 2009, 2011; Crast et al. 2009; Macfarlane and Graziano 2009), but only a few have provided a detailed kinematic analysis of non-human primates' grasping behavior. The majority of those studies were conducted observing captive macaques living in non-natural conditions (Fogassi et al. 1991; Roy et al. 2000, 2002, 2006; Sacrey et al. 2009; Jindrich et al. 2011) with some body parts constrained during movement. Only a few investigators have sought to observe them in their natural habitat living in totally unconstrained conditions (Christel and Billard 2002; Sartori et al. 2013a, b).

According to the majority of those studies, hand positioning depends on the size of the object to be grasped (e.g., Fogassi et al. 1991; Roy et al. 2000, 2002, 2006; Pouydebat et al. 2009; Sartori et al. 2013a). The amount of time it takes to complete a movement is also affected by the object's size: reaching to grasp a small object takes longer, in fact, than grasping a larger one (e.g., Fogassi et al. 1991; Roy et al. 2000; Sartori et al. 2013a). It follows then that peak wrist velocity is slower and the moment when the animal's fingers start to close around an object takes place earlier for precision with respect to whole-hand grips (Fogassi et al. 1991; Sartori et al. 2013a).

Most kinematic studies in non-human primates focusing on planning and control of hand orientation during grasping movements have tended to consider actions performed by animals in sitting positions (e.g., Fogassi et al. 1991; Scott and Kalaska 1997; Christel and Billard 2002; Roy et al. 2000, 2002, 2006; Jindrich et al. 2011; Sartori et al. 2013a, b). It is important to remember, nevertheless, that non-human primates reach-to-grasp objects from a variety of postures which, in fact, seem to influence how the hand is used (Hopkins 1993). Prosimians, being without well-developed precision grips, for example, use their hands differentially when they are reaching from a bipedal as compared to a tripedal posture (Hopkins 1993; Hopkins et al. 1993; Olson et al. 1990; Spinozzi and Truppa 1999). Reghem et al. (2013) contributed to this body of literature by outlining differences in the amplitude of upper limb joints across five primate species (lemur, capuchin, chimpanzee, gorilla and human) during unconstrained grasping conditions in which the animals were free to choose their body postures (Reghem et al. 2013). Further data are needed if investigators are to fully understand the influence of posture on grip morphology and hand use.

Another aspect that needs to be clarified is whether hand patterning for precision and whole-hand grasps while stopping after quadrupedal locomotion (i.e., freezing in a tripedal stance) are similar to that observed when an animal is already in a sitting position. The question is whether quadrupedal locomotion and the resulting unstable tripedal stance during reach-to-grasp movements affect the concomitant planning and execution of prehensile activities. The present study attempts to address and to answer that question by comparing the kinematic patterning of reaching to grasp actions by macaques living in totally unconstrained conditions while they were sitting and while they stopped walking in a tripedal stance posture as they roamed freely.

Materials and methods

Species studied

Ten adult macaque monkeys (*Macaca fascicularis*), all belonging to a single free-ranging troop made up of 65 animals living in Pulau Besar, Langawi, Malaysia, were studied. The troop included five males and five females, all with an estimated age of no <4 years. The study was carried out in accordance with the ethical principles issued by the World Medical Association (Declaration of Helsinki).

Data collection

A total of 10 h of video footage was filmed using a digital camcorder (100 frames/s) between November 2, 2008,

and November 27, 2008, during daylight hours (exclusively between 10.00 and 14.00). In view of the difficulty of 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 film the exemplars being observed (Altmann 1974). As the study aimed to capture the animals in natural conditions/habitat, a zoom lens was utilized to film them from a distance as they sat on the ground or moved from place to place going about normal activities. Just as the footage already described in the literature (e.g., Fogassi et al. 1991; Roy et al. 2000, 2002, 2006; Sartori et al. 2013a, b), the monkeys' movements were filmed in the sagittal plane to avoid motion artifacts. It is important to underline that all the objects that were grasped were indigenous to that geographic area and were not placed there by the experimenters. The areas where the monkeys were filmed were naturally scattered with clay balls and stones of different sizes. Our attention was focused on analyzing movements directed toward small balls of clay (~1 cm) leading to precision grips and round stones (~4 cm) leading to whole-hand grips. These were chosen because they resembled the spherical items used in previous kinematic studies focusing on macaques (Fogassi et al. 1991; Roy et al. 2000, 2002, 2006; Sartori et al. 2013a, b).

Grip classification

The grips appearing in the video sequences were classified depending on the areas of skin surface making contact with the objects being grasped. Two operators who were unaware of the study hypothesis and blinded to the experimental conditions were instructed to classify the grips as pinched (precision) when the distal pad of the thumb was opposed to the radial side of the index finger (used to manipulate small objects such as seeds, soil fragments or blades of grass) or as whole hand (power) when all four fingers and the palm were wrapped around an object in one direction while the thumb was wrapped around it in the opposite one (used to manipulate large objects such as stones or pieces of fruit). Cohen's κ value of 0.9 confirmed the reliability of our data. It is nevertheless important to remember that in natural situations/environments, spontaneous movements do not necessarily fit into classical power and precision grip categories: At times three fingers can be involved, at others various finger combinations can be utilized often moving fluidly from one configuration to another. For the sake of comparison, the movements most closely resembling those studied in previous experiments were selected and further analyzed (Fogassi et al. 1991; Roy et al. 2000, 2002, 2006; Sartori et al. 2013a). The present study was exclusively concerned with right-hand

grasping movements performed by individuals handling objects while they were in a sitting position or while stopping after quadrupedal locomotion.

Posture classification

The reaching and grasping movements that were analyzed and compared were carried out while the individuals were in two different situations: (1) sitting posture or (2) tripedal stance. With regard to the latter situation, individuals were filmed as they approached, stopped briefly in a tripedal position and grasped an object of their interest. The degree of stability of the resultant posture was likely determined by the particular locomotor pattern the monkey was using. In our case, the specific gait pattern adopted by each monkey when approaching the item to be grasped was a 'diagonal sequence,' that is when the touchdown of a foot is followed by that of the opposite (contralateral) hand (Hildebrand 1985). This information is important given that the feet and hand forming the tripod of support most likely maintained the relative position they were in when the monkey stopped walking (i.e., the monkey freezed in position). Note that the onset of reach-to-grasp movement was defined as the time the individual's arm/hand not forming the tripod of support was rising from the ground and beginning the reach-to-grasp action. The object was at the same approximate distance for both conditions (20 ± 0.2 cm away from the individuals). The majority (85 %) of objects were located to the right and a few (15 %) were located in front of the animal.

Data analysis

The video sample was analyzed frame-by-frame using an in-house software developed to perform two-dimensional (2D) post hoc kinematic analysis. Markers were inserted post hoc via software on the anatomical landmarks identified in the videos (Fig. 1a) and were tracked throughout the time course of the movement sequence. Care was taken to compare only those movements that were carried out while the monkeys were in a sitting position (Fig. 1a) or while they were moving from one place to another as they picked up objects (Fig. 1b). For both conditions, the onset of movement was defined as the time the tangential velocity of the wrist marker crossed a threshold (5 mm/s) and remained above it for at least two frames. The end of the movement was defined as the time the fingers closed around the object, and there were no further changes in the distance between the index finger and the thumb. To avoid any skewing effect, only time frames in which reaching movements were performed along a plane that was perpendicular to the camera axis, and the animal was located in the central part of the image were selected and analyzed.
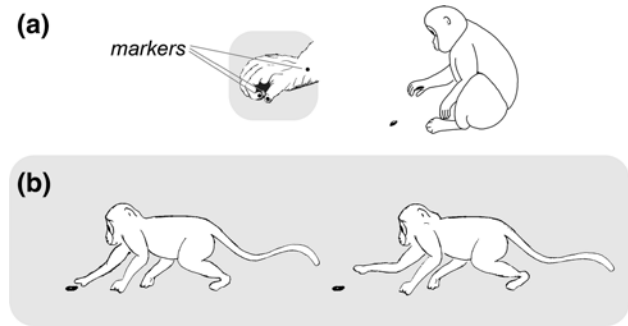
Fig. 1 Graphical representation of the monkeys' postural conditions. Schematic drawing of the monkeys' seated (**a**) and tripedal stance (**b**) postures as they reached and grasped. *Marke*r positions are also illustrated

The relative positioning of the video camera axis and the plane of motion were verified by measuring the length of selected bone elements (e.g., arm). This procedure was utilized to guarantee a constant point of reference during movements taking place on the plane perpendicular to the camera axis. A frame of reference identifying X and Y axis as horizontal (ground) and vertical directions was manually set by the 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 unit of measurement reference. Movement tracking procedures were performed to extract a number of kinematic parameters. As shown in Fig. 1a, markers were positioned on each individual's wrist to calculate the reaching component and on the nails of its index fingers and thumb to calculate the grip aperture as a function of time (Fogassi et al. 1991; Roy et al. 2000; Sartori et al. 2013a). In accordance with previous studies focusing on macaques (e.g., Fogassi et al. 1991; Roy et al. 2000; Sartori et al. 2013a), the following dependent measures were considered: (1) the movement duration time (i.e., the time between movement onset and when the monkey's hand grasped the object; (2) the time from the peak velocity to the end of the movement (deceleration time); (3) the time when the maximum distance between the thumb and the index finger took place; (4) the maximum distance between the thumb and the index finger. The absolute value of wrist velocity was computed on wrist trajectory data. More specifically, the used processing software implements the linear-phase autoregressive model-based derivative assessment algorithm (LAMBDA filter; D'Amico and Ferrigno 1990; see also Walker 1998). The implemented filter has been widely tested on natural and synthetic data (d'Amico and Ferrigno 1992). This algorithm exploits an autoregressive (AR) model of the original signal to estimate the filter low-pass cutoff frequency. The signal is then low-pass filtered in the frequency domain by a linear finite impulse response (FIR) filter where the

frequency spectrum of the data is obtained by fast Fourier transform (FFT). Derivatives are also computed in the frequency domain. Velocities in the time domain are then calculated by applying inverse fast Fourier transform (IFFT). The laterality quotient (LQ) was 77 ($\pm$15) with a LQ of 100 reflecting a full right-hand preference. Twenty movements of each of the four combinations (sitting/precision, sitting/whole hand, locomotion/precision and locomotion whole hand) being considered were chosen randomly from a larger sample for each of the monkeys being studied. Preliminary analyses were performed to ascertain if the velocity of quadrupedal locomotion could have determined differences in the dependent measures considered. The subjects were, in fact, subdivided into two groups depending on the velocity at which each was moving before they reached the point the movement sequence was analyzed (higher velocity—5 individuals, $M = 0.67$ m/s; lower velocity—5 individuals: $M = 0.42$ m/s). An ANOVA was performed to compare the two groups. As no significant differences were found ($P_s > 0.05$) for the dependent factors, the 'velocity' factor was collapsed. A repeated-measures analysis of variance (ANOVA) with types of condition (sitting, tripedal stance) and types of grip (precision grip, power grip) as within-subjects factors was carried out for each dependent measure. Post hoc pairwise comparisons were carried out using t tests, and the Bonferroni adjustment for multiple comparisons was applied. All the main assumptions behind this statistical model (i.e., normality and sphericity) were checked before running an ANOVA. The Kolmogorov–Smirnov test revealed that the normality assumption was satisfied (α-level: 0.05), and the Mauchly test showed that the sphericity assumption was not violated (α-level: 0.05).

Results

Reaching component

The main factor type of grip was significant for movement duration ($F(1,9) = 23.31$, $P < 0.001$), deceleration time ($F(1,9) = 12.23$, $P < 0.01$) and the peak velocity amplitude ($F(1,9) = 28.13$, $P < 0.0001$). In particular, the total duration of reach-to-grasp movements was longer for precision with respect to power grip (443 ± 42 vs. 392 ± 36 ms, respectively). A bell-shaped, single peaked asymmetric profile was found for wrist velocity which was characterized by a deceleration phase that was always longer than the acceleration one. As shown in Fig. 2a, the deceleration time was longer for precision with respect to power grips (226 ± 27 vs. 180 ± 22 ms, respectively). The peak velocity amplitude was higher for power with respect to precision grips ($1{,}202 \pm 145$ vs. 976 ± 104 mm/s, respectively; Fig. 2a). Neither the main factor type of posture nor the interaction between the type of posture and the type of grip was significant ($P_s > 0.05$), indicating that no difference was present depending on the type of condition (sitting, tripedal stance).

Grasping component

The main factor type of grip was significant for the time of the maximum grip aperture ($F(1,9) = 22.31$, $P < 0.001$) and the maximum grip aperture amplitude ($F(1,9) = 56.14$, $P < 0.0001$). In particular, the time of the maximum grip aperture occurred earlier for the precision with respect to power grips (275 ± 35 vs. 302 ± 41 ms, respectively; Fig. 2b). Grip aperture was larger for small objects
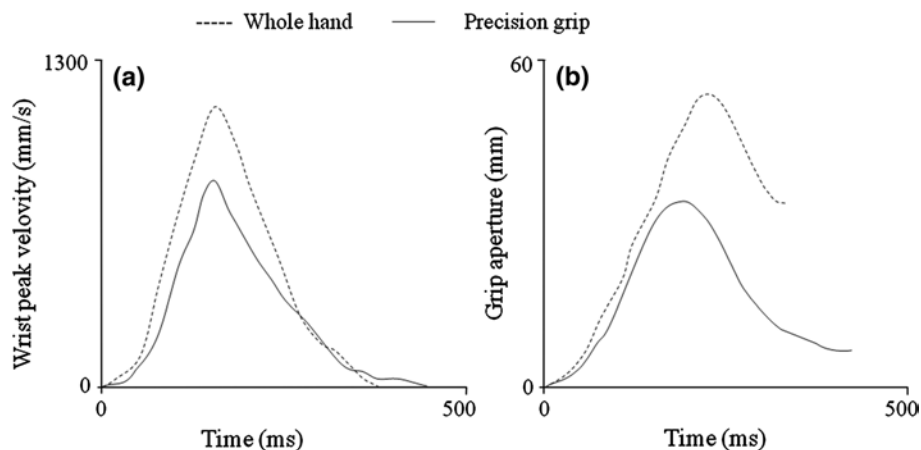
Fig. 2 Velocity and grip profiles. **a** The mean wrist peak velocity profile for power and precision grip movements in a representative subject ($N = 4$). The peak velocity is lower and the deceleration time is longer for precision grip movements than for whole-hand grips. **b** The mean grip aperture profile for power and precision grip movements in a representative subject ($N = 4$). The amplitude of maximum grip aperture is lower and it occurs at an earlier time for precision grip movements than for whole-hand grips

requiring a precision grip than for power grips used to grasp larger objects (30.0 ± 0.3 vs. 57 ± 0.8 mm, respectively; Fig. 2b). The interaction between the type of posture and the type of grip was significant for both the time and the amplitude of the maximum grip aperture ($F(1,9) = 12.32$, $P < 0.001$; $F(1,9) = 28.04$, $P < 0.0001$, respectively; Fig. 3a, b). Post hoc contrasts indicated that the time when the maximum grip aperture took place was earlier and the amplitude was smaller for precision with respect to power grips for the 'sitting' condition ($P_s < 0.05$); there were no differences in those variables for the 'tripedal stance' condition ($P_s < 0.05$). When, in fact, the monkeys were ambulating, the movement pattern remained the same regardless of the size of the object they were grasping. Post hoc contrasts across conditions revealed nevertheless an anticipated

maximum grip aperture during whole-hand movements and a wider grip aperture during precision grip movements for the 'tripedal stance' with respect to the 'sitting' condition ($P_s < 0.05$; Fig. 3a, b).

Discussion

The preeminent aim of the present study was to gain further knowledge about ecological and evolutionary aspects underlying grasping capabilities. In particular, we were interested in the kinematical correlates of reach and grasp in the hands of animals, which vary with the varying demands of posture and manipulative behavior. To this end, we compared free-ranging monkeys in the amount of difference between precision and power gripping kinematics performed in a sitting condition and while stopping after quadrupedal locomotion (i.e., tripedal stance). We hypothesized that the kinematic patterning could differ among the sitting and the tripedal stance condition due to the constraints associated with planning a grip while walking and performing the grip in an unstable position. The results indicate that there is a difference between the two grips in the sitting condition. But for the tripedal stance condition, the animal's tendency is to maintain a similar hand patterning for the two grips. Due to the difficulty in carrying out systematic studies in unconstrained conditions, little is known about how non-human primates organize grasping actions from different postures. Using our experimental protocol (post hoc digitalization), we were able to carry out a kinematic analysis of freely performed prehensile activities to grasp objects by macaques living in their indigenous habitat.

The literature findings concerning macaques grasping objects from a sitting position consistently indicate that, with respect to power grips, precision ones are characterized by longer lasting movements, longer wrist deceleration times, lower wrist peak velocity amplitudes and maximum grip apertures taking place earlier at a lower amplitude (e.g., Fogassi et al. 1991; Roy et al. 2000; Sartori et al. 2013a). As precision grips need more accuracy with respect to power ones, longer deceleration time seems predictable (Fitts 1954). There are usually no differences in the time that it takes to reach peak wrist velocity across the various types of grasping actions (Fogassi et al. 1991; Roy et al. 2000; Sartori et al. 2013a). The findings presented here with regard to the sitting condition fully agree, then, with previous reports indicating that when macaques are sitting, the type of grip to be carried out affects grasping kinematics.

Prehension movement in both humans (Jeannerod 1984) and other primates (Roy et al. 2000, 2002, 2006; Sartori et al. 2013a, b) is usually described in connection to
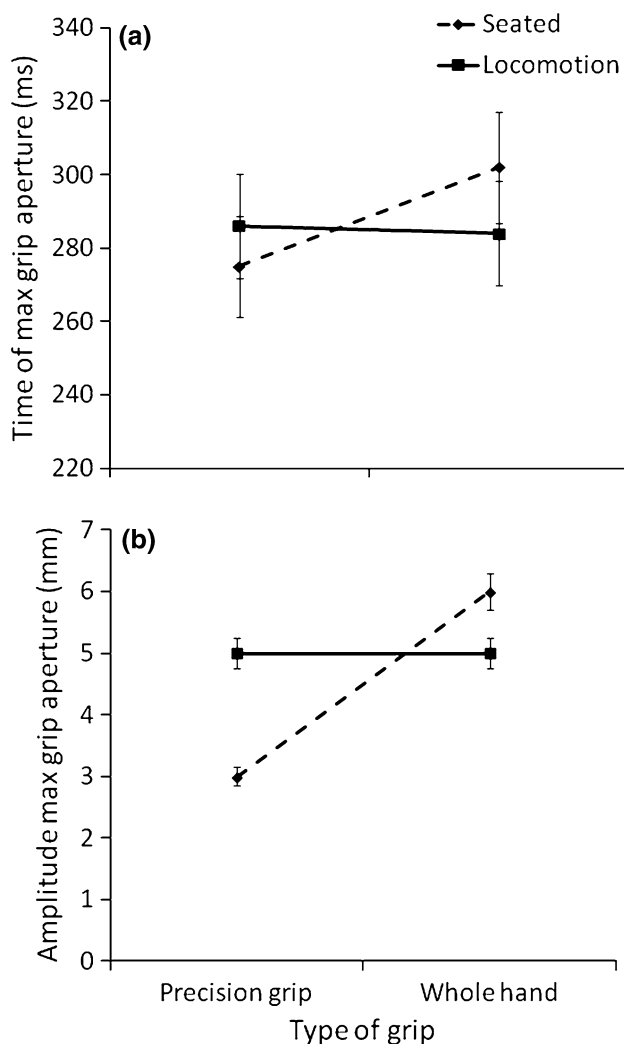
Fig. 3 Schematic representation of the interaction type of posture by type of grip. **a** The effect of the interaction type of posture by type of grip for the time of maximum grip aperture. **b** The effect of the interaction type of posture by type of grip for the amplitude of maximum grip aperture. *Bars* represent the standard error of means

its two major components: reaching and grasping. During the former, the actor brings its hand from its initial position to the target (proximal movements); during the latter the actor selects and controls its fingers depending on the size and shape of the object in question (distal movements). Some researchers have, however, questioned whether a dichotomy exists between reaching and grasping components. Some human studies have revealed that the component controlling proximal movements can access information concerning the size of the object to be grasped and can modify peak velocity and acceleration accordingly (e.g., Gentilucci et al. 1991; Jakobson and Goodale 1991; Smeets and Brenner 1999). Whereas our findings in seating macaques confirm this proposal, the results for the tripedal stance condition suggest that in some circumstances, the 'two independent channels' hypothesis still applies. The fact that variations in movement organization were evident only with regard to the grasping component confirms that the two parts can be dissociated.

During tripedal stance, macaques have displayed analogous kinematic patterns for both grip types as far as the time and the amplitude of maximum grip aperture were concerned. In other words, these parameters are similar regardless of the type of grip being utilized. Two factors might have contributed to this effect. First, as a large quantity of motor programming resources is devoted to maintaining balance and coordination during locomotion (e.g., Dunbar and Badam 1998; Larson 1998; Patel 2010), a compensatory strategy may be at play when a primate is simultaneously walking and planning a grasping action. Greater equilibrium constraints characterizing quadrupedal locomotion may place more demands on the central nervous system (CNS) with respect to the sitting position. Planning a single grip pattern for all prehensile activities could probably compensate for those constraints by simplifying motor programming. The process of selecting the appropriate muscles and joints needed to perform different types of grips is, according to this thesis, modulated by a single spatial–temporal template also controlling an action's coordination. Second, the unstable condition determined by the tripedal stance might have determined the particular kinematic pattern the monkey is using. In this respect, our findings suggest that an animal's posture has an important effect on kinematic patterns in terms of how an object is grasped. In other words, anticipating the maximum grip aperture time during whole-hand grasping movements and widening hand aperture for precision grip movements probably ensure safer establishment of contact points in unstable conditions (i.e., tripedal stance), thereby diminishing the possibility of error. Some data pertinent to human reach-to-grasp research have also led to analogous conclusions. Similar compensatory patterns have, in fact, been described in human experiments in which the target is visually unavailable or participants were instructed to carry out actions quickly (Wing et al. 1986).

In general, the implications of our findings are that grips to be utilized by macaques are determined not only by the physical dimension of the object to be grasped, but also by the dynamic aspects of the entire action sequence. A posture-linked strategy would permit the neural system to compensate for postural and joint kinematic instability characterizing reach-to-grasp actions in tripedal stance. The neural organization for object prehension in non-human primates appears, in fact, to be determined by an intricate, complex, not entirely understood interaction between spinal and cortical neural mechanisms (Rizzolatti and Luppino 2001; Castiello 2005). The present study offers new pieces to the puzzle of how those circuits modulate unconstrained grasping behavior in macaques.

In the end, our findings seem to have posed more questions than they have answered: do conditions of dynamic stability (i.e., when macaques continue to walk as they pick up objects) lead to the same or different results as those linked to static stability and do postural adjustments of proximal joints influence the distal component of an action are some of the questions that further studies will attempt to answer. For the time being, the findings outlined here regarding naturally free-ranging macaques complement previous reports and provide new insights into grip kinematics in non-human primates that may ultimately have implications in connection to evolutionary models of manual abilities.

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