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

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

33

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.

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164 **Two-Digit Approach**

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

168

169 --- Insert Figure 2 about here ---

170

171 **The Effects of Object Size**

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

178 With the foregoing details in mind, it is worth noting that a naturalistic study, by Sartori and
179 colleagues (2013a), examining macaques employing PG movements to grasp small objects and PoG
180 movements to grasp large ones (Fig. 3a), reported that each type of movement was characterized by
181 a specific kinematic signature that mirrored human data. Movements toward smaller objects led to a
182 prolonged movement duration, relative to movements toward larger objects. The deceleration time
183 was longer for the small objects, relative to the larger ones, whereas the peak velocity amplitude
184 was higher for larger objects than for smaller objects (Fig. 3b). The latency of peak velocity did not
185 differ, with respect to object size. The grasping component was characterized by a maximum grip
186 aperture, smaller and attained earlier for smaller objects, relative to larger ones (Fig. 3c). Turning to
187 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.

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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).

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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 tripod 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., tripedal stance; Fig. 6b; Sartori et al. 2014a).
271 Individual macaques were filmed on their approach, when they stopped briefly in a tripedal
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 tripedal 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 ---
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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

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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.

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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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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.

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

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

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

605 Another important consideration involves the developmental trajectory. Some studies
606 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 ± 21 ms vs
902 215 ± 20 ms). And that the time of maximum grip aperture was reached later for the snatching than
903 for the unconstrained (289 ± 32 ms vs 315 ± 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

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

919

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

925

926 Figure 10. (a) Objects grouped into four classes indicated by the labels. (b) Hand postures over time
927 reflect the evolution of hand shaping during reaching. Behavioral task. (c) Macaque monkeys grasp
928 a wide range of objects presented on a PC-controlled turntable. During a recording session the
929 animals wore an instrumented glove holding electromagnetic sensor coils for tracking finger, hand,
930 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	RH	Naturalistic	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	RH	Naturalistic	Balls of clay	PG/PoG	Movement duration; time/amplitude wrist peak velocity	Time/amplitude maximum grip aperture
Sartori et al., 2014a	10	RH	Naturalistic	Small/large objects	PG/PoG	Movement duration; deceleration time; time/amplitude wrist peak velocity	Time/amplitude maximum grip aperture
Sartori et al., 2014b	20		Naturalistic	Small/large objects	PG/PoG		Maximal hand aperture
Sartori et al. 2015	6	RH	Naturalistic	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	RH	Naturalistic	Food items	PG	Lateral deviation wrist trajectory; Maximum wrist trajectory height	
Christel and Billard, 2002	5	RH /LH	Semi-naturalistic setting	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	RH	Laboratory setting	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	RH	Laboratory setting	Large or small cylinders		Movement duration Time/amplitude wrist peak velocity	Time/amplitude maximum grip aperture
Roy et al., 2002	3	RH	Laboratory setting	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	RH (1) LH (1)	Laboratory setting	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	RH (1) LH (1)	Laboratory setting	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	LH	Multidigit/ laboratory studies	25 objects (cubes, spheres, cylinders)		Wrist	MCP carpal metacarpal; CMP opposition/reposition adduction/abduction and flexion/extension; SME index
Schaffelhofer et al., 2015a	2	UN	Multidigit/ laboratory studies	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	UN	Multidigit/ laboratory studies	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	RH	Multidigit/ laboratory studies	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	<i>Size</i>	=		=		=		NF	
	<i>Distance</i>	≠		≠		=		NF	
	<i>Location</i>	NT							
	<i>Speed</i>	=		=		=		≠	
Laboratory Behavioral	<i>Size</i>	=		=		≠		NF	
	<i>Distance</i>	=		=		=		NF	
	<i>Location</i>	=		=		=		NF	
	<i>Speed</i>	NT							
Laboratory Neurophysiology	<i>Size</i>	NT							
	<i>Distance</i>	NT							
	<i>Location</i>	NT							
	<i>Speed</i>	NT							
Seminaturalistic	<i>Size</i>	NT							
	<i>Distance</i>	NT							
	<i>Location</i>	NT							
	<i>Speed</i>	NT							

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

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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	<i>Size</i>	=		=		NT		NT			
	<i>Distance</i>	≠		≠							
	<i>Location</i>	NT									
	<i>Speed</i>	≠		=							
Laboratory Behavioral	<i>Size</i>	=		=		=		=			
	<i>Distance</i>	NT									
	<i>Location</i>	=		=						NT	
	<i>Speed</i>	NT									
Laboratory Neurophysiology	<i>Size</i>	NT				=		NT			
Seminaturalistic	<i>Size</i>	NT				NT		NT			
	<i>Distance</i>	NT									
	<i>Location</i>	NT									
	<i>Speed</i>	NT									

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



Side grip



Precision grip

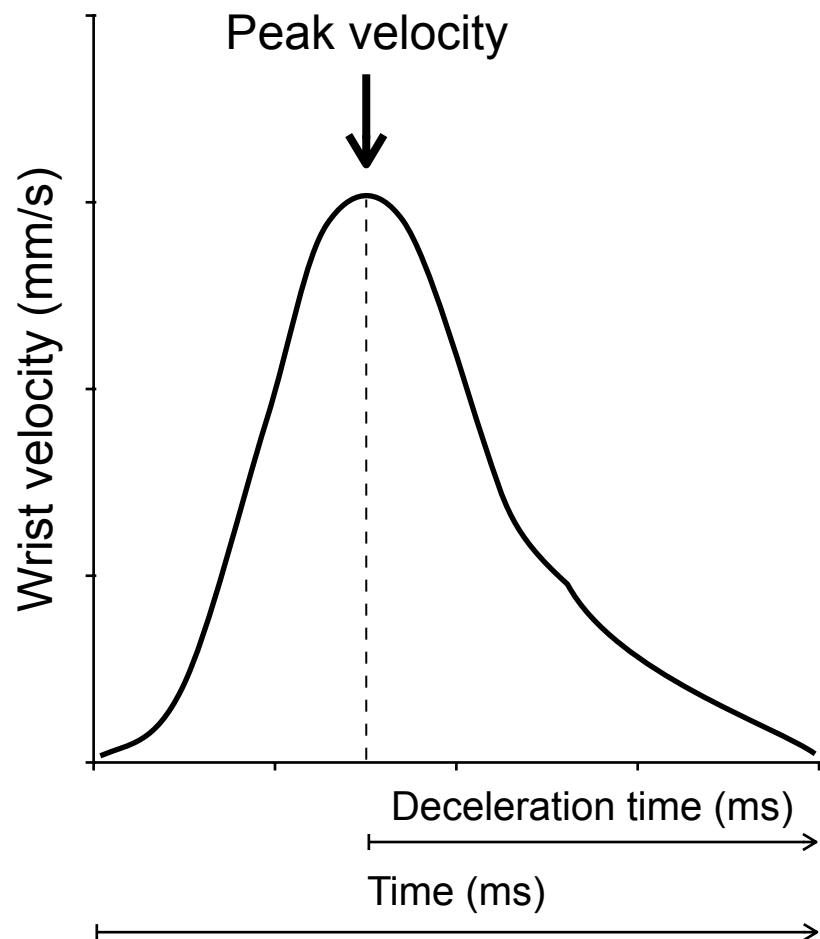


Thumb-to-Second-Third grip



Power grip

a)



b)

