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A review and consideration on the kinematics of reach-to-grasp movements in macaque monkeys

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The bases for understanding the neuronal mechanisms that underlie the control of reach-to-grasp movements among nonhuman primates, particularly macaques, has been widely studied. However, only a few kinematic descriptions of their prehensile actions are available. A thorough understanding of macaques' prehensile movements is manifestly critical, in light of their role in biomedical research as valuable models for studying neuromotor disorders and brain mechanisms, as well as for developing brain-machine interfaces to facilitate arm control. This article aims to review the current state of knowledge on the kinematics of grasping movements that macaques perform in naturalistic, semi-naturalistic, and laboratory settings, to answer the following questions: Are kinematic signatures affected by the context within which the movement is performed? In what ways is kinematics of humans' and macaques' prehensile actions similar/dissimilar? Our analysis reflects the challenges involved in making comparisons across settings and species due to the heterogeneous picture in terms of the number of subjects, stimuli, conditions, and hands used. The kinematics of free-ranging macaques are characterized by distinctive features that are exhibited neither by macaques in laboratory setting nor human subjects. The temporal incidence of key kinematic landmarks diverges significantly between species, indicating disparities in the overall organization of movement. Given such complexities, we attempt a synthesis of extant body of evidence, intending to generate some significant implications for directions that future research might take, to recognize the remaining gaps and pursue the insights and resolutions to generate an interpretation of movement kinematics that accounts for all settings and subjects.

34 A wide variety of tasks, employing numerous techniques, have been used to furnish a  
35 detailed characterization of reach-to-grasp movements, at both the neural and behavioral levels  
36 (Bennett & Castiello 1994; Corbetta & Santello, 2018; Nowack & Hermsdorfer 2009; Wing et al.  
37 1996). In neural terms, research has shown that analogous cortical areas are involved in controlling  
38 the prehensile actions of both humans and macaques (e.g., Begliomini 2008; Castiello 2005;  
39 Filimon 2010; Culham et al. 2006; Rizzolatti and Luppino 2001). In behavioral terms, the extent to  
40 which such similarity, at the neuronal level, actually translates into comparable kinematics, with  
41 regard to processing objects' features and contextual factors, remains substantially less clear. This  
42 ambiguity owes to the vast quantities of available psychophysical data related to human prehensile  
43 movements, relative to the scarce and largely heterogeneous data available to inform accounts of  
44 the kinematics of macaques' reach-to-grasp movements.

45 This work is an attempt to summarize the current state of knowledge on the kinematic  
46 organization that underlies the formation of reach-to-grasp movement patterns in macaques. To do  
47 this, we first established the goal of qualitatively categorizing the prehensile actions produced in a  
48 naturalistic setting, as this body of evidence can operate as a sort of referential platform, enabling us  
49 to identify the grip types that primates can, theoretically, learn and perform in a laboratory setting.  
50 We then plan to move onto an examination of the kinematics of those reach-to-grasp movements  
51 that are employed to manipulate objects of different sizes and shapes, at various distances, in  
52 naturalistic, semi-naturalistic, and laboratory settings. Studies that examine hand shaping by  
53 analyzing the distance between the thumb and the index finger, and derivatives of that method (i.e.  
54 the two-digit approach; e.g., Jeannerod 1984), as well as multi-digit grasping (e.g. Santello and  
55 Soechting 1998) will be reviewed. The article also aims to compare the body of evidence that exists  
56 for macaques to the evidence developed with regard to humans. Each section starts with a brief  
57 summary of the primary results obtained from human subjects, for a specific experimental  
58 manipulation; the summary is intended to function as a reference point for the research on  
59 macaques subsequently presented. Finally, we will highlight those factors that, from our

60 perspective, should inform future research, to determine the basis for making valid comparisons  
61 across settings and species.

62

### 63 **A Description of Grasping Configurations in Naturalistic Settings**

64 The acknowledged diversity of grasping behavior among macaque monkeys is manifest in  
65 data assembled from naturalistic and ethological research observations of semi-free-ranging rhesus  
66 macaques living in their natural habitat, with grips classified according to the skin surface areas in  
67 contact with the object (for a review, see Macfarlane and Graziano 2009). The salient conclusion of  
68 that study is that macaque monkeys employ a wide and varied assortment of grips that fall into two  
69 broad functional categories: object manipulation (most grips are of this type) and climbing. The  
70 following focuses on the grips aimed at object manipulation that most closely resemble those  
71 examined in subsequent sections of this review (variants of precision and power grips). They are  
72 presented according to incidence, from most frequent to least:

73 (i) The side grip (Fig. 1a) involves pinching an object between the thumb and the index  
74 digit. When using this grip, the distal thumb pad opposes the radial side of the second digit (but this  
75 corresponding opposition might occur anywhere along that digit). Macaques deploy this grip to  
76 manipulate small objects, such as blades of grass and pieces of fruit.

77 (ii) The precision grip (Fig. 1b), hereafter referred to as “PG”, involves opposing the distal  
78 pad of first digit to that of the second digit. This grip involves a larger area of pulp-to-pulp contact,  
79 relative to the pad-to-side grip. Macaques adopt this grip for grooming activities, and also to  
80 manipulate objects, like pieces of grass or dirt.

81 (iii) The thumb-to-second/third grip (Fig. 1c) features collaboration of the second and third  
82 digits in opposition to the thumb. The grip is generally used to hold medium-sized objects, such as  
83 pieces of fruit.

84 (iv) The power grip (Fig. 1d), hereafter referred to as “PoG”, is characterized by five parallel  
85 fingers wrapped, in the shape of a fist, around an object, often a larger one than the other grips can  
86 negotiate.

87 Together, these four grip types account for approximately 70% of simple grips (typically, a  
88 simple grip is used to grasp a single object, while a complex grip involves the application of  
89 multiple grips to one or more objects at the same time) that macaques use (MacFarlane and  
90 Graziano, 2009). Because kinematic studies have not paid substantial attention to the side grip or  
91 the thumb-to-second/third grip, these two grips will not be subject to explicit examination in the  
92 sections of the manuscript that follow.

93

94 --- Insert Figure 1 about here ---

95

## 96 **Quantitative Assessment of Grasping Configurations**

97 By contrast to the large quantity of psychophysical data available on human reach-to-grasp  
98 movements (Bennett and Castiello 1994; Corbetta and Santello, 2018; Jeannerod 1988; Nowack and  
99 Hermsdorfer 2009; Wing et al. 1996), there is a paucity of information on the kinematics of reach-  
100 to-grasp movements in macaques; what little exists has been gathered entirely from naturalistic,  
101 semi-naturalistic and experimental settings, such as those outlined below (see Table 1).

102

103 --- Insert Table 1 about here ---

104

105 The kinematics of reach-to-grasp movements presented for all the naturalistic studies has  
106 been generated via digitalization techniques using video footage of these primates in their natural  
107 habitat, spontaneously reaching to grasp objects (e.g., Sartori et al. 2013a). The kinematics of the  
108 macaque’s prehension, in the semi-naturalistic setting, was reconstructed from three-dimensional  
109 (3D) video images (Christel and Billard 2002). Behavioral and neurophysiological studies

110 examining macaques' upper limb kinematics in a laboratory setting, where the animal was  
111 constrained in a primate chair, used optoelectronic techniques (e.g., Roy et al. 2000). We did not  
112 consider psychophysical investigations which (i) were restricted to the reaching component, (ii)  
113 show poor temporal resolution (Fogassi et al. 2001; Gardner et al. 1999), along with those that (iii)  
114 considered the stages of the prehension task but did not report on specific parameters (Chen et al.  
115 2009; Gardner et al. 2007a, b, c), or (iv) examined a task that was fundamentally different from the  
116 majority of those outlined in this review (i.e., swinging objects; Bansal et al. 2011; Vargas-Irwin et  
117 al., 2010; Zhuang et al. 2010).

118

### 119 **A direct comparison between humans and macaques: a semi-naturalistic study**

120 To our knowledge, only one study has been designed with the aim of directly comparing the  
121 kinematics of prehensile actions in macaques and to those in humans. Here, the macaques'  
122 movements were recorded in a semi-naturalistic setting (Christel and Billard 2002). The macaques  
123 studied were free-ranging, within a relatively large area in their normal habitat, spontaneously  
124 performing PG movements in a quadrupedal stance or in a sitting or squatting position, with the arm  
125 either flexed or stretched. The human participants were, instead, seated at a table and instructed to  
126 carry out similar tasks that involved grasping small pieces of food, using a precision grip. To  
127 reproduce the time constraints that impact the macaques' response to group competition, a  
128 metronome was introduced, to pace the human participants' movements. The investigators reported  
129 that, whereas the macaques were faster than the humans, during the reaching phase, they moved at a  
130 similar pace to the humans during retrieval. The monkeys were able to execute their movements  
131 more rapidly, during the reaching phase, by rotating their wrists and opening their hands with  
132 greater speed. The angular velocity and acceleration of the finger aperture and the wrist were, in  
133 fact, significantly higher in the macaques than in the humans. Some have hypothesized that the  
134 primates were able to move more quickly because they have lighter and greater muscular strength  
135 (in proportion to their body mass) relative to humans (Cheng and Scott 2000; see also Billard 2001;

136 Billard et al. 2001). Study results also revealed that the macaques executed steeper and wider  
137 excursions of the elbow and wrist, a smaller abduction of the shoulder joint, and a greater  
138 displacement of the torso relative to human movement. Notably, despite the greater instability of  
139 the macaques' postures and joint kinematics, both species had similarly smooth hand paths (Christel  
140 and Billard 2002). In light of these data it has been proposed that macaques might have a more  
141 demanding way of controlling their muscles (i.e., sharp breaks and starts), relative to humans, who  
142 make smoother transitions in speed (Christel and Billard 2002). It is interesting to observe that,  
143 notwithstanding the similar qualities shared by humans and macaques, the interspecies distinctions,  
144 in terms of kinematic irregularities, specifically in elbow-shoulder posture might stem from a  
145 different control system (Christel and Billard 2002). Macaques rely on their arms for at least two  
146 main behaviors: locomotion and object manipulation. From an evolutionary perspective, it is  
147 reasonable to hypothesize that neural control for locomotion evolved in the central nervous system  
148 earlier than the mechanism for fine object manipulation and, as a result, a macaque's brain might  
149 switch almost constantly between these two activities. A possible way of simplifying this overlap  
150 involves separating the higher-and lower-motor control centers that guide grasping behavior and  
151 locomotive activity, respectively. Further studies are necessary to assess this hypothesis as well as  
152 the possibility of different brain areas to control locomotion and reaching. Although this study is a  
153 worthwhile attempt to identify the interspecies differences and similarities, it should here be noted  
154 that the stimuli used in this study (i.e., raisins and peanuts) varied with regard to the motivational  
155 status they would be assigned by macaques and humans, respectively. In fact, macaques are used to  
156 quickly executing grasping movements, aimed at snatching up food items of a similar size and  
157 rapidly scanning material to distinguish food from non-food; humans are involved with and  
158 motivated to execute the task of grabbing food in ways that are significantly different from such  
159 primates. Further, postural differences might have played a role in highlighting the reported  
160 differences.

161



## Two-Digit Approach

Figure 2 provides a schematic representation of the main dependent variables used to characterize reach-to-grasp movements, in both humans and macaques, for the studies reported in this section.

--- Insert Figure 2 about here ---

## The Effects of Object Size

The reach-to-grasp literature on humans demonstrates consistency across studies with regard to results such as a longer movement duration, a prolonged arm deceleration (i.e., the time from peak velocity to the movement's end), a lower arm peak velocity amplitude, and a predictably diminished amplitude of maximum grip aperture for smaller stimuli, relative to larger stimuli (Castiello et al. 1993; Castiello 1996; Gentilucci et al. 1991; Jakobson and Goodale 1991; Jeannerod, 1984).

With the foregoing details in mind, it is worth noting that a naturalistic study, by Sartori and colleagues (2013a), examining macaques employing PG movements to grasp small objects and PoG movements to grasp large ones (Fig. 3a), reported that each type of movement was characterized by a specific kinematic signature that mirrored human data. Movements toward smaller objects led to a prolonged movement duration, relative to movements toward larger objects. The deceleration time was longer for the small objects, relative to the larger ones, whereas the peak velocity amplitude was higher for larger objects than for smaller objects (Fig. 3b). The latency of peak velocity did not differ, with respect to object size. The grasping component was characterized by a maximum grip aperture, smaller and attained earlier for smaller objects, relative to larger ones (Fig. 3c). Turning to the laboratory setting, Fogassi and colleagues (1991) examined the kinematics of one macaque,

188 trained to reach for and grasp either a large or a small cylinder, using a PoG and a PG, respectively.  
189 They observed a kinematic patterning that resembled the one characterizing macaques' actions in a  
190 naturalistic environment (Sartori et al., 2013a) and humans (e.g. Gentilucci et al., 1991). Further  
191 behavioral laboratory experiments (Roy et al. 2000, 2002; fig. 3d) did not demonstrate differences  
192 in the latency of peak velocity, with respect to object size (Fig. 3e) and the amplitude of maximum  
193 grip aperture increased with object size (Fig. 3e) as found by Fogassi and colleagues (1991).  
194 However, by contrast to findings related to the unconstrained actions of macaques (Sartori et al.,  
195 2013a), in humans (e.g., Gentilucci et al., 1991) and findings of the experimental study by Fogassi  
196 and colleagues (1991), object size influences neither the amplitude of the velocity peak nor the time  
197 at which maximum grip aperture occurred. In particular, for one monkey (of the three tested), the  
198 latency and amplitude of maximum grip apertures decreased for small objects, and unexpectedly  
199 increased for others. This mixed picture emerges more conclusively upon inspection of Figure 4.  
200 The observable percentage of movement duration where the incidence of key kinematic landmarks  
201 is dependent on object size differs widely across studies, settings and species. It is worth noting  
202 that, in human adults, the temporal incidence of such landmarks is largely rather stable across  
203 studies, resting around the values depicted in Figure 4. This suggests that, for macaques, setting  
204 type is pivotal to determining kinematical timing.

205  
206 --- Insert Figures 3 and 4 about here ---  
207

## 208 **The Effects of Object Distance**

209 Some studies report kinematic changes among humans, with respect to object distance (e.g.  
210 Gentilucci et al., 1991; Jakobson and Goodale, 1991). Researchers have noted observations of  
211 longer movement duration, prolonged arm deceleration time, and lower arm peak velocity  
212 amplitude, together with a delayed amplitude of maximum grip aperture for objects that are farther  
213 away, relative to objects in closer proximity (Gentilucci et al., 1991; Jakobson and Goodale, 1991).

214 A naturalistic study, by Sartori et al. (2013b), evaluated macaques grasping objects located  
215 at various distances (Fig. 5a). Although the total duration of the movements and the time of the  
216 peak wrist velocity did not differ significantly across the three distances considered, there was a  
217 higher peak velocity amplitude for movements performed to secure more distance with respect to  
218 closer objects (Fig. 5b). The data demonstrate a strong correlation between distances and peak  
219 velocities (Fig. 5c). In accordance with the ‘isochrony principle’ (Viviani and McCollum 1983), a  
220 gearing down/up of movement velocity, depending on the amount of distance to cover, produced a  
221 constant duration of movement. For the grasping component, the time to maximal aperture did not  
222 increase as distances lengthened. In a laboratory setting, Fogassi and colleagues (1991) found  
223 further evidence of the isochrony principle, when one macaque reached toward and grasped objects  
224 at different distances.

225 Observation of humans and macaques reflects significant contrasts between them. Monkeys  
226 acting in a naturalistic setting consistently apply the isochrony principle (to wit, the peak velocity  
227 amplitude increases with distance, while the movement time remains constant). These kinematic  
228 signatures have not, to date, been detected consistently in macaques’ laboratory studies (only in one  
229 monkey in the study by Fogassi et al., 1991) or in human studies (a few participants in one study;  
230 Jeannerod, 1984). Regarding the grasping component the time to the maximal aperture did not  
231 increase with distance remaining invariant in free-ranging macaques. This latter effect has not been  
232 detected in any study of humans or macaques.

233

234 --- Insert Figure 5 about here ---

235

## 236 **The effects of movement direction**

237 Studies examining human movement direction (Connolly and Goodale 1999; Paulignan et  
238 al. 1991, 1997) have revealed longer movement times, with later and higher peaks in wrist velocity,  
239 for right-hand movements heading leftward, rather than rightward. For the grasping component, a

240 delayed time to the maximum grip aperture for movements toward objects on the left has been  
241 noticed (Connolly and Goodale 1999; Paulignan et al. 1997).

242 Roy and colleagues (2002) examined the effect of object location, in terms of leftward and  
243 rightward movements, in macaques acting constrained in a laboratory setting. The study involved  
244 only movements made with the right hand. The objects were spaced evenly and aligned  
245 perpendicularly to the monkey's sagittal axis, situated so that the central and lateral (left and right)  
246 objects were at the same distance from the home pad (Fig. 5d). The study's most salient finding was  
247 that movements toward objects on the left took significantly longer than those directed to either the  
248 right or toward the central object. The differences between the movements directed to the right and  
249 to the central objects were minor and attained statistical significance in only one monkey.  
250 Corresponding with an increase in movement times for leftward-directed movements, grasping for  
251 leftward objects was characterized by smaller velocity peaks, with respect to movements rightward  
252 or the center (Fig. 5e). The impact of object location on the time to maximum grip aperture was  
253 homogeneous across the studied monkeys (Fig. 5e): it was always reached later for movements  
254 leftward, relative to those directed centrally or rightward. Intra-individual differences in grip  
255 amplitude were also observed: two of the monkeys demonstrated smaller grip apertures for  
256 rightward movements, while a third displayed the highest grip aperture for rightward movements.  
257 These data suggest that some cross-species similarities can be understood with regard to longer  
258 movement times, as well as later and higher wrist velocity peaks for right-hand movements,  
259 heading leftward. Like humans, for the grasping component, the animals presented a delayed time  
260 to the attainment of maximum grip aperture for movements toward objects located on the left  
261 (Connolly and Goodale 1999; Paulignan et al. 1997).

262  
263

## 264 **The Effects of Posture**

265 No studies of humans have examined the extent to which 'macaque-like' body postures (i.e.,  
266 seated and tripedal stance) impact kinematic parameterization of reach-to-grasp movements,

267 thereby rendering most cross-species comparisons impossible. To date, only the macaques’  
268 naturalistic study outlined below has tackled this issue. Postural effects were gauged by examining  
269 the macaques’ grip behaviors in two postural positions: in a sitting position (Fig. 6a) or paused and  
270 still, following quadrupedal locomotion (i.e., tripodal stance; Fig. 6b; Sartori et al. 2014a).  
271 Individual macaques were filmed on their approach, when they stopped briefly in a tripodal  
272 position, and then grasped an object of interest. The object/s was/were at the same approximate  
273 distance from the subject’s initial position in both situations studied. The kinematic signatures of  
274 grasping in a seated position mirrored those described above for the ‘object size’ effect (see Fig.  
275 6c). Instead, the primates displayed analogous kinematic patterns, for both the PG and the PoG,  
276 with regard to time and amplitude of the maximum grip aperture, when the prehensile action took  
277 place in a tripodal stance (please refer to the solid lines in Figs. 6c,d). One factor could  
278 hypothetically account for this finding: given the quantity of motor programming resources devoted  
279 to maintaining balance and coordination during locomotion (e.g., Dunbar and Badam 1998; Larson  
280 1998; Patel 2010), primates probably apply a compensatory strategy when they are simultaneously  
281 walking (i.e., locomotion) and while planning a grasping action. Theoretically, quadrupedal  
282 locomotion imposes greater demands on the central nervous system, relative to retain a seated  
283 posture. Adopting a hybrid grip pattern for different-sized objects seems to compensate for this  
284 disparity of required effort. It cannot be excluded, however, that this effect might be simply related  
285 to important biomechanical constraints that do not require neural explanations. Further research to  
286 clarify this aspect is needed.

287  
288 --- Insert Figure 6 about here ---  
289

## 290 **The Effects of Speed**

291 When human beings rush to execute rapid reach-to-grasp movements, they open their hands  
292 more widely than they do when moving at a natural speed, thereby increasing their tolerance for

293 positioning errors that derive from the higher wrist variability (Wing et al. 1986). A greater hand  
294 aperture represents an error-compensating adjustment, to avoid a collision of the thumb or fingertip  
295 with the object in question.

296 Monkeys' activities, as they snatch food items from one another (i.e., snatching condition)  
297 or in the absence of competition or threats from rivals (i.e., unconstrained condition) have been  
298 compared to characterize the impact of speed on the kinematics of prehensile actions (Sartori et al.  
299 2015). The type of action (snatching vs. unconstrained) affected both the reaching and the grasping  
300 components of the movements (Figs. 7a,b). In terms of movement time, snatching movements  
301 required less time than unconstrained movements. Wrist peak velocity was higher and manifested  
302 earlier for snatching movements than for unconstrained movements. Further, during the  
303 deceleration phase, a break-point, generally occurring at 80% of the way through the movement's  
304 duration, was only observed among those in the snatching condition (Fig. 7a). The break-point  
305 coincided temporally and correlated with the time of the maximum grip aperture (Fig. 7a; Sartori et  
306 al. 2015), reflecting a high degree of temporal association between the reaching and the grasping  
307 components when a great deal of accuracy (such as that involved in quickly grasping small objects)  
308 is required.

309 The consistent temporal synchronization of reaching and grasping components seems to be  
310 an exclusive trait of free-ranging macaques. The temporal modulation of hand aperture seems,  
311 nevertheless, to distinguish the two species from each other: the time of the maximum grip aperture  
312 is often attained earlier in humans, for faster actions, whereas the inverse condition obtains for  
313 macaques. Like humans, monkeys demonstrated an increase in the amplitude of maximum grip  
314 aperture for the fast condition.

315

316 --- Insert Figure 7 about here ---

317

318

## 320           **Selective Grasping**

321           Although many different objects are present in a visual field, information specific to just one  
322 of these objects uniquely determines the spatiotemporal coordinates of the endpoint of a reaching  
323 gesture, which include orientation, aperture of the hand, etc. This leaves us with a question,  
324 however: Are, the other objects, each of a distinctive size, shape, color and weight, motorically  
325 represented? As the hand is clearly able to (and does) move around and/or above irrelevant objects,  
326 such objects are certainly represented internally. To wit, when a target object is not alone, but rather  
327 flanked by other objects, is the information related to and available from the flankers overlooked?  
328 In humans, information from even irrelevant objects influences motor outputs (Castiello 1999; Tipper  
329 et al. 1998). For instance, when grasping a large target, flanked by an object suitable to a small  
330 grasp, the amplitude of the maximum hand aperture is smaller than it would have been had the  
331 target been presented alone (Castiello 1996). The inverse occurred when grasping a small object,  
332 flanked by a large one. For another example, if an object is close to target, whether it is an obstacle  
333 or not, it renders the reaching trajectory toward the target wider and higher (Tipper et al. 1997).

334           A naturalistic study conducted by Sartori et al. (2014b) investigated macaques grasping  
335 objects in two situations: in the first, the grasped object was located to the monkey's left (Fig. 8a) or  
336 its right (Fig. 8b), and no other objects were within reaching distance; in the second, the grasped  
337 object, either to the right or to the left, was flanked by other objects located to the monkey's right  
338 and within reaching distance (Fig. 8c, d). The hand aperture correlated with the size of the object in  
339 the absence of any other potentially distracting objects in the vicinity. To wit, the maximal hand  
340 aperture was significantly smaller for the smaller objects than for large ones, and vice versa (control  
341 conditions in Fig. 8e; please refer to the 'the effects of object size' section). The study's most  
342 important finding was that, in the other situations, where the target object was not alone, but rather  
343 was in the vicinity of flanking objects the results indicated that the flankers' information did not go  
344 unnoticed, as the aperture of the hand used to grasp the target was affected by the flanker. As

345 revealed in Figure 8e (i.e., incongruent conditions), when the animal grasped a large target, flanked  
346 by an object invoking a small grasp, the amplitude of the maximum hand aperture was smaller than  
347 it would have been if the target had been presented in isolation. The inverse result occurred, when  
348 the animal grasped a small object, flanked by a large one.

349

350 --- Insert Figure 8 about here ---

351

352 In another naturalistic study (Bulgheroni et al. 2017), macaques were observed as they  
353 reached for an object (i) when no other objects were in the vicinity (Figs. 8a,b), (ii) when a nearby  
354 object was present but did not represent an obstacle (i.e., not impeding a movement or requiring a  
355 change in trajectory; Fig. 8c), and (iii) when a nearby object that did represent a potential obstacle  
356 was present (Fig. 8d). The results indicated that the presence of a nearby object did indeed affect the  
357 wrist trajectory (see Figs. 8c,d), as it demonstrated greater deviations from the path (i.e., solid lines  
358 in Figs. 8c,d) with the potential obstacle, relative to the no-nearby-object-condition (i.e., dashed  
359 lines in Figs. 8c,d). Data on the maximum trajectory height (the maximum height reached by the  
360 arm trajectory from the ground) revealed that when the nearby object actually functioned as an  
361 obstacle, the arm trajectory was higher, relative to the no-obstacle-condition (Fig. 8f). When a  
362 nearby object was present but represented no real impediment, maximum trajectory was higher, as  
363 in the presence of a real obstacle (Fig. 8f). These findings suggest that, the presence of a nearby  
364 object, whether it is actually an obstacle or not, renders the reaching trajectory toward the target  
365 wider and higher. The type of representation invoked by the nearby object(s) contains information  
366 about the action that it/they prompt(s), and this information is nested within the one programmed  
367 for the target object. Monkeys are sensitive to non-goal-related-targets' motoric features, given their  
368 potential role as targets capable of triggering action. As the results presented here exactly mirror  
369 those obtained in studies of humans (Castiello 1996, 1999; Tipper et al. 1997, 1998), free-ranging  
370 macaques and humans appear to share a number of kinematic features and neural responses, with



371 regard to the selection mechanisms linked to action control (Allport 1987). This make sense, given  
372 that animals have evolved neural information processing systems to facilitate interaction with the  
373 environment, thereby maximizing its probability of survival and reproduction. Primates and humans  
374 both recognize that, to attain this goal, they must extract appropriate information about the  
375 environment via perceptual systems and in a form that can be deployed to guide actions.

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377  
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### **The Effects of End Goal**

380 How an object is grasped does not depend exclusively on the properties of the object, but is  
381 also influenced by the action's end-goal. In humans, a number of studies have examined how end-  
382 goals influence the execution of reach-to-grasp movements (e.g., Ansuini et al. 2014 for a review).  
383 In these studies, the end-goal varied, while the grasped object, as well as the context, remained  
384 constant. This aspect has been tested in two-digit grasp studies, as well as in multi-digit grasp  
385 studies, exploring the way that the whole hand is shaped during the moment in which the reach-to-  
386 grasp movement unfolds. For instance, Marteniuk et al. (1987), by requesting participants to grasp a  
387 disk and either fit it carefully or throw it, demonstrated that deceleration time was longer for the  
388 fitting condition than for the throwing one. Ansuini et al. (2008), by conducting an analysis of digit  
389 kinematics, revealed that when the bottle was grasped with the intent to pour, both the middle and  
390 the ring fingers were extended farther than they would have been for purposes of displacing,  
391 throwing, or passing it.

392 In macaques, this issue has been tackled only in one neurophysiological study conducted by  
393 Bonini and colleagues (2012). They assessed possible kinematical differences between conditions  
394 where the monkey grasped-to-eat or grasped-to-place different target objects (i.e., pieces of food or  
395 metallic objects), using different types of grip (Fig. 9a). The study focused on two primary  
396 parameters: the maximal distance between the tip of the thumb and the index finger, and the peak  
397 wrist tangential velocity. The study results revealed that hand aperture and peak wrist velocity were  
398 not significantly different when the monkey executed a grasp-to-eat motion or a grasp-to-place

399 motion concerning piece of food (Fig. 9b,c). However, peak wrist velocity was significantly higher  
400 when the monkey executed a grasp-to-place motion on a piece of food, rather than on a metallic  
401 object. Although some differences concerning the end-goal, at the level of the reaching component,  
402 might suggest that, like humans, macaques program their movements differently, pursuant to an  
403 end-goal, the heterogeneity of the dependent measures and conditions tested in the two species  
404 make it advisable to be cautious about drawing any firm conclusion on the matter.

405

406 ----- Insert Figure 9 about here -----

407

## 408 **The Multi-digit Approach**

409 The laboratory studies examined in this section all focused on simultaneous motion, at the joints of  
410 all five digits, during reach-to-grasp movements. In these studies, dimensionality-reducing  
411 techniques (e.g., principal component analysis, [PCA]) were used chiefly to identify the kind of  
412 control strategies underlying the organization of a complex system, like the hand. Employing these  
413 techniques has demonstrated that, in humans, the linear combination of a small number of hand  
414 postures can generate the hand shapes needed to grasp a large variety of objects (Santello et al.  
415 2002; Santello and Soechting 1998).

416 In one study (Mason et al. 2004), macaques performed sensorily- or visually-cued reach-to-  
417 grasp tasks, where the size, shape, and orientation of the objects varied (see Fig. 10a). The wrist-  
418 speed profile was bell-shaped for the reaching component, and the divergence in hand paths, at the  
419 end of the reaching movement, depended on the orientation of the hand preparing to grasp the  
420 object. Hand shaping was initiated at the beginning of the reaching movement and continued  
421 throughout, trying to match object properties, even when the primate was unable to see either the  
422 hand or the object (Fig. 10b). Two synergies identified via PCA were determined to account for  
423 most of the kinematic variability: the first, consisting of an open hand with partially-flexed fingers,

424 explained 93% of the variability; and the second, consisting of an extension of all joints, accounted  
425 for another 4–5% of the variance.

426 A subsequent study, using similar procedures (Mason et al. 2006), investigated the extent to  
427 which individual fingers acted synergistically during the pre-shaping process. Individual fingers  
428 were found to move with a stereotyped temporal profile coupled across the fingers. As such, a  
429 temporal coordination of individual finger seems to be embedded in the overall hand-shaping  
430 synergies. These findings suggest that a control strategy simplifying grasping uses stereotypic  
431 timing for finger movements, relying on amplitudes to match an object's properties. As the  
432 temporal evolution of finger movements is stereotypic and tightly coordinated, the motor system  
433 varies the amplitude of the finger movements to achieve the desired hand shape. That the timing of  
434 the fingers' inflection points was stereotypic and tightly coupled means that the fingers moved  
435 together with the spatiotemporal unity required to shape the hand preparing to grasp an object. The  
436 speed of the finger joint angles, during hand shaping, suggests that this parameter is also vital to the  
437 controlled timing of the task (Prosise et al. 2015; Vinjamuri et al. 2009).

438 Confirmation that grasp shapes for an object during reach is a process that may be mediated  
439 by dedicated grasping synergy derives from studies that used instrumented gloves, rather than three-  
440 dimensional motion analysis systems to monitor joint angles. Overduin and colleagues (2010; see  
441 also Overduin et al. 2008) quantified the object information conveyed by the sensors embedded in  
442 the glove, in terms of the sensorimotor efficiency index (SME; Santello and Soechting 1998). The  
443 SME is an absolute measure of performance that can be defined as the ratio between the  
444 information transmitted by the object and the maximum amount of information transmissible by an  
445 object. As in earlier studies (Mason et al. 2004), sensory data confirmed that grasp pre-shaping for  
446 an object, during reach, is a process that may be mediated by a dedicated grasping synergy  
447 (Overduin et al. 2008). Using a similar technique, Schaffelhofer and colleagues (2015a; see also  
448 Schaffelhofer and Scherberger 2012) proposed a musculoskeletal approach to the study of the upper  
449 extremity, thereby employing a nonlinear transfer function, from the joint domain to the muscle

450 domain. This enables a compact representation and a high level of decoding accuracy concerning  
451 large repertoires of grasping actions (Fig. 10c). The researchers used PCA, to interpret and visualize  
452 the large repertoire of grasping movements in both degrees of freedom (DOF) and the  
453 musculotendon unit (MTU) space. Notably, the DOF and the MTU space demonstrated a strong  
454 similarity within PCA coordinates. Almost the same cluster overlaps were observed for the DOF  
455 and the MTU representation. Eight PCA components were determined to be sufficient to account  
456 for more than 95% of variance across all conditions in the MTU space, whereas in the DOF space,  
457 around 11 components were required to account the same amount of variance. The lower  
458 dimensional representation in the MTU space is remarkable, as the number of MTU (i.e., 50)  
459 involved in grasping strongly exceeded the number of DOF (i.e., 27). Overall, this model employs a  
460 nonlinear transfer function, from the joint domain to the muscle domain, to enable a more compact  
461 representation and a higher level of decoding accuracy of large repertoires of grasping actions than  
462 was possible via the traditional method of joint kinematics recording.

463         Neurophysiological studies aimed at uncovering how the kinematics of reach-to-grasp  
464 movements are encoded at the neuronal level used similar procedures, like PCA (Mason et al. 2001;  
465 Mollazadeh et al. 2014; Saleh et al. 2010; Schaffelhofer et al. 2015b) or a more novel version of this  
466 technique, known as demixed principal component analysis (dPCA; Takahashi et al. 2017). Such  
467 studies confirmed results obtained in studies in which surgical procedures were not performed, in  
468 terms of synergies. Furthermore, the results are in line with human studies aimed at decoding  
469 kinematics of individual fingers' movement at neural level with electrocorticograms (ECoG;  
470 Kubanek et al. 2009). The decoding of continuous grasping movements shows that the many  
471 degrees of freedom inherent to finger movements can be represented by a few principal component  
472 representations (Flint et al. 2017).

473         Altogether, these findings have shown that, as is the case for humans (Santello et al. 2002;  
474 Santello and Soechting 1998), for macaques, the linear combination of a small number of hand  
475 postures can generate the hand shapes needed to grasp a large variety of objects. The need to

476 simplify control strategies concerned with the reduction of the number of degrees of freedom, to  
477 minimize the complexity of the control problem, has been asserted by various authors, on the basis  
478 of human and macaque data (Arbib et al. 1985; Iberall and Fagg 1996). One solution to the  
479 complexity problem involves the use of a small number of synergies (D'Avella et al. 2003;  
480 Schieber and Santello 2004). Synergistic hand shaping would involve movement of the digits in a  
481 highly coordinated, dependent pattern. In terms of homologies, it must be noted that, on some  
482 occasions, the variance accounted for by the PCAs and the SME is somewhat lower in monkeys  
483 than in humans, but this difference probably reflects the broader selection of objects used in human  
484 studies. Basically, however, the postures and the timing of hand shaping are common to humans  
485 and monkeys.

486

487 --- Insert Figure 10 about here ---

488

489 The multi-digit studies mentioned above focused primarily on variations in the digit and  
490 wrist angles used to grasp various objects, without conducting a simultaneous examination of the  
491 impact of object and location. To plug this gap, Rouse and Schieber (2015) focused on analyzing  
492 joint angles, from the shoulder to the five digits. The variation of each angle, depending on the  
493 location, on the object, and on the interaction between these two factors, was calculated as a  
494 function of time. Two main phases were identified: an early phase involving location effects from  
495 the shoulder to the digits, followed by a phase driven by object effects at the level of joint angles  
496 distal to the shoulder. The effects, relative to the interaction between location and object, were  
497 rather small. Whereas location did not influence grasp shape, the object influenced the reach  
498 trajectory. These findings suggest that controlling reach-to-grasp movements develops via two  
499 sequential phases: a first phase, concerned with the arm bringing the hand toward the object; and a  
500 second phase, shaping the arm/hand ensemble to grasp and manipulate the object. A pause occurred  
501 in many joint angles, at the time of the transition from one phase to another. These pauses might be

502 indicative of a shift from an initial phase that guides the extremity to the intended location, to a  
503 subsequent phase that prepares the extremity for grasping and manipulating the intended object.  
504 These observations are consistent with human studies by Jeannerod (1984, 1986) who observed  
505 similar pauses in hand opening, at approximately the time of peak transport velocity.

506

## 507 **Conclusions**

508 First and foremost, an inspection of Table 2 seems to confirm the existence of some  
509 similarities between macaques and humans, when certain conditions for a comparison are met. For  
510 instance, macaques tested in both naturalistic and behavioral laboratory settings seem to modulate  
511 the kinematics according to object size, as humans do. However, the information depicted in Figure  
512 4 suggests that this might not be the case, and that a certain degree of caution should be used when  
513 declaring similarities. Here, the temporal distribution of key kinematic variables reveals interspecies  
514 differences. To wit, both humans and macaques modulate temporal aspects of kinematics depending  
515 on object properties, but in some cases, the form of such modulation differs. When we inspect the  
516 time of the maximum aperture for the grasping component and the time of peak velocity for the  
517 reaching component, with respect to the object size, the results for macaques examined in different  
518 settings are scattered, diverging from the human data (Fig. 4). Rather, a similarity across species  
519 emerges, as far as object distance is concerned. The time to peak velocity takes a similar percentage  
520 of movement time for macaques in naturalistic setting as it does for humans. Overall then, it would  
521 seem that the mode of timing the kinematic patterning, related to the intrinsic (i.e., size) and  
522 extrinsic (i.e., location) properties of objects adheres to different rules for macaques acting in  
523 different settings than for humans. This is an important issue because the incidence of these  
524 measures is an essential condition for a successful reach-to-grasp movement. The very fact that  
525 such timing varies across settings and species is suggestive of the existence of diverse modes for  
526 programming the action. This aspect it is also important because it seems that even though humans  
527 and macaques mobilize similar neural structures for reaching to grasp, this may not translate into

528 macaques and humans sharing conceptual motivation for movement beyond the purely  
529 physiological trait. In other words, that they use the same neural structures does not mean that both  
530 species motorically interpret their perceptions (of objects and context) in the same way.

531  
532 --- Insert Table 2 about here ---

533  
534 A second critical aspect that emerges during an inspection of Table 2, is that the majority of  
535 conditions tested in naturalistic and behavioral laboratory settings have not yet been assessed in  
536 semi-naturalistic and neurophysiological settings. We feel that this gap in the literature must be  
537 filled, particularly for studies conducted in neurophysiological settings. The overarching aim of  
538 these investigations is to gain a more robust understanding of how kinematic parameterization can  
539 be accurately decoded from the cortical areas dedicated to the planning and execution of reach-to-  
540 grasp movements, given the important implications such knowledge would have for the neural  
541 guidance of hand prosthetics. Although some work in terms of hand shaping (i.e., multi-digit  
542 approach) confined to whole hand grasping movements has been done in macaques (Schaffelhofer  
543 et al. 2015a) and humans (Flint et al. 2017), knowing how the neural decoding of kinematics is  
544 modulated according to distances, locations, sizes of objects and type of grasp appears pivotal for  
545 implementing flexible myoelectric prosthetics. Needless to say, the effect of the movement speed  
546 would also be a relevant aspect for comparing macaques' and humans' movements, given that  
547 macaques move much more quickly than humans do and that their mode of organizing reach-to-  
548 grasp movements may present some peculiarities, as reported above (i.e., isochrony, break point).  
549 Continuing forth from this analysis, it is notable that choosing a grip does not depend exclusively  
550 on the visual properties of the target object, but rather on the environment within which the action  
551 takes place, the meaning invested in the object, and what the individual intends to do with the  
552 object. To date, these aspects have been only marginally addressed. Incorporating the components  
553 of selection and intention into the investigation of reach-to-grasp movements in macaques is  
554 crucial, if this animal model is ever intended to assist in implementing devices used by humans.

555 This aspect could be investigated via the observation of macaques achieving different goals with the  
556 same object, as has already been tested in humans. Generally, extending the research into more  
557 naturalistic, less constrained settings, wherein macaques interact with familiar objects that are, in  
558 reality, part of their behavioral repertoire, would afford invaluable information on the very nature of  
559 these mechanisms. The development of wireless recording systems would make it feasible to record  
560 neural activity in macaques in naturalistic settings, facilitating the study of a greater number of  
561 subjects, thereby to furnishing the observations with more statistical power.

562         Aside from rendering research across settings and species more homogeneous, there are  
563 other factors that, in our opinion, must be considered to enable future research to better characterize  
564 the kinematics underlying reach-to-grasp movements in macaques, which in turn would allow for a  
565 more meaningful comparison with human movements (Napier, 1956; Cutkosky, 1989; Bullock and  
566 Dollar, 2011). It is worth noting that, in humans, lateralized and cognitive functions are largely  
567 linked to handedness-related differences. The majority of the human population (90%) is right  
568 handed, across all human societies and over long time periods (Cashmore et al. 2008; Fitch and  
569 Braccini 2013). When comparing the population-level hand dominance among humans and  
570 nonhuman primates, the results appear to be inconsistent, because assessing hand preference  
571 depends strictly on the tasks employed and the statistical approaches used to characterize hand  
572 preference (Hopkins 2013a, b). It is worth noting that handedness-related tasks (e.g., food reaching,  
573 haptic reaching, joystick tasks, quadrupedal reaching, and bimanual feeding) vary greatly across  
574 studies. According to Fagot and Vauclair (1991), the task and task demands are relevant factors in  
575 determining the strength of lateralization observed in nonhuman primates. In particular, tasks that  
576 require bimanual coordination are more prone to elicit a stronger manual laterality in non-human  
577 primates, relative to actions that are simple and routine. These latter tasks would also be poor  
578 indicators of hand preference, due to their low cognitive and motor involvement (Fagot and  
579 Vauclair 1991; Regaiolli et al. 2018). Papademetriou and colleagues (2005) performed a meta-  
580 analysis of 62 studies representing 31 species (including prosimians, New World monkeys, Old



World monkeys, and apes) that indicated a population-level left-handed bias for prosimians and Old World monkeys, and determined that six out of 12 studies indicated a population-level right-handed bias among apes. Further evidence of a population-level bias for the right handedness has been reported in relation to chimpanzees, with three populations undergoing a task requiring coordinated bimanual actions (*tube task*). The results revealed an approximate 2:1 ratio of right-to-left-handed individuals among a population of captive chimpanzees (Hopkins et al. 2004). Evidence collected regarding macaques' one-hand preference is hardly unambiguous. The heterogeneity of results can be ascribed to several factors, ranging from differences in temperament (Thierry 2007) to age and the rearing history of the subjects (Hopkins et al. 2003). No population-level bias in hand use was reported when subjects were observed in unimanual tasks (Howell et al. 2007; Nelson et al. 2011), whereas bimanual tasks (such as the tube task) revealed a population-level preference for the right hand (Westergaard and Suomi 1996) or the left hand (Westergaard et al. 1997).

These considerations should be taken into account, when interpreting the studies cited in this review. In the majority of studies, the researchers measured the exemplars' hand performance during task execution, without any consideration of individual differences in hand preference or, more importantly, differences between humans and non-human primates, in terms of population-level motor bias. For example, the right hand has been measured in the majority of naturalistic and behavioral laboratory (although the left hand was blocked) studies adopting the two-digit approach. Conversely, the majority of multi-digit studies considered the left hand or either the left or the right hand, in different exemplars. Given that additional gap in the research, it remains difficult to engender a homogeneous picture, and this complicates the issue of homology. Ideally, the left and the right hand should be subject to equally thorough investigative measures. Consider that both right-and left-handed humans exhibit very distinctive neural and kinematic reach-to-grasp patterning, when using a non-dominant hand (Begliomini et al. 2008; Gonzalez et al. 2006, 2007).

Another important consideration involves the developmental trajectory. Some studies revealed that infant macaques develop the capacity to reach and grasp starting from the third week

607 of life (e.g., Nelson et al. 2011) whereas in humans, not until infants reach approximately nine  
608 months of age that their hands start to shape in response to object properties (Von Hofsten &  
609 Ronnqvist 1988). This suggests that, in a short period of time, infant macaques develop the capacity  
610 to move about in an environment and interact with objects in an adult-like fashion (Sclafani et al.  
611 2015). A carefully-designed kinematical investigation could determine whether this is truly the case  
612 or if the seemingly mature pattern disguises a simpler developmental trajectory that merely shifts,  
613 from broad to refined motor skills.

614         Although ever more information is constantly being collected, with regard to the behavioral  
615 manifestations of reach-to-grasp movements in macaques, a substantial amount information has yet  
616 to be revealed or understood, about the variables involved, the organization of prehensile activities  
617 among these primates, and interspecies similarities and differences. Recent methodological  
618 advances should pave the way for a more direct and complete examination of the kinematics  
619 underlying hand movements in these primates, across various settings. Carefully-designed studies  
620 will conclusively answer the remaining questions and hopefully lead to innovative experiments that  
621 would facilitate a more sophisticated mode of comparison between humans and macaques. This is  
622 critical, given that the neuronal mechanisms responsible for the control of reach-to-grasp movement  
623 have already been studied, particularly in macaque monkeys. Comprehending the similarities  
624 linking human and macaque movement behavior is essential, if we ever hope to capitalize on the  
625 animal model for human benefit. There is not previously published comparative account that details  
626 the reach-to-grasp kinematics of macaque monkeys. The purpose of the present review was to  
627 provide such a description.

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858

859 Figure captions

860 Figure 1. The main categories of grips used for manipulation of objects. For each grip type, the  
861 surface area of contact is shown in grey on the hand diagram (modified from MacFarlane and  
862 Graziano 2009).

863

864 Figure 2. Graphical representation of the wrist velocity profile (a) and of the grip aperture (b).

865

866 Figure 3. (a) A schematic drawing showing the seated posture adopted by the animal during reach-  
867 to-grasp movements. In the upper call-out, a precision grip involving the tip of the forefinger and  
868 thumb to hold small objects is represented. In the lower one, a power grip in which all four fingers  
869 are opposed to the thumb to hold larger objects is represented. (b) Wrist peak velocity and (c) grip  
870 aperture for power (left panel) and precision (right panel) grip movements in a representative  
871 subject. (d) The setting for laboratory behavioral experiments. For the size experiment a small (S)  
872 or a large (L) cylinder (1.5 or 2.5 cm diameter, respectively) was presented on a tray fitted onto the  
873 primate chair. (e) Time plots of grip aperture and wrist velocity for a representative movement  
874 directed to either the small object or the large object.

875

876 Figure 4. Changes in the relative timing (expressed as a percent of total movement time) of time to  
877 peak velocity (TPV) and the time of maximum grip aperture (TGA) as a function of object size for  
878 the macaques' studies considered in the present review. Dashed vertical lines indicate an  
879 approximate mean value for human studies considering small and large stimuli located at a distance  
880 comparable to the macaques studies (ca 20 cm).

881

882 Figure 5. (a) Overlays show the movements performed by the animal at three different distances. (b)  
883 The average peak wrist velocity (left panel) for objects located at different distances and (c) the  
884 correlation between mean peak wrist velocity and distance from the target (right panel). Modified

885 from Sartori et al. 2013a and Sartori et al. 2013b. (d) Laboratory location experiment. Three  
886 cylinders were aligned perpendicularly to the monkey's sagittal axis. (e) Wrist velocity and grip  
887 aperture profiles of 3 individual movements directed to the 3 object locations. Note that leftward  
888 movements showed later wrist velocity and grip aperture peaks (modified from Roy et al. 2000,  
889 2002).

890

891 Figure 6. Graphical representation of the monkeys (a) sitting and (b) in a tripedal stance as they  
892 reached and grasped. A schematic drawing of the interaction between the type of posture and the  
893 type of grip for the time (c) and the amplitude (d) of the maximum grip aperture. Bars represent the  
894 standard error of means. Note that for the tripedal stance the values for these measures remain  
895 invariant independently from the type of grasp (modified from Sartori et al. 2014a).

896

897 Figure 7. Superimposition of the velocity and grip profiles for (a) the snatching and (b) the  
898 unconstrained conditions. In panel 'a' arrows indicate the correspondence between the time at  
899 which the maximum grip aperture and the beginning of the low velocity phase occur for a  
900 movement in the snatching condition (modified from Sartori et al. 2015). Please note that wrist peak  
901 velocity was reached earlier for the snatching than for the unconstrained condition ( $161 \pm 21$  ms vs  
902  $215 \pm 20$  ms). And that the time of maximum grip aperture was reached later for the snatching than  
903 for the unconstrained ( $289 \pm 32$  ms vs  $315 \pm 26$  ms).

904

905 Figure 8. A schematic drawing depicting the three experimental conditions and mean wrist  
906 trajectories. The left (a) and the right (b) target is reached in isolation. (c) The left target along with  
907 the distractor (solid line represents the mean trajectory path). For the sake of comparison, the  
908 dashed line represents the mean trajectory path for the left target without distractors. (d) The right  
909 target with the distractor (solid line represents the mean trajectory path). For the sake of  
910 comparison, the dashed line represents the mean trajectory path for the right target without

distractors. (e) A graphic representation of the interaction “condition by stimulus size” for the test conditions. Grip apertures for large and small objects for the control (no distractor), congruent (target and distractor of a similar size), and incongruent (target and distractor of a different size) experimental conditions are represented. Bars represent the standard error of means. (f) representative example of maximum trajectory height for the right target alone (solid line) and for the right target along with the distractor (dashed line) conditions. Values on the axis are in millimetres (mm). Axis z = sagittal axis; axis y = vertical axis. The arrow indicates the point of maximum trajectory height (modified from Bulgheroni et al. 2017 and Sartori et al. 2014b).

919

Figure 9. (a) The grip types employed for grasping target objects. (b) Maximal finger aperture during the execution of grasp-to-eat, grasp-to-place an object, and grasp-to-place food with finger prehension (FP), precision grip (PG), and side grip (SG). (c) Wrist velocity peak during the execution of grasp-to-eat, grasp-to-place an object, and grasp-to-place food with FP, PG, and SG (modified from Bonini et al. 2012)

925

Figure 10. (a) Objects grouped into four classes indicated by the labels. (b) Hand postures over time reflect the evolution of hand shaping during reaching. Behavioral task. (c) Macaque monkeys grasp a wide range of objects presented on a PC-controlled turntable. During a recording session the animals wore an instrumented glove holding electromagnetic sensor coils for tracking finger, hand, and arm movements (modified from Mason et al. 2004; 2006 and from Schaffelhofer et al. 2015a).

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Table 1. A brief overview of the kinematical studies carried out in macaques in different settings. In parentheses further specifications regarding the number of participants.

Study	n	hand	Type of study	Type of Object	Type of Grip	Dependent measures	
						Reaching component	Grasping component
Sartori et al., 2013a	20	<i>RH</i>	<i>Naturalistic</i>	Balls of clay; Round stones	PG/PoG	Movement duration; time/amplitude wrist peak velocity; deceleration time	Time/amplitude maximum grip aperture
Sartori et al., 2013b	20	<i>RH</i>	<i>Naturalistic</i>	Balls of clay	PG/PoG	Movement duration; time/amplitude wrist peak velocity	Time/amplitude maximum grip aperture
Sartori et al., 2014a	10	<i>RH</i>	<i>Naturalistic</i>	Small/large objects	PG/PoG	Movement duration; deceleration time; time/amplitude wrist peak velocity	Time/amplitude maximum grip aperture
Sartori et al., 2014b	20		<i>Naturalistic</i>	Small/large objects	PG/PoG		Maximal hand aperture
Sartori et al. 2015	6	<i>RH</i>	<i>Naturalistic</i>	Food items	PG	Movement duration; Time/amplitude wrist peak velocity; Deceleration time; Breakpoint (Low velocity phase)	Time/amplitude maximum grip aperture
Bulgheroni et al., 2017	6	<i>RH</i>	<i>Naturalistic</i>	Food items	PG	Lateral deviation wrist trajectory; Maximum wrist trajectory height	
Christel and Billard, 2002	5	<i>RH</i> / <i>LH</i>	<i>Semi-naturalistic setting</i>	Food items	PG	Movement duration; Angular displacement; Angular speed velocity; Angular acceleration	Time/amplitude maximum grip aperture; Angular velocity and acceleration of fingers' aperture
Fogassi et al., 1991	1	<i>RH</i>	<i>Laboratory setting</i>	Stimuli of three different sizes	PG/PoG/FG	Movement duration; Time/amplitude wrist peak velocity	Time/amplitude maximum grip aperture
Roy et al., 2000	2	<i>RH</i>	<i>Laboratory setting</i>	Large or small cylinders		Movement duration Time/amplitude wrist peak velocity	Time/amplitude maximum grip aperture
Roy et al., 2002	3	<i>RH</i>	<i>Laboratory setting</i>	Concentric white plastic cylinders		Movement duration; Time/amplitude wrist peak velocity, acceleration and deceleration	Time/amplitude maximum thumb-index and thumb-middle finger grip aperture

Table 1 continued

Mason et al., 2004	2	<i>RH</i> (1) <i>LH</i> (1)	<i>Laboratory setting</i>	Set of 16 objects divided into 4 classes of cubes, rectangular polygonal and cylinders		Distance between the thumb IP joint and the middle finger DIP joint	Maximum grip aperture
Mason et al., 2006	2	<i>RH</i> (1) <i>LH</i> (1)	<i>Laboratory setting</i>	Set of 16 objects divided into 4 classes of cubes, rectangular polygonal and cylinders		Arm peak velocity	Time/amplitude maximum grip aperture; Distance between the thumb IP joint and the middle finger DIP joint
Overduin et al., 2010	1	<i>LH</i>	<i>Multidigit/ laboratory studies</i>	25 objects (cubes, spheres, cylinders)		Wrist	MCP carpal metacarpal; CMP opposition/reposition adduction/abduction and flexion/extension; SME index
Schaffelhofer et al., 2015a	2	<i>UN</i>	<i>Multidigit/ laboratory studies</i>	Set of 48 objects divided into 7 categories (rings, cubes, spheres, horizontal cylinders, boxes, vertical cylinders and specials)	PG/PoG	Shoulder elevation rotation and adduction/abduction; forearm rotation; elbow flexion; wrist flexion/extension, adduction/abduction and pronation/supination	MCP flexion/extension and adduction/abduction, DIP flexion/extension, PIP flexion/extension
Schaffelhofer and Scherberger, 2012	2	<i>UN</i>	<i>Multidigit/ laboratory studies</i>	Set of 48 objects divided into 7 categories Rings, cubes, spheres, horizontal and vertical cylinders, boxes, specials	PG/PoG	Wrist flexion/extension, adduction/abduction, pronation/supination; elbow flexion; shoulder elevation, rotation and adduction/abduction	MCP adduction/abduction, flexion/extension; PIP; DIP
Rouse and Schieber, 2015	3	<i>RH</i>	<i>Multidigit/ laboratory studies</i>	4 objects in 8 different positions (perpendicular cylinder, coaxial cylinder, button, sphere)		Shoulder; elbow; wrist	MCP joints, Thumb, PIP flexion/extension

Table 1 continued

Schaffelhofer et al., 2015b	2	LH	Neurophysiological	Set of 48 objects divided into 7 categories (rings, cubes, spheres, horizontal cylinders, boxes, vertical cylinders and specials)	PG/PoG	Shoulder elevation, rotation, and adduction/abduction; forearm rotation; elbow flexion/extension; wrist flexion/extension, deviation and pronation/supination	MCP joints, DIP joints, PIP flexion/extension
Takahashi et al., 2017	2	LH	Neurophysiological	Set of 5 objects in different orientations (cylinder horizontal, out and vertical, small disc horizontal, out and vertical, key, large disc horizontal and vertical, ring horizontal and vertical)	Diverse grips	Humerus flexion/extension, adduction/abduction and rotation; elbow flexion/extension; wrist pronation/supination, abduction/adduction and flexion/extension	MCP flexion/extension and adduction/abduction; PIP flexion/extension

935 Notes. FP = Fingers grip; PG = Precision grip; PoG = Power grip; SD = Side grip; IP = Interphalangeal Joint; DIP = Distal Interphalangeal Joint; PIP =  
936 Proximal Interphalangeal Joint; MCP = Metacarpal Phalangeal Joint; CMP = Carpometacarpal; SME = Sensorimotor Efficiency; LH = Left hand. RH = Right  
937 Hand; UN = Hand used unspecified.

Table 2a. Differences and similarities in the modulation of the main dependent measures characterizing the reaching component depending on object size, object distance, object location and movement speed between macaques and humans.

Type of setting	Experimental manipulation	Movement Duration		Deceleration Time		Amplitude Peak Velocity		Breakpoint	
		M	H	M	H	M	H	M	H
Naturalistic	Size Distance Location Speed	=		=		=		NF	
		≠		≠		=		NF	
		NT							
		=		=		=		≠	
Laboratory Behavioral	Size Distance Location Speed	=		=		≠		NF	
		=		=		=		NF	
		=		=		=		NF	
		NT							
Laboratory Neurophysiology	Size Distance Location Speed	NT							
		NT							
		NT							
		NT							
Seminaturalistic	Size Distance Location Speed	NT							
		NT							
		NT							
		NT							

Notes. M = Macaques; H = Humans; NF = Not found; NT = Not tested; '=' = same modulation for humans and macaques; '≠' = different modulation for humans and macaques



Table 2b. Differences and similarities in the modulation of the main dependent measures characterizing the grasping component depending on object size, object distance, object location and movement speed between macaques (M) and humans (H).

Type of setting	Experimental manipulation	Time Maximum Grip Aperture		Amplitude Maximum Grip Aperture		Evidence of Synergies		Sensorimotor Efficiency Index	
		M	H	M	H	M	H	M	H
Naturalistic	Size Distance Location Speed	=		=		NT		NT	
		≠		≠					
		NT							
		≠		=					
Laboratory Behavioral	Size Distance Location Speed	=		=		=		=	
		NT							
		=		=		NT			
				NT					
Laboratory Neurophysiology	Size Distance Location Speed			NT		=		NT	
Seminaturalistic	Size Distance Location Speed			NT		NT		NT	
				NT					
				NT					
				NT					

Notes. NT = Not tested; '=' = same modulation for humans and macaques; '≠' = different modulation for humans and macaques



Side grip



Precision grip

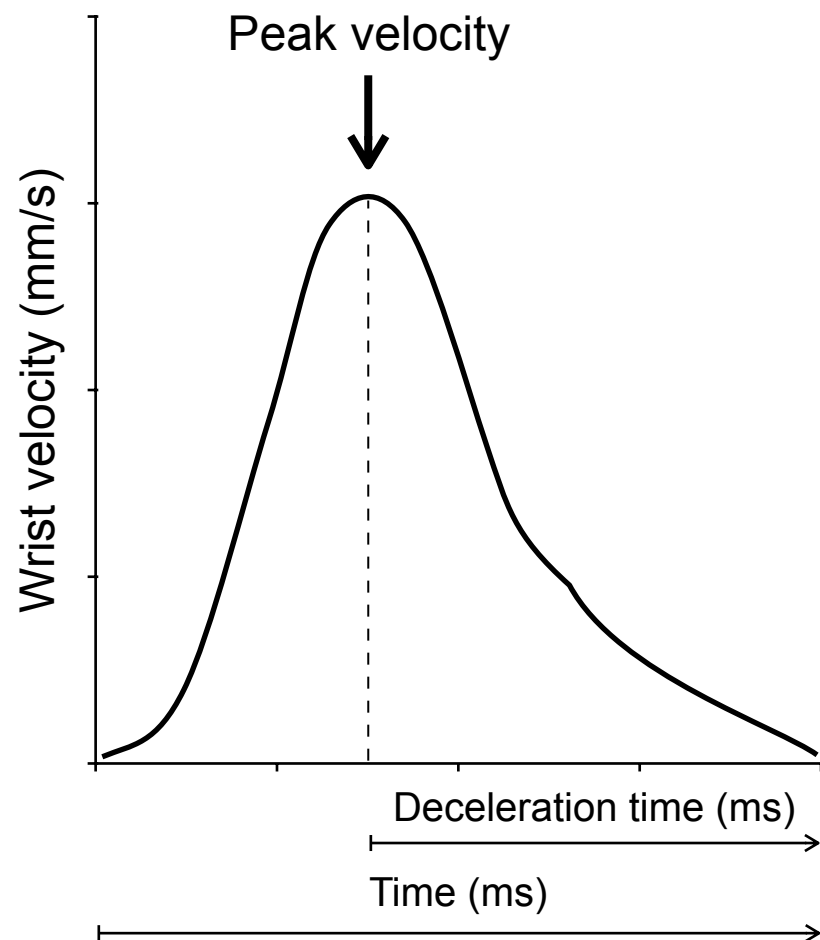


Thumb-to-Second-Third grip



Power grip

a)



b)

