SENSORIMOTOR DEPRIVATION INDUCED BY IMMOBILIZATION MODIFIES THE KINEMATIC OF A REACHING-TO-GRASP.

M. Bassolino, M. Jacono, M. Bove, L. Fadiga, Thierry Pozzo

► To cite this version:

M. Bassolino, M. Jacono, M. Bove, L. Fadiga, Thierry Pozzo. SENSORIMOTOR DEPRIVATION INDUCED BY IMMOBILIZATION MODIFIES THE KINEMATIC OF A REACHING-TO-GRASP.. Neuroscience, 2012, epub ahead of print. 10.1016/j.neuroscience.2012.04.019 . hal-00705304

HAL Id: hal-00705304

<https://u-bourgogne.hal.science/hal-00705304>

Submitted on 12 Jun 2012

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 “SENSORIMOTOR DEPRIVATION INDUCED BY IMMOBILIZATION MODIFIES THE
2 KINEMATIC OF A REACHING-TO-GRASP”

3

4 *Michela Bassolino^{1,2}, Marco Jacono¹, Marco Bove³, Luciano Fadiga^{1,4}, Thierry Pozzo^{1,5}*

5

6 1.IIT, Istituto Italiano di Tecnologia, Genoa, Italy;

7 2. DIST, University of Genoa, Italy;

8 3. Departement of Experimental Medicine, Section of Human Physiology, University of Genoa,
9 Italy;

10 4. DSBTA, Section of Human Physiology, University of Ferrara, Italy;

11 5. INSERM, U887, Motricité-plasticité, Dijon, France.

12

13

14

15 ACKNOWLEDGEMENTS

16

17 ABSTRACT

18 During reaching-to-grasp, the hand shape has to adapt according to the target object (*the grasp*
19 *component*) which the arm is approaching (*the transport component*). This requires a sophisticated
20 coordination between the two components, involving a continuum of feedforward and feedback
21 processes. A constant stream of sensorimotor information seems to be essential to successful
22 perform the task and a transient reduction of these would affect the movement. To test this
23 hypothesis, the right hand and wrist joint of 7 healthy subjects was immobilized with a removable
24 bandage for 10 hours. We compared the kinematic of a reaching-to-grasp performed before and
25 after immobilization as well as with a control group (i.e. not immobilized). Additionally, hand
26 posture was measured by recording the angular position of 16 joint angles of the fingers and thumb
27 at the time of the contact with the object. Further, time series of angular displacement were
28 analyzed by means of Principal components analysis (PCA) to evaluate a potential effect of
29 immobilization on fingers' coordination. Here we found that after immobilization the total duration
30 of reaching movement increased together with an anticipation of the time to peak velocity.
31 Moreover, the maximum grip aperture significantly increased and the hand posture at the end of the
32 grasp changed in the two groups of participants. Nevertheless, the patterns of co-variation between
33 the angular excursion of the digits remained similar before and after immobilization. All together,
34 the present findings demonstrate that a temporary reduction in sensory and motor information
35 modify the kinematic of a reaching-to-grasp both in the transport and grasp phases. However, the
36 two components showed a different recovery time course: while reach duration returned to the
37 baseline value at the lasts repetitions of the task, the maximum grip aperture increased trial after
38 trial.

39

40 INTRODUCTION

41 Reaching-to-grasp is a daily life common motor task, fundamental for interaction with the
42 surrounding environment. It plays a central role in the early development of perception and action
43 (see Piaget 1952, 1954), probably because the hand provides an efficient tool to continuously verify
44 motor and sensory predictions. Two main components contribute to organize these sensorimotor
45 activities. A first progressive opening of the grip, with straightening of the fingers is followed by a
46 gradual closure until it matches the object's dimension and orientation (*the grasp component*, Arbib
47 1981; Jeannerod 1984, for a review Castiello 2005). Contemporaneously, the hand, moving towards
48 the object, follows a characteristic path and timing (*the transport component*, Jeannerod 1999.) A
49 successful performance requires a sophisticated coordination between the two components (Wing et
50 al. 1986; Wallace and Weeks 1988; Jakobson and Goodale 1991; Gentilucci et al. 1992;
51 Paulignan et al. 1991). At last, a synergistic control of each finger's position is essential to correctly
52 adapt the hand shape to the target object (Santello et al. 1998). All these phases involve a
53 continuum of feedforward and feedback processes (Seidler et al., 2004). Predictions about the state
54 of the motor system and environment in addition to sensory feedback can be used to update
55 parameters of the next motion (e.g. Gentilucci et al. 1997). Thus, a constant stream of sensorimotor
56 information seems to be essential for action execution. The presence of these mechanisms raises a
57 fundamental question: what is the effect of a transient lack of sensory information and motor
58 commands in a reaching-to-grasp? Differently stated, what is the behavioral consequence of a short
59 period of immobilization that induces a temporary reduction in sensory and motor information?

60 Previous investigation showed that upper limb immobilization for 12 hours induced
61 significant changes in somatosensory-evoked potentials (SEPs), motor-evoked potentials (MEPs)
62 and slow wave activity during sleep over the sensorimotor areas corresponding to the immobilized
63 limb (Huber et al., 2006). However, little is known on the functional effect of hand and arm
64 immobilization (Moisello et al., 2008). The underlying assumption is that if action execution
65 generates crucial input to the brain to update the next motor command, reaching-to-grasp movement
66 would be significantly affected after upper limb immobilization. To this aim, the right hand and
67 wrist joint of 7 healthy subjects was immobilized with a removable bandage for 10 hours. Two
68 different effects of the short term immobilization on the kinematic of a reaching-to-grasp could
69 occur: **first**, a short period of immobilization would not produce any behavioral effect, as it is
70 sometimes the case during daily life situations in which the arm motion is limited, such as after a
71 long travel or sleeping. **Alternatively**, immobilization may modify the kinematic of a task strongly

72 dependent of sensorimotor information such as reaching-to-grasp. In this context, an adaptation
73 process could be also expected after the immobilization period. If so, a detailed analysis of reaching
74 and grasping, separately, might also reveal different recovery time courses in the two components.

75

76

77 METHODS

78 *Participants.*

79 Thirteen healthy volunteers (7 female, 6 male) participated in the study. All participants were right
80 handed, as determined by the Edinburgh Handedness Inventory (Oldfield, 1971). They reported
81 normal or corrected-to-normal vision, no previous history of neurological disorders or recent
82 orthopedic problems for the right upper limb. All subjects gave their informed consent to participate
83 in the study, which was performed with approval of the local ethics committee and in accordance
84 with the Declaration of Helsinki. All participants were naive to the purpose of the study and
85 received an attendance fee at the end of experiment.

86 *Experimental protocol.*

87 If present, the effect of immobilization could be also dependent on the degree of precision required
88 in the task. To this aim, subjects were instructed to grasp, lift and back down a little yellow wooden
89 pencil (7 cm in length, 1 cm in diameter) with a precision grip and a yellow tennis ball (6 cm in
90 diameter) with a power grip. A power grip is achieved by moving the whole hand, while a precision
91 grip involves grasping an object between the tips of the thumb and index finger (see for example,
92 Napier 1956) in such a way that there is precise control of the position of the object and the
93 grasping forces (Jones & Lederman, 2006). Movement were shown by the experimenter at the
94 beginning of each experimental section. Participants sat in front of a table where on each trial, the
95 experimenter placed the objects to grasp on a marked point. They started and finished each trial in
96 the same fixed position (called “pinch”): they kept the index in contact with the thumb, holding the
97 two fingers on a marked point. This point was drawn on the table 30 centimeters far from the
98 objects. After a brief familiarization phase, they repeated the movement 15 times for each object in
99 a self-paced mode. Subjects were instructed to start the movement when they preferred, after a
100 verbal go-signal given by the experimenter. When the subjects ended the movement, the object was
101 removed and the next one was set. The order of objects presentation was randomized. We compared
102 the kinematic of the reaching-to-grasp in a group of 6 subjects (Control Group, CG) who repeated
103 the task in two following days (first day=Pre, second day=Post), with another group of 7 subjects
104 (Immobilization Group, IG) who did the same task after 10 hours of immobilization (Post) and one
105 day before (Pre). All participants did the task at about 6.30 p.m. The two groups were matched for
106 age and gender (IG: mean age 27.00 ± 1.07 years, range 25-29, 4 female; CG: mean age $27.17 \pm$
107 1.33 years, range 25-29, 3 female).

109 *Immobilization procedure.*

110 In the IG, subjects were instructed to not move the right hand and the wrist joint for 10 hours from
111 the morning (at about 8.30 a.m.) to the evening (at about 6.30 p.m.). We wrapped subjects' hand
112 and wrist with a soft painless bandage used in everyday clinical practice by physiotherapists.
113 Participants wore also a cotton support that limited the arm movement and hold the elbow joint in a
114 comfortable way at 90 degree flexion. As soon as the experimenter removed the bandage, subjects
115 performed the grasping task.

116 *Data acquisition.*

117 The 3d kinematic data were recorded with an optical motion capture system (Vicon), at a frequency
118 of 100 Hz. Retro-reflective markers (4 and 6 mm in diameters) were placed on the hand (19
119 markers), in particular on the metacarpal-phalangeal and the proximal interphalangeal joints, on the
120 nails of each fingers, on the radial and the ulnar styloid process and on the lateral epicondyle of the
121 humerus. At the beginning of each trial, before assuming the "pinch position" (see above), to be
122 sure that all markers were visible by the recording system, the subjects were requested to keep the
123 hand palm-down on the table with the thumb on a marked point. This recorded position was also
124 used as a reference value of participants' hand size and in particular, of the thumb-index distance.
125 Software made with Matlab® (Mathworks, Natick, MA) was employed to filter (Butterworth filter,
126 second order $f_c = 5\text{Hz}$) and analyze the data. Both reaching and grasping components were
127 evaluated. Moreover, we measured also 16 hand angles to describe the hand posture at the time of
128 the contact with the object and their co-variation during the whole motion.

129 *Reach component.*

130 To determine the onset and the end of the reaching movement, we considered the velocity profile of
131 the wrist, applying on it a threshold of the 5% of its maximum (see Santello et al., 2002). Thus, the
132 onset and the end of the reaching movement were respectively set at the first and at the last frame in
133 which subjects moved with a wrist velocity equal to this threshold. We measure the following reach
134 parameters: *reach duration*: the total duration of reaching phase (ms); *time to peak velocity*: the
135 ratio between the time at which the maximum velocity occurred and the total reach duration (%).

136 *Grasp component.*

137 The distance between the two markers located on the nails of thumb and index fingers was
138 calculated during the whole grasping task. The velocity profile of the displacement of this distance
139 was then considered to determine the onset and the end of the duration of the grasping movement.
140 Starting with the hand in “pinch position”, the grasp time course is typically constituted by a phase
141 of finger opening till a maximum (maximal finger aperture) followed by a phase of finger closing
142 on the object (Jeannerod, 1984). Thus, the velocity profile of the variation of the index-thumb
143 distance started from an initial value of zero, when the fingers were in pinch position, was then
144 characterized by a positive peak corresponding to the phase of finger opening, reached the zero at
145 the time of maximal finger aperture and showed a negative peak in the phase of finger closing. The
146 beginning of the grasp was set at the first frame in which the two fingers started to open from the
147 pinch position (i.e., when the velocity of the variation of index-thumb distance increased respect to
148 the initial zero value). On the contrary, the end of the grasp corresponded to the first frame after
149 finger closing in which the time course of the index-thumb distance reached the zero and remained
150 stable at this value at least for 10 following samples (i.e., during the contact with the object). To
151 avoid any effect due to different sizes of participants’ hands, for each subjects we normalized the
152 index-thumb distance measured during the motion with respect to the corresponding distance
153 recorded when the participant kept the hand still on the table at the beginning of the task (“hand
154 size”, see Data Acquisition). We measured the following grasp parameters: *maximum grip*
155 *aperture*: the maximum value of the index-thumb distance (aperture / “hand size”, %); *time to*
156 *maximum grip aperture*: the ratio between the time at which the maximum grip aperture occurred
157 and the total duration of grasping phase (%); *final grip aperture*: the index-thumb distance at the
158 end of the grasp movement (aperture / “hand size”, %).

159

160 *Angular displacements.*

161 To describe the hand shape during the grasp movement, we considered 16 angles. In particular, we
162 measured the angular excursions at the metacarpal-phalangeal of the second, third, fourth and fifth
163 finger (respectively I_MCP, M_MCP, R_MCP, L_MCP) and proximal interphalangeal joints (PIP:
164 I_PIP, M_PIP, R_PIP, L_PIP) of the same fingers. For the thumb, we considered the metacarpal-
165 phalangeal (T_MCP) and interphalangeal joints (T_IP). Therefore, we evaluated the abduction
166 angles (ABD) of all digits. During the movement, hand rotated with respect to the 3d space of the
167 data acquisition system. To avoid any difference in the measure of the angles due to this 3d rotation,

168 first we introduced a local Cartesian coordinate system X–Y–Z (F1) attached on the palm of hand
169 defined by the plane passing through the index and little metacarpal-phalangeal joints and the radial
170 styloid, as previously described by Carpinella et al. (2006) (see Fig. 1). The ABD angle of each
171 finger was defined as the angle between the Y-axis and the projection on the XY plane of the MCP
172 joint of each finger. Second, concerning the measure of MCP and PIP joint angles, to keep away
173 from any difference due to the abduction, the angular excursions were evaluated in a new frame of
174 reference (F2). This was defined by a new plane obtained by the rotation of F1 with respect to the X
175 axis and attached on each finger at the MCP and PIP joints respectively. MCP and PIP angles were
176 calculated according to Denavit-Hartenberg convention (Denavit J. & Hartenberg. R.S. 1955). The
177 angular excursion at the PIP joints were evaluated as the angles between the markers placed on
178 nails, proximal interphalangeal and metacarpal–phalangeal joints. Concerning the thumb, the
179 metacarpal–phalangeal (T_MCP) and the interphalangeal joints (T_IP) angles were measured as the
180 others fingers. Moreover, we also evaluated the thumb rotation (T_ROT) and abduction angle
181 (T_ABD), respectively as elevation and azimuth angle (polar coordinates) of the metacarpal–
182 phalangeal joint referring to trapezio-metacarpal joint. Angles at the end of grasping movement
183 were calculated to describe the posture of the hand at the time of the contact with the object.

184

185 INSERT FIGURE 1 AROUND HERE

186

187 Time series of finger angular displacement were further analyzed by means of Principal
188 components analysis (PCA) to evaluate a potential effect of immobilization on fingers'
189 coordination.

190 *Principal component analysis.*

191 PCA was applied to the angular displacements of all 16 angles in the Post condition both in CG and
192 IG. All time series were time-normalized to 100 points by using Matlab. Each sample of time was
193 considered as a single observation lying an ambient vector space whose dimension was given by the
194 number of time series included in the analysis. For instance, consider a simple input dataset
195 composed of thirty-two columns (16 angular displacements recorded during each trial for the pencil
196 and 16 angular displacements for the ball) and 100 rows (normalized time). PCA could be thought

197 as a generalization of a correlation analysis in a high dimensional space. In this case, PCA extracted
198 the commonality between the angular displacements, which was sometimes referred as
199 “waveforms” because it especially focused on the shape of the angular time series. To this aim, each
200 eigenvector was defined as a one-dimensional vector subspace (i.e., a certain direction in the
201 thirty-two dimensional vector space). These eigenvectors represented a well adapted basis of the
202 thirty-two dimensional vector space, characterizing the most important directions (in the sense of
203 the variance account for: VAF), and, in this setting, principal component was simply the projection
204 of the data onto a subspace spanned by a certain eigenvector. The ratio between the first eigenvalue
205 and the sum of all eigenvalues could be viewed as an index of the whole-hand coordination (this
206 value is commonly called the VAF by the PC1 and is referred to as PC1%). A PC1% value equal to
207 100% mean that the trajectory in the space of angles was a straight line (i.e., all angles were linearly
208 correlated together). However, a low PC1% value indicated that only one principal component
209 could not describe precisely the whole-hand movement. Therefore, we also reported the second PC
210 whose VAF was denoted by PC2%. Here, instead of using independent PCAs (a PCA for each trial,
211 each condition, and each participant), we used two PCAs, one for the IG and one for CG, taking
212 together the two objects (pencil and ball), whose input dataset consisted of respectively 3360 or
213 2880 columns (16 angles for each objects, that is 32 in total, 15 trials, 7 participants for IG or 6 for
214 the CG) and 100 rows (normalized time), considering only the Post condition. In this manner, the
215 PCA automatically extracted the commonality between the shapes of the angular displacements (as
216 in the study by Berret et al., 2009). Therefore, to statistically compare the VAF by PC1 and PC2,
217 we also computed PCAs subjects by subjects.

218 *Statistical analysis.*

219 *Reach and grasp components.* To evaluate the effect of 10 hours of immobilization, we compared
220 the kinematic of the grasping task in the CG and the IG. To this aim, we performed separate
221 analysis of variance (ANOVAs) with repeated measures on each parameter calculated in every trial
222 for all subjects with CONDITION (“Pre” and “Post”) and OBJECTS (“Pencil” and “Ball”) as
223 within-subjects factors and with GROUP (Immobilization vs Control) as between-subjects factor.
224 While no variation in the motor performance of the CG was expected in the task recorded during
225 the two days, in the IG we hypothesized some differences concerning the kinematic of reaching-to-
226 grasp after immobilization .

227 *Angular displacements.* To directly compare the effect of immobilization on angular displacements,
228 we considered each angle subtracting the value obtained in the Pre from the corresponding measure
229 recorded in the Post. In this way, we can evaluate if the angular excursion remained constant or not
230 in the two experimental conditions. In particular we compared the CG and the IG performing
231 separate ANOVAs on the normalized data with OBJECTS (“Pencil” and “Ball”) as within-subjects
232 factor and GROUP (Immobilization vs Control) as between-subjects factor. While no difference
233 was expected in the CG for all the angles, in the IG a higher positive value at MCP or PIP joints
234 indicated a wider flexion after immobilization. On the contrary, a negative value revealed a more
235 extended posture of fingers. For the ABD angles of middle, ring and little fingers a higher positive
236 difference could be obtained if the fingers were more adducted after immobilization. On the
237 contrary, for the index and thumb the adduction was indicated by negative values, while positive
238 values meant abduction. Moreover, a wider negative value of the T_ROT corresponded to an
239 increased of the internal rotation of this finger with respect to the hand space.

240 *Principal Component Analysis.* To understand if the covariation between the angular excursions of
241 the digits were affected by immobilization, we compared the VAF for each subject by means of two
242 separate ANOVAs, one for PC1 and the other for PC2, with GROUP (Immobilization vs Control)
243 as between-subjects factor. Moreover, we evaluated the correlation coefficients of the most
244 common and the second angular waveform in the dataset, respectively described by PC1 and PC2,
245 in IG and CG.

246 *Recovery.* Finally, we check if, after immobilization, there was a recovery trial after trial (i.e. 15
247 repetitions for each object). Thus, we performed linear regression analysis on *reach duration* and
248 *maximum grip aperture* as a function of the number of trials, for each subject of IG and CG in the
249 Post condition. Then, we statistically compared the slopes of the linear regression lines by means of
250 2 separate ANOVAs (one for *reach duration* and one for *maximum grip aperture*) with “OBJECT”
251 (“Pencil” and “Ball”) as within-subjects factor and “GROUP” (Immobilization vs Control) as
252 between-subjects factor. Moreover, in the IG and CG, we evaluated the coefficient of correlation
253 between the *reach duration* and the *maximum grip aperture* as a function of the number of trials. To
254 this aim, we considered the mean value among all participants in the IG and in the CG, at each
255 trial.

256 Significance threshold was set at $p < 0.05$. If ANOVAs showed significant interaction effects, we
257 performed post hoc tests using the Newman-Keuls procedure to directly compare the experimental
258 factors.

259

260

261 RESULTS

262 As soon as we removed the bandage (10 hours of immobilization), subjects were equally able to
263 correctly grasp the objects as before immobilization and comparable to the CG. However, while in
264 the CG no difference was shown comparing the Pre and Post conditions, in the IG a different
265 kinematic for reach and grasp components, both in precision and power grip, was described after
266 immobilization (Fig.2 and 3). Therefore, the hand posture at the end of grasping task changed in the
267 two groups (Fig.4). Nevertheless, the patterns of co-variation between the angular excursion of the
268 digits remained similar (Fig. 5). Finally, after immobilization reach duration decreased trial after
269 trial in contrast to maximum grip aperture that increased during the repetitions (Fig. 6).

270 *Reach and grasp components.*

271 For all reach and grasp parameters, excepted for the time to maximum grip aperture (see below), the
272 critical interaction GROUP X CONDITION is statistically significant ($p < 0.05$). In particular,
273 Newman-Keuls post-hoc comparisons revealed that in the IG Pre and Post conditions were
274 different, while this was not the case in the CG ($p > 0.05$). The results obtained in conditions without
275 immobilization, that is in Pre for IG and in the Pre and Post for CG, were never statistically
276 different (in both comparisons $p > 0.05$). For all parameters, the interaction GROUP X CONDITION
277 X OBJECT was not statistically significant, underlining that the effect of immobilization was
278 similar both in the precision and the power grip.

279 IG participants spent more time in the reaching in the Post condition (802 ms) with respect to the
280 Pre (776 ms, critical interaction GROUP X CONDITION: $F(1, 193) = 6.98$, $p < 0.01$). Moreover,
281 after immobilization the *time to peak velocity* occurred significantly earlier (40%) than in the Pre
282 (42%, GROUP X CONDITION: $F(1, 193) = 4.46$, $p < 0.05$). Thus, immobilization affected both
283 duration and timing of the reaching movement.

284

285 INSERT FIGURE 2 AROUND HERE

286

287 After immobilization participant opened their hand wider compared to Pre values, or CG. Indeed,
288 post hoc comparisons revealed a significant increase of *maximum grip aperture* after

289 immobilization (70% of “hand size”) compared with the Pre (66%, $p<0.001$) in the IG (critical
290 interaction GROUP X CONDITION ($F(1,193) = 4$, $p< 0.05$). However, even if, the maximum grip
291 aperture increased after immobilization, the time in which the peak aperture occurred (*time to*
292 *maximum grip aperture*) was similar in both groups (GROUP X CONDITION: $F(1, 193)=0.11$,
293 $p>0.05$). Moreover, a significant increase of *final grip aperture* in the Post condition in the IG
294 indicated that after immobilization participants kept their hand more open also at the end of the
295 grasp (Pre=40%, Post=44%, GROUP X CONDITION: $F(1,193) = 9.2$, $p<0.01$).

296

297 INSERT FIGURE 3 AROUND HERE

298

299 *Angular displacements.*

300 In order to verify if after immobilization the increase in the final grip aperture was associated to a
301 different hand posture, we compared the value of the 16 angles of the fingers at the time to contact
302 with the object. The hand posture changed before and after immobilization. Indeed, in the IG the
303 hand posture was characterized by wider flexed MCP joints of the middle, ring, little and thumb
304 fingers associated with a higher extension of PIP joints of all fingers. This effect was comparable
305 for the two objects, excepted for L_PIP and T_IP (see Table 1). Therefore, the index and ring
306 fingers were closer each other, more adducted. A similar effect was present also for the little finger
307 only during precision grip. Finally, after immobilization also the thumb was nearer the palm, being
308 more adducted (for the Ball) or internal rotated (for the Pencil). Statistical analysis and values are
309 reported in Table1.

310

311 INSERT TABLE 1 AROUND HERE

312

313 INSERT FIGURE 4 AROUND HERE

314

315 *Principal Component Analysis .*

316 PCA was applied to the angular displacements of the sixteen angles to understand if different
317 patterns of co-variation of the digitis were present after immobilization. PCA showed that the first
318 two principal components could account for a large proportion of the variance, i.e., 90.6 % and
319 89.9% for the Post conditions in the IG and the CG, respectively, without any difference for the two
320 objects. This implied that before immobilization there was a high degree of co-variation between
321 the fingers that remained unvaried after non-use. The present result is in line with previous studies
322 in which the first two components could account for the majority of the variance, without
323 distinguishing the type of grip (e.g., precision or power) or different target object (for example
324 Santello et al., 2002). Moreover, also comparing the VAF by PC1 and PC2 through separate PCAs
325 for each subjects, no difference was showed in the IG and the CG. Furthermore, the waveforms of
326 the first two principal components were remarkably similar (PC1: $r^2=0.99$, $p<0.00001$; PC2: $r^2=0.99$
327 , $p<0.00001$).

328

329 INSERT FIGURE 5 AROUND HERE

330

331 *Recovery.*

332 ANOVA on slopes of *reach duration* calculated on 15 successive trials revealed a statistical
333 difference in IG and CG ($F(1,11) = 9.59$, $p<0.01$, mean slope IG= -8.8, mean slope CG= -0.7).
334 Indeed, the *reach duration* in IG was inversely correlated with trials ($r= -0.8$, $p<0.001$), while there
335 was no correlation in the CG ($r= -0.2$, $p= 0.53$) (Figure 6, panel A). This showed that after
336 immobilization, subjects took more time to perform the reach in the first trials, but during the task,
337 this effect reduced until getting values comparable with those obtained in the CG at the last three
338 repetitions. Similarly, concerning the *maximum grip aperture*, ANOVA on slopes demonstrated a
339 significant difference in IG and CG ($F(1,11) = 6.85$, $p<0.02$, slope IG= 0.004, slope CG= -0.004).
340 While the *maximum grip aperture* in CG was inversely correlated with trial number ($r= -0.7$,
341 $p<0.01$), in the IG the correlation was positive ($r= 0.7$, $p<0.01$) (Figure 6, panel B). Thus, in the CG
342 participants decreased the index-thumb distance during the repetitions; on the contrary this distance
343 increased trial by trial in the IG. Consequently, in IG the *maximum grip aperture* and the *reach*
344 *duration* were inversely correlated ($r= -0.7$, $p<0.01$): while participants reduced the reach duration
345 (i.e. recovery of immobilization effect), they opened their hand wider (Figure 6, panel C). On the

346 contrary, there was no correlation in CG between *maximum grip aperture* and the *reach duration*
347 ($r = 0.3$, $p < 0.05$) (Figure 6, panel D). In other words, while reach duration recover nominal value
348 trial after trail in the Post, maximum grip aperture followed an opposite mechanism.

349 INSERT FIGURE 6 AROUND HERE

350

351

352 DISCUSSION

353 Findings demonstrated that 10 hours of immobilization were sufficient to modify the kinematic of
354 reaching and grasping, anyhow preserving the capability of participants to perform the task. Further,
355 a different recovery was observed in the two components. As far as we know, this is the first
356 demonstration of modifications in the kinematics of a reaching-to-grasp induced by a short term
357 period of immobilization in healthy subjects.

358 *General behavioural effects on reach and grasp*

359 Firstly, concerning the reach, after immobilization both duration and timing were affected. In
360 particular, reach duration increased and the time to peak velocity occurred earlier, indicating a
361 longer deceleration phase. Additionally, the movement remained under feedforward control with a
362 bell shape velocity profile with any online adjustment. Secondly, immobilization increased the
363 maximum grip aperture (the peak of index-thumb distance) that, as for the transport component,
364 was produced without online adjustments. How can we explain these modifications? The concept of
365 internal models suggests that specialized neural networks would relate motor commands to sensory
366 signals of body motion (forward models) and desired movements to appropriate motor commands
367 (inverse model) (Desmurget et al., 2000; Wolpert et al., 1998). As such, sensory information from
368 the moving limbs strongly contributes to regulate the motor command and to define hand shaping.
369 Thus, successful reaching-to-grasp movement requires continuous adaptation of fingers
370 coordinative patterns in order to accurately grasp the object. Immobilization induced a reduction of
371 dynamic sensory information (mainly from proprioception and vision), usually generated by arm
372 motion (i.e. dynamic proprioception, Burke et al. 1976). Evidences from animal models and human
373 studies showed that this input is thought to have direct access to contralateral sensory and motor
374 cortical areas (Heath et al. 1976; Hore et al., 1976). For instance Huber and colleagues (2006), using
375 EEG recording in healthy subjects after upper limb immobilization, described a significant
376 reduction of the amplitude of the P45 component which classically represents the proprioceptive
377 information processing within the sensorimotor areas (Allison et al. 1992). However, during
378 immobilization motor planning and consecutive forward (prediction of sensory consequence of
379 movement) and inverse (motor command) models remained available, but no more updated because
380 of the lack of motor output. This could lead to an inaccurate prediction of sensory consequences of
381 motor command. In support to this, variability of imagined walking (Courtine et al. 2004) or writing
382 (Papaxanthis et al. 2002) movements steadily increased as time elapsed between overt (i.e. real

383 execution) and covert (i.e. imagined action) performances. This resulted from the absence of
384 sensory feedback, which appears essential to accurately execute the tasks. Consequently, the present
385 increase in the duration of transport, in the deceleration phase and in the amplitude of the grip
386 aperture may represent an adaptative process in order to maintain a successful motion without
387 online regulation. A wide opening of the hand might be employed to maximize the likelihood to
388 successfully grasp the object (Grosskopf et al. 2006) and it could be the consequence of a motor
389 strategy design to increase the tolerance for programming errors (Jakobson and Goodale 1991).
390 According to this, a higher maximum finger opening was previously described in conditions which
391 impede the accuracy of reaching (Grosskopf et al. 2006), such as fast movements (Wing et al. 1986;
392 Wallace and Weeks, 1988), movements in the dark (Jakobson and Goodale 1991; Churchill et al.
393 2000; Schettino et al. 2003) or anaesthesia (Gentilucci et al. 1997). Extending the duration of the
394 motion (and in particular, here, the deceleration phase) may contribute to improve the action
395 accuracy (Fitts, 1954; Tanaka et al. 2006) after sensorimotor deprivation induced by immobilization.
396 We can also suppose that because of the decrease of dynamic proprioceptive information during
397 immobilization, visual inputs could be more reliable when participants start to move again, as soon
398 as the bandage was removed. Since the visual loop is slower respect to the proprioceptive one
399 (Jeannerod 1988), it is likely that the increased reach duration reflects an attempt to perform the
400 movement using mostly visual inputs. Comparably, in deafferented patient Gentilucci et al. (1994)
401 described an abnormal lengthening of movement (and in particular of deceleration phase), reported
402 as a tentative to compensate for the proprioceptive deficit through vision.

403 *Final hand posture*

404 Inspection of fingers' position after immobilization revealed that participants adopted a different
405 hand posture characterized by wider flexed MCP joints (except for the index) accompanied by a
406 higher extension of PIP joints, with all fingers (little only for the ball) closer each other and more
407 adducted. A greater distance between the tips of the index and thumb fingers observed at the end of
408 the grasping motion (see above "final grip aperture") is congruent with this hand posture. This
409 effect could result from the hand position imposed by the bandage used to constraint the fingers
410 extended and close each other during immobilization. Such possibility cannot be ruled out and
411 could have been tested by immobilizing subjects in another position, i.e. with fingers flexed.
412 However, we choose a comfortable position avoiding an over-stretching of agonist/antagonist
413 muscles. Moreover, this explanation seems not compatible with the specific thumb position (more
414 internally rotated for the pencil and more adducted for the ball) that significantly changed with

415 respect to the immobilization posture. One possibility to explain these postural effects is that the
416 thumb would compensate for the extension of the fingers. Indeed, by rotating or moving more
417 internally the thumb, subjects could increase the opposition between the digits and the thumb and
418 better stabilize the grip. This is in agreement with the idea that thumb will drive the adaptations in
419 contrast to the others fingers (Frak et al. 2001; Galea et al. 2001; Smeets and Brenner 1999; Wing
420 and Fraser 1983). Biomechanically, there is a structural separation of the extrinsic muscles of the
421 thumb from the multi-tendoned muscles acting on the other digits (Landsmeer JMF et al., 1986),
422 permitting more selective, independent movement of the thumb (Schieber MH. Et al., 1991).

423 *Fingers coordination*

424 We found that only two principal components could account for a large proportion of the variance,
425 showing that the motion of the hand during the movement is characterized by consistent, joint-
426 specific co-variation in angular excursion. The presence of these co-variation patterns indicates that
427 not all the finger joints were controlled independently, resulting in a reduction in the number of
428 mechanical degrees of freedom (Santello et al. 1998, 2002). Interestingly, despite kinematic
429 changes and modifications in hand posture after non-use, finger coupling was not affected. Such
430 robustness of fingers coordination could be due to the well-documented presence of biomechanical
431 couplings among digits (Lang and Schieber 2004, Schieber 1991). Zatiorsky et al. (2000), for
432 instance, described the tendency of fingers to generate forces as a consequence of an “enslaving”
433 phenomenon that activates simultaneously the other fingers. Moreover, other studies demonstrated
434 the consistency of joint co-variation despite the modifications of hand postures and kinematics in
435 grasping multiple objects under different conditions (i.e. modulating visual or proprioceptive input)
436 (Thakur et al. 2008, Mason et al. 2001, Santello et al. 1998, 2002) and in complicated hand
437 gestures, such as finger spelling (Jerde et al. 2003; Weiss and Flanders, 2004) or typing (Fish and
438 Soechting, 1992; Soechting and Flanders, 1997).

439 *Reaching versus Grasping*

440 When considering transport and grasp component trial by trial, CG participants always kept the
441 same reach duration while maximum grip aperture decreased. Consistency of reach duration
442 probably resulted from the lack of experimental constraint on movement velocity (i.e. participants
443 were in a self-paced mode). In contrast, a reduced hand opening seems a consequence of a learning
444 effect due to the repetitions of the task (Lin et al. 2007). Accordingly, developmental studies in
445 children have showed that, in parallel with the refinement of other hand motor skills, the grip

446 aperture becomes progressively smaller during the first decade of life (Kuhtz-Buschbeck et al. 1998;
447 Smyth et al. 2004). In IG participants increased reach duration after non-use. Thus, one may
448 suppose a reduction of transport duration trial by trial. Surprisingly, we observed an opposite
449 recovery processes for reach and grasp components: while reach duration returned to the baseline
450 value at the last repetitions of the task, the maximum grip aperture increased trial after trial.
451 Similarly, when reaching is under time constraint, several authors noted an increase of maximum
452 grip aperture (Wing et al. 1986; Wallace and Weeks, 1988; Bootsma et al. 1994; Mason and
453 Carnahan 1999), as a strategy to grasp with a greater “safety margin” (Grosskopf et al. 2006). Why
454 reach and grasp recovered differently? One possibility concerns the effect of immobilization on
455 distal (wrist and fingers for the grasp) and proximal (shoulder and elbow for the transport) parts.
456 Actually, the bandage worn by participants prevented any hand and wrist motions, but did not
457 completely block shoulder movements. Further, reaching is organized bilaterally, so it can be
458 controlled adequately by the ipsilateral hemisphere (Brinkman & Kuypers, 1973). On the contrary,
459 grasping depends more on contralateral primary motor cortex (Jeannerod 1986; Porter & Lemon,
460 1993). Thus, we can suppose that the activity of the ipsilateral “not immobilized” motor cortex
461 could support the recovery for the reaching, but not for the grasp component. In support of this
462 hypothesis, in another study, we demonstrated that the cortical excitability is reduced in the motor
463 cortex contralateral to the immobilized arm, while not in the ipsilateral one (Bassolino et al., 2009
464 XXX). This could confirm a potential role of the ipsilateral motor cortex in the fast improvement
465 observed only for the transport component. Finally, the different recovery processes could also be
466 related to an optimal strategy (Todorov and Jordan, 2002; Guignon et al., 2007). Indeed, reduction
467 of reach duration would decrease the energetic cost mainly due to arm displacement, and become a
468 priority compared to grip aperture.

469

470 *Conclusion*

471 The present findings demonstrated that ten hours of hand and forearm immobilization affect the
472 reaching-to-grasp movement, lengthening the duration and modifying the timing of the transport
473 phase, increasing the amplitude of grip aperture and altering the final hand posture. Thus, a transient
474 lack of sensory information and motor commands modify the kinematic of a very well known motor
475 task. These results could be due both to peripheral or cortical effects. Findings from previous
476 studies support the latter hypothesis (Huber et al., 2006; Facchini et al. 2002; Bassolino et al.,

477 2009XXX). However, to answer this question, direct evidence of cortical changes after ten hours of
478 arm immobilization are required.

479

480
481 **FIGURE 1**

482 **METHODS.** On the left, markers displacement and F1 with x and y axis, the system of reference
 483 built on the hand plane by means of A, B and C points. Upper on the right, the y axis of F1 and F2.
 484 F2 was obtained by the rotation of F1 with respect to the X axis and attached on each finger at the
 485 MCP and PIP joints respectively. Lower on the right, angles at MCP (metacarpal–phalangeal) and
 486 PIP (proximal interphalangeal) joints of index finger.

487

488 FIGURE 2

489 REACH COMPONENT: the velocity profile and time to peak (upper graph) and the reach duration
 490 (lower graph) in the IG for the pencil (left column) and the ball (right column). Immobilization
 491 affected the reach phase both in timing (first line) and duration (second line). Light and dark gray
 492 represent the Pre and the Post condition respectively. Error bars indicate the standard errors, and *
 493 shows $p < 0.05$.

494

495 FIGURE 3

496 GRASP COMPONENT: the distance between index and thumb at the peak (maximum grip
 497 aperture) with the percentage of time in which occurred (time to maximum finger aperture) and at
 498 the end of the grasp (final grip aperture) in the IG for the pencil (left column) and the ball (right
 499 column). After immobilization, the index and thumb distance significantly increased. Gray and dark
 500 bars represent the Pre and the Post condition respectively. Error bars show the standard errors. *
 501 shows $p < .05$.

502

503 FIGURE 4

504 STATIC HAND POSTURE. Representations of the hand posture in one typical subject (mean of all
 505 trials) when he grasped the pencil (lower line) and the ball (upper line) at the time of the contact
 506 with the object before (“blue shadow color”) and after immobilization (“skin natural color”). After
 507 non-use, the hand posture was characterized by more flexed fingers at the MCP joints and more
 508 extended PIP joints. Therefore, index, ring and little fingers were more adducted. Moreover, a
 509 stronger opposition of the thumb (more internal rotated for the pencil and more adducted for the
 510 ball) was evident.

511 FIGURE 5

512 PRINCIPAL COMPONENT ANALYSIS. On the left, means of the percentage of variance
 513 explained by the first two principal components (VAF) in the IG and CG. No significant difference
 514 was shown. Error bars is related to the standard errors. On the right, the principal components. The
 515 PC1 is the most common angular waveform found in the dataset and PC2 is the second angular
 516 waveform. Correlation coefficient (r^2) between the IG (solid line) and the CG (broken line) is
 517 reported.

518

519

520 FIGURE 6

RECOVERY. The linear regression lines of reach duration (panel A) and maximum grip aperture (panel B) on the number of trials, for the IG (dark grey) and CG (light grey). Participants in the IG reduced the reach duration trial by trial, while this parameter did not change in the CG. Concerning maximum grip aperture, in the IG, participants increased the hand aperture during the repetitions, while in the CG, subjects progressively reduced that aperture. In panel C, the inverse correlation between the mean values of reach duration and the maximum grip aperture at each trial in the IG; on the contrary, no correlation between these two parameters is showed for the CG (panel D).

528

	MCP					PIP								ABD		
	I	M	R	L	T	I	M	R	L		T		I	M		
									P	B	P	B				
IG post-pre	1.0 (0.8)	5.9 (0.8)	4.6 (0.8)	3.5 (1.0)	4.3 (0.6)	-2.8 (0.8)	-11.7 (1.2)	-8.2 (1.0)	-5.5 (1.2)	-6.2 (1.1)	-3.0 (0.3)	-2.7 (0.7)	-3.7 (0.7)	0.3 (0.3)		
CG post-pre	1.8 (0.8)	2.4 (0.9)	2.1 (0.9)	1.3 (1.1)	1.8 (0.7)	1.4 (0.9)	-1.5 (1.3)	-1.6 (1.0)	-3.2 (1.3)	1.7 (1.2)	0.3 (0.3)	-1.7 (0.8)	2.5 (0.5)	0.6 (0.3)		
p		**	**	*	**	**	**	**		**	**		**			

529

530

531 TABLE1

532 ANGULAR DISPLACEMENTS: STATISTICAL ANALYSIS.

533 Normalized data (Post-Pre) in Immobilization (IG) and Control group (CG): post hoc comparisons
534 of the Group or when significant, of the Group X Object interaction (P= pencil, B= ball) are shown.
535 At MCP and PIP joints a positive and negative value point out respectively wider flexed or
536 extended posture. For the middle, ring and little ABD angles a positive difference reveals that the
537 fingers were more adducted. On the contrary, for the index and thumb the adduction is identified by
538 negative values. A higher negative value of the T_ROT corresponds to an increased internal
539 rotation of this finger toward the hand palm. Standard error of mean values are in parentheses. *
540 indicates p<0.05, ** indicates p<0.005.

541

542
543

REFERENCES

544

545 Allison, T., G. McCarthy, and C. C. Wood. "The relationship between human long-latency somatosensory evoked
546 potentials recorded from the cortical surface and from the scalp." *Electroencephalogr Clin Neurophysiol* 84 (1992):
547 301-314.

548 Arbib, M.A. *Perceptual structures and distributed motor control*. 1981.

549 Berret, Bastien, François Bonnetblanc, Charalambos Papaxanthis, and Thierry Pozzo. "Modular control of pointing
550 beyond arm's length." *J Neurosci* 29 (2009): 191-205.

551 Bootsma, R. J., R. G. Marteniuk, C. L. MacKenzie, and F. T. Zaal. "The speed-accuracy trade-off in manual
552 prehension: effects of movement amplitude, object size and object width on kinematic characteristics." *Exp Brain Res*
553 98 (1994): 535-541.

554 Brinkman, Kuypers HGJM. "Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the
555 split-brain rhesus monkey." *Brain* 96 (1973): 653-74.

556 Burke, D, KE Hagbarth, L Löfstedt, and BG Wallin. "The responses of human muscle spindle endings to vibration of
557 non-contracting muscles." *J Physiol* 261 (1976): 673-93.

558 Carpinella, I., P. Mazzoleni, M. Rabuffetti, R. Thorsen, and M. Ferrarin. "Experimental protocol for the kinematic
559 analysis of the hand: definition and repeatability." *Gait Posture* 23 (2006): 445-454.

560 Castiello, Umberto. "The neuroscience of grasping." *Nat Rev Neurosci* 6 (2005): 726-736.

561 Churchill, A., B. Hopkins, L. Rönqvist, and S. Vogt. "Vision of the hand and environmental context in human
562 prehension." *Exp Brain Res* 134 (2000): 81-89.

563 Courtine, Grégoire, Charalambos Papaxanthis, Rodolphe Gentili, and Thierry Pozzo. "Gait-dependent motor memory
564 facilitation in covert movement execution." *Brain Res Cogn Brain Res* 22 (2004): 67-75.

565 Denavit, J., and R.S. Hartenberg. "A kinematic notation for lower-pair mechanisms based on matrices." *J. Appl. Mech*
566 23 (1955): 215-221.

567 Desmurget, and Grafton. "Forward modeling allows feedback control for fast reaching movements." *Trends Cogn Sci* 4
568 (2000): 423-431.

569 Facchini, Stefano, Michela Romani, Michele Tinazzi, and Salvatore M Aglioti. "Time-related changes of excitability of
570 the human motor system contingent upon immobilisation of the ring and little fingers." *Clin Neurophysiol* 113 (2002):
571 367-375.

572 Fish, J., and J. F. Soechting. "Synergistic finger movements in a skilled motor task." *Exp Brain Res* 91 (1992): 327-334.

573 Fitts, P. M. "The information capacity of the human motor system in controlling the amplitude of movement." *J Exp*
574 *Psychol* 47 (1954): 381-391.

575 Frak, V., Y. Paulignan, and M. Jeannerod. "Orientation of the opposition axis in mentally simulated grasping." *Exp*
576 *Brain Res* 136 (2001): 120-127.

577 Galea, M. P., U. Castiello, and N. Dalwood. "Thumb invariance during prehension movement: effects of object
578 orientation." *Neuroreport* 12 (2001): 2185-2187.

579 Gentilucci, M., I. Toni, E. Daprati, and M. Gangitano. "Tactile input of the hand and the control of reaching to grasp
580 movements." *Exp Brain Res* 114 (1997): 130-137.

581 Gentilucci, M., I. Toni, S. Chieffi, and G. Pavesi. "The role of proprioception in the control of prehension movements: a
582 kinematic study in a peripherally deafferented patient and in normal subjects." *Exp Brain Res* 99 (1994): 483-500.

583 Gentilucci, M., S. Chieffi, M. Scarpa, and U. Castiello. "Temporal coupling between transport and grasp components
584 during prehension movements: effects of visual perturbation." *Behav Brain Res* 47 (1992): 71-82.

585 Grosskopf, Alexandra, and Johann P Kuhtz-Buschbeck. "Grasping with the left and right hand: a kinematic study." *Exp*
586 *Brain Res* 168 (2006): 230-240.

587 Guigon, Emmanuel, Pierre Baraduc, and Michel Desmurget. "Computational motor control: redundancy and
588 invariance." *J Neurophysiol* 97 (2007): 331-347.

589 Heath, C. J., J. Hore, and C. G. Phillips. "Inputs from low threshold muscle and cutaneous afferents of hand and
590 forearm to areas 3a and 3b of baboon's cerebral cortex." *J Physiol* 257 (1976): 199-227.

591 Hore, J., J. B. Preston, and P. D. Cheney. "Responses of cortical neurons (areas 3a and 4) to ramp stretch of hindlimb
592 muscles in the baboon." *J Neurophysiol* 39 (1976): 484-500.

593 Huber, Reto, et al. "Arm immobilization causes cortical plastic changes and locally decreases sleep slow wave activity."
594 *Nat Neurosci* 9 (2006): 1169-1176.

595 Jakobson, L. S., and M. A. Goodale. "Factors affecting higher-order movement planning: a kinematic analysis of human
596 prehension." *Exp Brain Res* 86 (1991): 199-208.

597 Jeannerod, M. "Visuomotor channels: their integration in goal-directed prehension." *Hum. Mov. Sci.* 18 (1999): 201–
598 218.

599 Jeannerod, M. "The formation of finger grip during prehension. A cortically mediated visuomotor pattern." *Behav Brain*
600 *Res* 19 (1986): 99–116.

601 Jeannerod, M. "*The neural and behavioural organization of goal-directed arm movements*". Clarendon, Oxford (1988)

602 Jeannerod, M. "The timing of natural prehension movements." *J Mot Behav* 16(3) (1984): 235-54.

603 Jones, L.A. *Human hand function*. 2006.

604 Kuhtz-Buschbeck, J. P., H. Stolze, K. Jöhnk, A. Boczek-Funcke, and M. Illert. "Development of prehension movements
605 in children: a kinematic study." *Exp Brain Res* 122 (1998): 424-432.

606 Landsmeer, J. M. "A comparison of fingers and hand in varanus, opossum and primates." *Acta Morphol Neerl Scand* 24
607 (1986): 193-221.

608 Lang, Catherine E, and Marc H Schieber. "Human finger independence: limitations due to passive mechanical coupling
609 versus active neuromuscular control." *J Neurophysiol* 92 (2004): 2802-2810.

610 Lin, K-C., C-Y. Wu, T-H. Wei, C-Y. Lee, and J-S. Liu. "Effects of modified constraint-induced movement therapy on
611 reach-to-grasp movements and functional performance after chronic stroke: a randomized controlled study." *Clin*
612 *Rehabil* 21 (2007): 1075-1086.

613 Mason, A. H., and H. Carnahan. "Target viewing time and velocity effects on prehension." *Exp Brain Res* 127 (1999):
614 83-94.

615 Mason, C. R., J. E. Gomez, and T. J. Ebner. "Hand synergies during reach-to-grasp." *J Neurophysiol* 86 (2001): 2896-
616 2910.

617 Moisello, Clara, et al. "Short-term limb immobilization affects motor performance." *J Mot Behav* 40 (2008): 165-176.

618 Napier, J. R. "The prehensile movements of the human hand." *J Bone Joint Surg Br* 38-B (1956): 902-913.

619 Oldfield, R. C. "The assessment and analysis of handedness: the Edinburgh inventory." *Neuropsychologia* 9 (1971): 97-
620 113.

621 Papaxanthis, Charalambos, Thierry Pozzo, Xanthi Skoura, and Marco Schieppati. "Does order and timing in
622 performance of imagined and actual movements affect the motor imagery process? The duration of walking and writing
623 task." *Behav Brain Res* 134 (2002): 209-215.

624 Paulignan, Y., M. Jeannerod, C. MacKenzie, and R. Marteniuk. "Selective perturbation of visual input during
625 prehension movements. 2. The effects of changing object size." *Exp Brain Res* 87 (1991): 407-420.

626 Piaget, J. *The construction of reality in the child*. 1954. New York: Ballantine Books

627 Piaget, J.. *The origins of intelligence in children*. 1952. New York: Norton and Company Inc.

628 Porter, R.& Lemon, R *Corticospinal Function and Vol-untary Movement*. 1993. Oxford: Clarendon Press

629 Santello, M., M. Flanders, and J. F. Soechting. "Postural hand synergies for tool use." *J Neurosci* 18 (1998): 10105-
630 10115.

631 Santello, Marco, Martha Flanders, and John F Soechting. "Patterns of hand motion during grasping and the influence of
632 sensory guidance." *J Neurosci* 22 (2002): 1426-1435.

633 Schettino, Luis F, Sergei V Adamovich, and Howard Poizner. "Effects of object shape and visual feedback on hand
634 configuration during grasping." *Exp Brain Res* 151 (2003): 158-166.

635 Schieber, M. H. "Individuated finger movements of rhesus monkeys: a means of quantifying the independence of the
636 digits." *J Neurophysiol* 65 (1991): 1381-1391.

637 Seidler, Thiers G. "Feedforward and feedback processes in motor control." *Human Movement Science* 18 (1999): 201-
638 218.

639 Smeets, J. B., and E. Brenner. "A new view on grasping." *Motor Control* 3 (1999): 237-271.

640 Smyth, Mary M, Kirsty A Peacock, and Janet Katamba. "The role of sight of the hand in the development of prehension
641 in childhood." *Q J Exp Psychol A* 57 (2004): 269-296.

642 Soechting, J. F., and M. Flanders. "Flexibility and repeatability of finger movements during typing: analysis of multiple
643 degrees of freedom." *J Comput Neurosci* 4 (1997): 29-46.

644 Tanaka, Hirokazu, John W Krakauer, and Ning Qian. "An optimization principle for determining movement duration."
645 *J Neurophysiol* 95 (2006): 3875-3886.

646 Thakur, Pramodsingh H, Amy J Bastian, and Steven S Hsiao. "Multidigit movement synergies of the human hand in an
647 unconstrained haptic exploration task." *J Neurosci* 28 (2008): 1271-1281.

648 Todorov, Emanuel, and Michael I Jordan. "Optimal feedback control as a theory of motor coordination." *Nat Neurosci* 5
649 (2002): 1226-1235.

650 Wallace, S. A., and D. L. Weeks. "Temporal constraints in the control of prehensile movement." *J Mot Behav* 20
651 (1988): 81-105.

652 Weiss, Erica J, and Martha Flanders. "Muscular and postural synergies of the human hand." *J Neurophysiol* 92 (2004):
653 523-535.

654 Wing, A. M., A. Turton, and C. Fraser. "Grasp size and accuracy of approach in reaching." *J Mot Behav* 18 (1986): 245-
655 260.

656 Wing, A. M., and C. Fraser. "The contribution of the thumb to reaching movements." *Q J Exp Psychol A* 35 (1983):
657 297-309.

658 Wolpert., D.M., and M. Kawato. "Multiple paired forward and inverse models for motor control." *Neural Networks* 11
659 (1998): 1317–1329.

660 Zatsiorsky, V. M., Z. M. Li, and M. L. Latash. "Enslaving effects in multi-finger force production." *Exp Brain Res* 131
661 (2000): 187-195.

662