

1 **Augmented manipulation ability in humans with six fingered hands**

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18 19 **Abstract:**

20 Neurotechnology attempts to develop supernumerary limbs, but can the human brain deal
21 with the complexity to control an extra limb and yield advantages from it? Here, we analyzed
22 the neuromechanics and manipulation abilities of two polydactyly subjects who each possess
23 six fingers on their hands. Anatomical MRI of the supernumerary finger (SF) revealed that it is
24 actuated by extra muscles and nerves, and fMRI identified a distinct cortical representation of
25 the SF. In both subjects, the SF was able to move independently from the other fingers.
26 Polydactyly subjects were able to coordinate the SF with their other fingers for more complex
27 movements than five fingered subjects, and so carry out with only one hand tasks normally
28 requiring two hands. These results demonstrate that a body with significantly more degrees-
29 of-freedom can be controlled by the human nervous system without causing motor deficits or
30 impairments and can instead provide superior manipulation abilities.

31
32 **Contributions:** Conceived and designed the study: CM, LB, MM, HC, AS, EB; Polydactyly
33 subjects recruitment: CM, LB, EB; Performed the experiments: LB, MA, MM, HC, MB, ASB,
34 TP, RS, OB; Analyzed and interpreted the data: CM, LB, MA, MM, HC, TP, AC, AS, EB; Wrote

35 the manuscript: CM, MA, AS, EB; All co-authors have read and edited the manuscript and
36 agree with its content.

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43 **Introduction**

44 Additional artificial limbs that are seamlessly controlled concurrently to the natural limbs, and
45 can assist actions with little cognitive effort, are a popular idea in science fiction and art.
46 Inspired by this vision, engineers have undertaken to design wearable robotic limbs (1,2), and
47 recent neuroscience studies have aimed at developing ways to interface such limbs with the
48 nervous system (3-6). However, is the human brain able to control a body with additional
49 degrees-of-freedom (dof), as the range of possible movements increases exponentially with
50 every dof (see Supplementary Note), and could this enhance functional abilities? Furthermore,
51 how can the nervous system represent an extra limb and its relation to other limbs? The
52 challenging, massive reorganization of neural representation required for individuals with
53 abnormal body structure is illustrated through phantom limbs experienced by amputees and
54 even by individuals with a congenitally missing limb (7,8). While the physiological
55 consequences of a missing limb have been studied, none of the corresponding fundamental
56 issues of movement augmentation have yet been examined in the literature.

57 Here we address these issues by analyzing for the first time the neuromechanics and
58 manipulation abilities of the right hand in two polydactyly subjects (17 years old subject P1
59 and his 52 years old mother, subject P2), who both have six anatomically fully developed
60 fingers on the two hands (Fig.1A, Supplementary Fig.1). Polydactyly, the congenital physical
61 anomaly of hands with more than five fingers, is not rare in humans, with an incidence of
62 around 0.2% (9) and archaeology has demonstrated the presence of polydactyly individuals
63 already in the mesoamerican civilisation (10). However, supernumerary fingers are often
64 removed at birth (11) as they are deemed not useful and are often not fully developed.

65 The combinatorics of polydactyly's genetics have been analyzed in seminal 19th century
66 works (12), and the genes responsible for polydactyly have been identified recently (13).
67 However, the neuromechanics and functionality of polydactyly hands raise many questions
68 that have never been investigated: First, is the movement of the additional finger actuated by
69 other fingers' muscles, or does it have its own dedicated muscles and nerves? Second, how
70 independent is the extra finger from the other fingers? Does its movement accompany the
71 movement of common fingers, like in the little and ring fingers (14), or does it move
72 independently from other fingers like the thumb? Third, hand movements are already among
73 the most complex movements humans can perform, requiring a large area of the sensory and
74 motor cortices to control them (14-16). Therefore, how could the cortex control a hand with
75 several additional dof? Fourth, what is the perceived body representation of polydactyly
76 hands? Fifth, and most importantly, are the supernumerary fingers (SF) functional, and can
77 they provide advantages in terms of additional manipulation abilities? The present case study
78 examines these questions on two subjects with preaxial polydactyly with an SF between

79 thumb and index finger. The results reveal dedicated muscles, nerves and neural resources
80 that offer these polydactyly augmented manipulation abilities.

81

82 **Results**

83 *The SF is actuated by dedicated muscles and nerves*

84 We first examined the anatomy of the six-fingered right hand of subject P1 (Fig.1,
85 Supplementary Movie 1). The most radial digit or 'thumb' has two phalanges and the other
86 five fingers three phalanges (Fig.1A,B). The left and right hands of P1 have a similar shape,
87 likewise for P2 (Supplementary Fig.1). A magnetic resonance imaging (MRI) analysis revealed
88 that the right hand of P1 had four digits with similar anatomy to the ulnar four fingers of
89 common hands (Fig.1B). The thumb's bones are similar in morphology to that of a normal
90 thumb and have similar musculotendinous and neurovascular structures. However, the
91 thumb's carpometacarpal joint is of the ball-and-socket type (Fig.1D), with three dof including
92 torsion, while a normal thumb's carpometacarpal joint is a saddle joint that does not allow
93 torsion. The extra or *supernumerary finger* (SF) with three phalanges has a saddle joint similar
94 to that of a normal thumb (Fig.1E). It has two extrinsic flexor tendons as well as a normal
95 extensor apparatus (Fig.1C), in addition to dedicated digital nerves. Hence, *this polydactyly*
96 *hand is controlled by more muscles and nerves than normal five fingered hands*. Critically
97 there are intrinsic muscles whose origin is the second metacarpal and whose insertion is to
98 the proximal phalanx of the finger, similar to the muscles of a normal thumb and yielding a
99 spherical range of motion (Fig.1B,C).

100 *Neuromechanics of polydactyly hands* Using a dedicated interface to measure the force
101 exerted by individual fingers (Fig.2A, Supplementary Movie 2), we could then examine the
102 fingers' biomechanical characteristics. The maximal force was similar in 6- and 5-fingered
103 subjects (Fig. 2B; two-sided Wilcoxon rank sum test, $p=0.80$, $W=18$, 95% CIs [-14N,12N],
104 average across fingers 6- vs. 5-fingered subjects, $N_{1,2}=2,13$) and the maximum force exerted
105 by the SF was similar to the strongest other fingers (two-sided Wilcoxon signed-rank test,
106 $p=0.50$, $W=3$, 95% CIs [0.21N,1.2N] SF vs. the average across thumb, index and middle
107 finger, $N_{1,2}=2,2$). Force variability increased with the force level in the SF like in other fingers
108 of the 6-fingered hands and in the 5-fingered hands (17, Fig.2C). The interdependency (or
109 'enslaving', 18) of all pairs of fingers was examined by instructing subjects to produce maximal
110 force with each individual finger separately, while measuring the force of all fingers without
111 providing visual feedback of the force exerted by the remaining fingers. The enslaving value
112 was computed as the magnitude of the force exerted by a finger relative to its maximal force.
113 The results of this analysis revealed that *the SF was independent from other fingers, with only*

114 *some dependence between the SF and the thumb* (Fig.2D). The other fingers had similar
115 dependencies as in common 5-fingered hands (Fig.2D) and enslaving magnitude was highly
116 correlated between 5- and 6-fingered subjects across finger pairs available in both hands
117 (Pearson correlation coefficient, $r=0.94$, $N=20$). The enslaving between SF and index, little,
118 middle, ring, little finger was not different from the enslaving between the thumb and the other
119 fingers in 5-fingered subjects (two-sided Wilcoxon rank sum test, $p=0.30,0.38,0.17,0.57$,
120 $W=23,22,25,20$, 95% CIs $[-0.12,0.18]$, $[-0.028,0.052]$, $[-0.028,0.10]$, $[-0.10,0.13]$ for index,
121 middle, ring and little finger, $N_{1,2}=2,13$). Enslaving for lower levels of force (10%, 20% and
122 30% of maximal force) was similar to enslaving at maximal force, in particular for 20% and
123 30% of maximal force (Supplementary Fig. 2). Furthermore, the independent controllability of
124 the SF was also exemplified by our polydactyly subjects being able to do pinch grips between
125 the SF and all other fingers (Supplementary Movie 3).

126 Next, we investigated the functional organization of the motor cortex in P1 using an individual
127 finger tapping task and functional MRI at 7T high resolution (19). In order to highlight the
128 specific representations of each finger (14), we compared the activity patterns generated by
129 individual finger movements (Supplementary Fig.3). The results show that the representation
130 of the SF in the primary sensorimotor cortices was distinct from the representations of all other
131 fingers, including the thumb (Fig.2E, Supplementary Fig. 4). This demonstrates that *separate*
132 *neural resources are used to control movements of the SF in this 6-fingered subject.*

133 *Mental representation of polydactyly hands*

134 To infer the mental representation of the hand in our polydactyly subjects, we asked them to
135 indicate their perceived location of landmarks on the hand (fingertip, 1st and 2nd knuckles, for
136 each finger) by pointing with the other hand to the corresponding target on a two-dimensional
137 graded grid placed above the hidden hand, following a tactile cue on the target. As we see in
138 Fig.2F, *the hand representation corresponds to its anatomy, with the SF perceived correctly*
139 *between the thumb and index.* We found similar localization errors in the 6-fingered and 5-
140 fingered subjects (two-sided Wilcoxon rank sum test, $p=0.33$, $W=7$, 95% CIs $[-$
141 $0.89\text{cm},0.47\text{cm}]$, average across fingers 6- vs 5-fingered subjects, $N_{1,2}=2,9$, cf. ref 20). This
142 morphologically correct representation of the fingers may support 6-fingered manipulation.

143 *Supernumerary finger yields augmented manipulation abilities*We then investigated the
144 fingers' functionality by measuring their movement during free manipulation of selected
145 objects with various shapes (21), as well as during common tasks (Supplementary Fig.5,
146 Supplementary Movies 4 & 5). An accurate motion capture system was used to record the
147 movement of the distal and proximal phalanges of each finger. Interestingly, we found the
148 same interdependencies between the fingers' movements (Fig.3A for object manipulation,

149 Supplementary Fig.6A for common tasks) as in the previous biomechanical investigation,
150 suggesting that the mobility and independence of the SF is not reduced during manipulation
151 ($r=0.88$, $N=30$, Pearson correlation coefficient between enslaving matrix in Fig.2D and
152 dependency matrix in Fig.3A for 6-fingered subjects; $r=0.87$, $N=30$, Pearson correlation
153 coefficient as before but using the dependency matrix for common tasks show in
154 Supplementary Fig. 6A). The interdependencies between the fingers' movements was highly
155 correlated between 5 fingered and 6 fingered hands for all fingers excluding the SF ($r=0.996$,
156 $N=10$, Pearson correlation coefficient for object manipulation; $r=0.995$, $N=10$, Pearson
157 correlation coefficient for object manipulation). The movements of the SF, like the thumb and
158 index finger's movements, could not be reconstructed from the movements of the other fingers
159 (Supplementary Fig.7). Consistently, an examination of the fingers' kinematic synergies (22)
160 revealed that movements of the 6-fingered hands had a higher number of effective degrees
161 of freedom than 5-fingered hands (Fig.3B,C, Supplementary Fig.6B,C; two-sided Wilcoxon
162 ranksum test, $p=0.019$, $W=29$, 95% CI [2.5,6.9], $N_{1,2}=2,13$ for object manipulation; $p=0.044$,
163 $W=19$, 95% CI [1.5,8.6], $N_{1,2}=2,8$ for common tasks). These results were confirmed by an
164 information theoretic analysis (Fig.3D, Supplementary Fig.6D) taking into account non-linear
165 relations. The movement of each finger was classified into one of three states {rest, flexion,
166 extension} yielding 3^f (f : number of fingers) different movement configurations on which the
167 joint entropy was calculated (Fig.3D, Supplementary Fig.6D). For finger combinations
168 available in both kinds of subjects the entropy for 6 fingered subjects was similar to 5 fingered
169 subjects (two-sided Wilcoxon rank sum test, $p=0.17,0.23,0.23,0.30,0.38$, $W=25,24,24,23,22$,
170 95% CIs in bits [-0.011,0.055], [-0.018,0.072], [-0.11,0.26], [-0.079,0.31], [-0.18,0.38], for the
171 first five finger combinations shown in Fig. 3D for object manipulation, $N_{1,2}=2,13$; two-sided
172 Wilcoxon rank sum test, $p=0.53,0.27,0.044,0.044,0.40$, $W=8,16,19,19,15$, 95% CIs in bits [-
173 0.080,0.11], [-0.056,0.16], [0.046,0.20], [0.12,0.47], [-0.097, 0.66] same combinations for
174 common tasks, $N_{1,2}=2,8$). However, the maximal entropy for 6-fingered hand movements was
175 substantially higher than for 5-fingered movements (two-sided Wilcoxon rank sum test,
176 $p=0.019$, $W=29$, 95% CI in bits [1.3,1.8], $N_{1,2}=2,13$ for object manipulation; two-sided Wilcoxon
177 rank sum test, $p=0.044$, $W=19$, 95% CI in bits [1.2,2.1], $N_{1,2}=2,8$ for common tasks). Moreover,
178 the entropy was higher than the maximum possible entropy for five fingers and close to the
179 maximum possible entropy for six fingers showing that subjects used a rich ensemble of
180 movement patterns. Furthermore, the SF was moved most of the time in coordination with
181 both the thumb and index finger, rather than moving alone or with only the thumb or the index
182 finger (Fig.3E, Supplementary Fig.6E). Consequently, the independence of the SF could not
183 simply be ascribed the function of replacing the thumb or index finger. Instead, 6-fingered
184 hands featured unique movement patterns involving thumb, SF and index finger. Importantly,
185 this did not come at the expense of slower movements (Fig.3F, Supplementary Fig.6F): the

186 movement speed was similar for 5- and 6-fingered subjects (two-sided Wilcoxon rank sum
187 test, $p=0.80$, $W=18$, 95% CIs [-1.0cm/s,1.5cm/s], average across fingers 6- vs 5-fingered
188 subjects, $N_{1,2}=2,13$, object manipulation; two-sided Wilcoxon rank sum test, $p=0.27$, $W=16$,
189 95% CIs [-0.28cm/s,4.2cm/s], average across fingers 6- vs 5-fingered subjects, $N_{1,2}=2,8$,
190 common tasks) Taken together *these results demonstrate that the movements of the 6-*
191 *fingered hands of our two subjects had increased complexity relative to common 5-fingered*
192 *hands.*

193 To examine whether the superior functionality of 6-fingered hands enabled our polydactyly
194 subjects to carry out tasks that cannot be completed with one 5-fingered hand, we designed
195 a video game stimulating subjects to coordinate finger movements at increasing speed
196 (Fig.3G, Supplementary Movie 6). The video game consisted of 6 boxes oscillating up- and
197 down at different frequencies on a computer screen; each time a box reached a target area at
198 the bottom of the screen, the subject had to press a key with the corresponding finger. The
199 aim was to keep both the fraction of missed key presses (false positives) and wrongly timed
200 key presses (false negatives; i.e. when the box was not in the white area) below a specified
201 threshold, for 2 minutes. When this objective was achieved subjects moved on to a harder
202 level. Across levels, the movement speed of the boxes increased, requiring temporally more
203 precise finger movements (Fig.3G). Subjects practiced the video game across five days,
204 training on each day using either (a) the 6 fingers of their right hand, or (b) 5 fingers from the
205 right without the SF and 1 finger from the left hand (Fig.3H). The slopes of the learning curves
206 (Fig. 3H) were not different between 5+1 and 6 finger control for both subjects ($p>0.05$,
207 Bootstrap test, see Methods). Hence, subjects achieved the same performance with 6 fingers
208 from one hand as with two hands, which is how the task would be carried out by normal 5-
209 fingered hands. *This demonstrates the augmented abilities for manipulation enabled by the 6-*
210 *fingered hand compared to a common 5-fingered hand.* Supplementary movie 7 further
211 illustrates the skill enabled by 6-fingered manipulation.

212

213 **Discussion**

214 Although polydactyly is not rare, and can be traced back at least 1000 years (10), only its
215 genetics has, until now, been studied. This may in part be due to the belief that supernumerary
216 fingers represent a malformation and are not useful, thus are generally removed at a young
217 age. However, our study with two preaxial polydactyly subjects from the same family reveals
218 fully functional supernumerary fingers (SF), demonstrates their utility and the augmented
219 manipulation capabilities they can provide. The observed SF has independent muscles,
220 nerves, a dedicated cortical representation and an anatomically correct mental representation.

221 Our polydactyly subjects can move the SF independently from the other five fingers and use
222 it to carry out unique manipulation behaviors in particular in conjunction with the thumb and
223 index finger.

224 Importantly, the possibilities offered by the SF biomechanics of our polydactyly subjects were
225 not reduced or even modified by the neural control, as demonstrated during manipulation of
226 various objects. The experiments demonstrated that they have no difficulty in controlling the
227 SF in coordination with and independently from the other fingers while no movement deficits
228 of the hand or other limbs were observed. The SF is used together with all other fingers for
229 more complex manipulation than in normal 5-fingered individuals, at a similar speed. In
230 particular, the highly mobile thumb and SF, both having a spherical workspace, allow these
231 polydactyly subjects a large versatility and dexterity, yielding a higher sensorimotor ability for
232 manipulation with one hand than in normal-bodied individuals. These superior abilities of our
233 polydactyly subjects, which may be specific to the preaxial group of polydactyly and to the
234 well-developed SF in our subjects, suggest to thoroughly evaluate the functionality of a SF in
235 polydactyly infants before deciding on whether to remove it.

236 The present study is the first demonstration that the human nervous system is able to develop,
237 embody and control multiple extra dof and integrate them into coordinated movements with
238 the other limbs, without any apparent movement deficits or conflicts in the sensorimotor or
239 mental representations. The exceptional manipulation abilities in our polydactyly subjects
240 suggest that it may be of value to augment normal 5-fingered hands with an artificial
241 supernumerary finger. For several years, roboticists have been attempting to develop extra
242 limbs to augment human movement abilities (1-2) and neural interfaces to control them (3-6).
243 The biomechanics and functionality of the polydactyly hands analyzed in this paper may be
244 used as a blueprint for the development of robotic hands. However, it remains unclear how to
245 implement real-time and embodied control of additional dofs yielding augmented manipulation
246 capabilities. Polydactyly individuals with functional SF offer a unique opportunity to investigate
247 the neural control of supernumerary limbs, analyze internal representations of the body and
248 the limits of sensorimotor capabilities in humans.

249

250 **Methods**

251 This section describes the series of experiments carried out by the two polydactyly subjects,
252 P1 and P2, to investigate the neuromechanics and functions of their hands. Some experiments
253 involved in addition a group of control subjects with 5-finger hands. The study was approved
254 by the institutional ethics committees at the University of Freiburg, Imperial College London,

255 EPFL and King's College London. Each subject gave informed consent prior to starting every
256 experiment.

257

258 *MRI analysis of hand anatomy*

259 The underlying anatomy of the hand of subject P1 was visualized using magnetic resonance
260 imaging (MRI) in the Department of Perinatal Imaging and Health, King's College London. T1
261 weighted, inversion recovery and proton density images were acquired with a 1.5 Tesla
262 Siemens Aera system (Erlangen, DE). Images could not be acquired from subject P2 due to
263 a metallic dental implant.

264

265 *Hand biomechanics*

266 A dedicated hand interface to measure the isometric force of each finger (shown in Fig. 2A)
267 was developed at the Human Robotics group, Imperial College London, to investigate the
268 force capability of either left or right fingers, in individuals with either 5-finger or 6-finger hands.
269 The hand was placed horizontally on the interface as shown in Fig. 2A. 5 or 6 of the 8 3D
270 printed supports, each affixed to a load cell (HTC), could slide linearly to accommodate a left
271 or right hand of any size so that the subject could comfortably exert a vertical force with the
272 tip of each finger.

273 Forces across all fingers were recorded at 128Hz. Experiments were carried out with this
274 interface on the two polydactyly subjects as well as on a population of 13 control subjects (6
275 females) with 5-finger hands between 25 and 35 years old. The subjects were seated in front
276 of a table with the interface positioned on top of it so that the forearm was resting on the table
277 in a natural position.

278 Initially, subjects were asked to exert the maximal possible force with a single finger. This
279 *maximal force* (MF) was recorded for each finger separately starting with the thumb and
280 ending with the little finger. Fig. 2B shows the MF for 5- and 6-finger subjects. Using this data,
281 the *enslaving* e_{ij} , characterizing the dependence between fingers i and j , was computed as

$$285 \quad e_{ij} = \frac{F_j(i)}{MF_j} \quad (1)$$

282 where i is the finger which generates MF while F_j is the force produced simultaneously by
283 finger j and MF_j is the maximal force of finger j . The enslaving for 5- and 6-fingered subjects
284 are presented in Fig. 2D.

286 Then the subjects were asked to control 10%, 20%, or 30% of MF during 15s long trials. Three
287 trials were carried out at each force level, totalizing $3 \times 3 \times 5 = 45$ or $3 \times 3 \times 6 = 54$ trials per session
288 for 5- and 6-fingered subjects respectively. 5-fingered subjects carried out only one session
289 while the 6-fingered subjects performed two (subject P1) or three (subject P2) sessions. The
290 data from this experiment was used to examine how the force variability depends on the
291 amount of force exerted. In each trial, the force variability was computed as the standard
292 deviation of the force across the time window [1300-1800]/128 s, which was selected so that
293 the subjects were correctly exerting the required force during this period in almost all trials.
294 Five trials (1 trial in a control subject, 2 trials in subject P1 and 2 trials in subject P2) were
295 excluded from the analysis as they showed extraordinary high fluctuations of the force across
296 time, indicating that the task was not carried out successfully on these trials. Fig. 2C shows
297 the standard deviation of the force as a function of the magnitude of the force for 5- and 6-
298 fingered subjects.

299 We also computed the enslaving for the 10%, 20%, or 30% MF tasks (Supplementary Fig.2).
300 The normalization by the maximal force (MF_j) was replaced by 10%, 20%, or 30% of the
301 maximal force respectively.

302

303 *Functional MRI*

304 P1 and a group of 9 control participants with 5-finger hands took part in the fMRI experiment.
305 P2 was excluded due to a metallic dental implant. In a block design, participants performed a
306 tapping movement during 20 seconds with a single finger (20 taps per block, 1 tap per second)
307 followed by 10 seconds of rest. Four blocks were performed for each finger in pseudo-
308 randomized order (24 trials for P1 and 20 trials for controls). P1 performed two sessions, one
309 for each hand. Controls performed only one session with the right hand. All participants were
310 trained on the movements before entering the fMRI scanner.

311 Images were acquired on a short-bore head-only 7T scanner (Siemens Medical, Germany)
312 with a 32-channel Tx/Rx rf-coil (Nova Medical, Germany). Functional images were acquired
313 using a sinusoidal readout EPI sequence (23) and comprised 28 axial slices. Slices were
314 placed over the central sulcus (approximately orthogonal to the central sulcus) in order to
315 cover the primary motor cortices (voxel resolution $1.3 \times 1.3 \times 1.3 \text{mm}^3$; TR= 2s, FOV=210mm,
316 TE=27ms, flip angle=75°, GRAPPA=2). Anatomical images were acquired using an
317 MP2RAGE sequence (24) in order to allow the precise localization of the precentral sulcus
318 (see below) and for display purposes (TE = 2.63ms, TR = 7.2ms, T11 = 0.9s, T12 = 3.2s,
319 TRmprage = 5s). To aid coregistration between the functional and the anatomical images, a
320 whole brain EPI volume was also acquired with the same inclination used in the functional

321 runs (81 slices, voxel resolution $1.3 \times 1.3 \times 1.3 \text{mm}^3$, FOV=210mm, TE=27ms, flip angle=75°,
322 GRAPPA=2). Subjects were scanned in supine position.

323 All images were analyzed using the SPM8 software (Wellcome Centre for Human
324 Neuroimaging, London, UK). Preprocessing of fMRI data included slice timing correction,
325 spatial realignment, smoothing (FWHM=2mm) and coregistration with anatomical images.
326 Caret 5 (Van Essen Laboratory, Washington University School of Medicine) was used for
327 surface visualization. To localize the voxels included in the analysis of activation patterns
328 (Supplementary Fig. 3), a first GLM analysis was computed, which included one regressor per
329 finger (6 for P1 and 5 for controls) and 6 rigid movements regressors. A functional mask for
330 finger movements was defined as the active voxels in the F-contrast associated with any type
331 of finger movement ($p < 0.05$ FWE). In addition, an anatomical mask corresponding to the
332 sensorimotor cortex was designed using published probabilistic cytoarchitectonic maps
333 (25,26,27). The anatomical mask included the primary motor cortex M1 (Brodmann areas 4a
334 and 4p) and the primary somatosensory cortex S1 (Brodmann areas 3a, 3b, 1 and 2). The
335 anatomical mask was back-projected onto the native space of each participant. This led to
336 2190 voxels in the left hemisphere of P1 for right finger movements, 2037 voxels in the right
337 hemisphere of P1 for left finger movements, and 343.8 ± 417.1 (mean \pm std) voxels in the left
338 hemisphere of controls for right finger movements (Supplementary Fig. 3).

339 To analyze the activation patterns within the selected voxels associated with each trial of finger
340 movement, a second GLM analysis was computed, which included one regressor for each
341 finger tapping trial (24 for P1 and 20 for controls) and 6 rigid movements regressors.
342 Separately for each participant, the beta estimates for each tapping trial were extracted within
343 the selected voxels (resulting in a trials \times voxels matrix). These high-dimensional patterns
344 were projected to 2 dimensions by classical multidimensional scaling (MDS), which finds low-
345 dimensional projections preserving approximately the pairwise distances between the high-
346 dimensional activation patterns (14). As distance metric for the MDS, we used the cross-
347 validated Mahalanobis distance (14). For the 5-finger control group, MDS was carried out for
348 each subject separately. As MDS projections induce an arbitrary rotation we aligned the
349 projections of the individual subjects using Procrustes alignment (14). Standard error ellipses
350 shown in Fig. 2E were computed from the covariance across subjects. As the Procrustes
351 alignment can also remove some of the true inter-subject variability (14), we used a Monte-
352 Carlo procedure to estimate a correction and adjusted the standard error ellipses accordingly
353 (14). For the polydactyl subject P1, we computed the covariance by bootstrapping the trials.
354 For each bootstrap sample an MDS projection was computed. The bootstrapped MDS
355 projections were aligned using Procrustes alignment. The standard error ellipses (Fig. 2E,

356 Supplementary Fig. 4) were computed from the covariance across bootstrapped MDS
357 projections, adjusted by correction factors estimated by a Monte-Carlo procedure (14).

358

359 *Finger localization task*

360 A finger localization task (20) was conducted to investigate the perceived hand shape of P1,
361 P2, and of a group of 9 controls. Participants were blindfolded and their hand was placed
362 below a structure topped by a 2D grid. They had to point on the grid with the index of the free
363 hand towards the cued locations on the tested hand. They were required to identify 3 locations
364 on each finger: the first knuckle, the second knuckle and the tip (total of 18 locations per hand
365 for P1 and P2, and 15 locations for controls). Each location was tested 6 times for P1 and P2,
366 4 times for controls. The task was conducted for both hands in P1 and P2, only for the right
367 hand in controls. The task was conducted once with tactile cueing, i.e. the target locations
368 were touched with a plastic filament, and once with verbal cueing, i.e. the target locations were
369 orally named. The localization error was measured for each tested location as the 2D-
370 Euclidean distance between the reported positions on the grid and the real positions of the
371 tested locations on the grid (Fig. 2F). Similar results were obtained with tactile and oral cueing,
372 we only report the results from tactile cueing.

373 *Object manipulation and common movement tasks*

374 *Experimental setup.* The subjects were seated in front of a desk during the two tasks described
375 below. An electromagnetic motion capture system (Polhemus Liberty 240/16-16) was used to
376 record the hand and finger movements during the object manipulation and the common
377 movement tasks (see Supplementary Fig. 5A). The hands were kept at 0.6m distance from
378 the main Polhemus system to maintain the recording noise below 0.005mm. In total 12
379 respectively 14 sensors were attached to the hand and fingers of 5- or 6-finger subjects using
380 medical tape. Every sensor measured 3 Cartesian coordinates for the position and 3 angles
381 for the orientation relative to the main station. Each sensor was connected to the Polhemus
382 system by plastic insulated aluminum wires. Two large sensors (9x11x6mm³ at maximum
383 positions, 9.1g) were placed on the skin on top of the middle and thumb metacarpal bones.
384 The others were small sensors (spherical, 17.3mm length, 1.8mm outer diameter, <1g) which
385 were placed at the distal and proximal phalanges of each finger. Measurements were recorded
386 at 120Hz.

387

388 *Object manipulation task.*

389 The two polydactyly subjects and 13 control subjects with 5-finger hands (6 female, mean age
390 24.8 with standard deviation 2.0) participated in an object manipulation task. The experimental
391 procedure for the object manipulation task was adapted from (21). We chose 50 objects with
392 different shapes, sizes, textures and materials (see Supplementary Fig. 5B). These objects
393 were without metal or paramagnetic materials so as to not interfere with the Polhemus
394 measurement based on magnetic fields. The subjects were blind-folded and were given the
395 objects one by one. They had to explore an object with one hand, and guess what it is (see
396 supplementary movie 4). Each object was explored for 30s. When an object was recognized
397 earlier than 30s, the subject was asked to explore special features of this object such as tips,
398 edges etc.

399

400 *Common movement tasks.* The two polydactyly subjects and 8 of the 13 subjects with 5-finger
401 hands who carried out the object manipulation task (5 female, mean age 24.3 with standard
402 deviation 2.0) also performed four common movement tasks (see also supplementary movie
403 5). *Tying shoe laces:* The end of two shoe laces were fixed on a table and the subjects were
404 required to tie the laces with two hands. *Flipping book pages:* The subjects were given a book
405 and had to flip pages using one hand only. *Napkin folding:* The subjects received a paper
406 napkin and had to fold it into a specific shape (as used in restaurants) and in a specific
407 sequence using both hands. *Rolling a towel:* Subjects were given a towel and asked to roll it
408 into cylinders using both hands. Five minutes of movement per task was recorded during
409 which subjects were asked to repeat the task as often as they wanted.

410

411 *Data analysis.* The position of every small sensor relative to the large sensor on the middle of
412 the metacarpal bones was used for further analysis. Raw positional measurements were
413 smoothed with a Savitzky-Golay filter (3rd order, length 41 sample points equivalent to 341.67
414 ms). Movement velocities were computed from raw positional measurements with a first
415 derivative Savitzky-Golay filter (3rd order, length 41 sample points equivalent to 341.67 ms).

416 *Analysis of finger (in)dependence.* To assess the (in)dependence of finger movements we
417 estimated the mutual information between the movements of different fingers. The mutual
418 information between two continuous stochastic signals X and Y is defined as:

419
$$I(X, Y) = \int_X \int_Y p(x, y) \log_2 \left[\frac{p(x, y)}{p(x)p(y)} \right] dx dy \quad (2)$$

420 where $p(x,y)$ is the joint probability density function of X and Y , $p(x)$ and $p(y)$ are the marginal
421 probability density functions of X and Y . Note that the mutual information is symmetric, i.e.
422 $I(X, Y) = I(Y, X)$. In case of multivariate Gaussian density functions (2) simplifies to

$$427 \quad I(X, Y) = \frac{1}{2} \log_2 \left[\frac{\det(\sigma_X) \det(\sigma_Y)}{\det(\sigma_{XY})} \right] \quad (3)$$

423 where σ_X , σ_Y are the covariance matrices of the marginal densities X and Y and σ_{XY} is the
424 covariance matrix of the joint density. A more intuitive understanding of the mutual information
425 can be gained for univariate normal signals X and Y for which equation (3) further simplifies
426 to

$$428 \quad I(X, Y) = \log_2 \sqrt{\frac{1}{1 - r(X, Y)^2}} \quad (4)$$

429 where $r(X, Y)$ is the Pearson correlation coefficient between X and Y . To estimate the mutual
430 information between two fingers we used the 6-dimensional position measurements from the
431 two sensors at each finger, estimated the covariance matrices from the time series of
432 movement positions and applied equation (3).

433

434 *Prediction of individual finger movements from movements of other fingers.* The movement of
435 each individual finger was predicted from the movements of the other fingers. For 6-fingered
436 subjects the prediction was carried out with and without the supernumerary finger; the latter
437 to facilitate comparison with the results from 5-fingered subjects. The x/y/z-positions of the
438 two sensors at each finger constituted the 6-dimensional movement vector of each finger.
439 These 6 components were individually predicted from the 24- or 30-dimensional movement
440 vectors of the remaining 4 or 5 fingers. Prediction was done using linear least-squares and
441 non-linear support vector regression. We used two-fold cross-validation with chronological
442 splits of the data to avoid overfitting. The quality of prediction was quantified by computing the
443 coefficient of determination (R^2) between predicted and actual movement for each component
444 of the 6-dimensional movement vector and then averaging the R^2 values across the 6
445 dimensions. We used support vector regression with a Gaussian kernel and the
446 hyperparameters (i.e. the kernel width as well as the regularization parameter) were optimized
447 on the training data set. We used the Matlab implementation ('fitcsvm') for support vector
448 regression and optimization of hyperparameters. To reduce computation time the data was
449 downsampled to 120/20=6Hz.

450

451 *Principal component analysis (PCA) of degrees of freedom (21,28,29).* PCA was performed
452 on the sensor x/y/z-positions measured with two sensors at each finger during the object
453 manipulation and the common movement tasks. The cumulated amount of variance captured
454 by an increasing number of principal components is plotted in Fig. 3B and Supplementary Fig.
455 6B. To compute the effective number of dof we applied two algorithms: the cross-validation
456 PCA with Eigenvector method recommended in (30) and the cross-validation PCA method
457 using expectation maximization for missing values as proposed in (31). Both methods use a
458 cross-validation procedure where the PCA is first computed from training data and then
459 applied to predict the samples of the test data while training and test data set are mutually
460 exclusive (30,31). In our case we used 10-fold cross-validation and chronologically split the
461 movement data separately for each task into 10 parts using in each fold 9 of those parts in the
462 training and 1 part in the test data. The first and last 10 seconds of the test data set were
463 excluded for each task to avoid any influence of the training on the test data due to the auto-
464 correlation of the movement. The mean squared error between prediction and actual data was
465 computed as a function of the number of principal components. The number of principal
466 components which yielded the smallest error was used as an estimate for the effective number
467 of dof and was computed for each subject separately. For each subject we averaged the
468 determined number of principal components across both methods (30,31) and used this as an
469 estimate of the number of degrees of freedom (Fig. 3C, Supplementary Fig. 6C).

470

471 *Information theoretic analysis of degrees of freedom.* In addition to the PCA analysis described
472 in the previous section, we analyzed the degrees of freedom using information entropy. In
473 contrast to the PCA, the analysis of information entropy takes into account potential non-linear
474 relationships between finger movements. Information entropy, on the other hand, requires an
475 estimate of the joint probability distribution of the finger movements. To compute this joint
476 probability distribution, we discretized the finger movements by classifying the movement state
477 of each finger into one of three conditions from the set $MS=\{\text{rest, flexion, extension}\}$, based
478 on the movements of the distal and proximal interphalangeal joints. Spherical coordinates
479 (distance, polar and azimuth angle) of the distal sensor relative to its proximal sensor were
480 computed. PCA was performed on the polar and azimuth angles and the movements along
481 the first principal component were used to represent the movements of each finger. For each
482 finger, the first derivative v of the first PC was calculated as the difference between two
483 consecutive time bins and used to derive the current movement state based on a threshold μ
484 $= 0.3 \text{ SD}(v)$: flexion for $v < -\mu$, extension for $v > \mu$, rest otherwise. Different threshold values
485 ($\mu = 0.4 \text{ SD}(v)$ or $\mu = 0.1 \text{ SD}(v)$), as well as different set of states (only two states: flexion for
486 $v < 0$ and extension for $v > 0$), did not change our general conclusion regarding the comparison

487 of the information entropy between 5 and 6-fingered subjects. We computed the information
488 or Shannon entropy (H) of the joint probability distribution of the movement states of all fingers
489 (p):

$$490 \quad H = - \sum_{s_1 \in MS} \sum_{s_2 \in MS} \cdots \sum_{s_n \in MS} p(s_1, s_2, \dots, s_n) \log_2[p(s_1, s_2, \dots, s_n)] \quad (5)$$

491 where $s_i \in MS$ is the state of finger i . For n fingers the number of different movement states is
492 3^n and the maximum entropy is therefore $\log_2(3^n)$ which is obtained when all possible
493 movement states have equal probability.

494

495 *Joint movement of thumb, index and supernumerary finger.* For each time point we computed
496 the movement speed for each finger as the magnitude of its 3-dimensional velocity vector at
497 the fingertip. We then classified the movement state of each finger in each time point as either
498 'rest' or 'moving' by comparing the speed to a threshold value which was chosen as the 10th,
499 30th or 50th percentile of the speed distribution across all time points and all fingers. From this
500 data we estimated the conditional probabilities that thumb and index finger or thumb alone or
501 index finger alone were moving given the supernumerary finger was moving. These
502 conditional probabilities were estimated for the three speed thresholds (Fig. 3E,
503 Supplementary Fig. 6E).

504

505 *Video game for 6 fingers*

506 Polydactyly subjects sat in front of a computer monitor (DELL U2713HM) approximately 0.6m
507 from the screen, on which six target boxes were displayed in the lower centre of a black
508 screen. During the experiment, oscillating cursors passed through the target boxes (Fig. 3G
509 and supplementary movie 6). Each of these oscillating squares had a different frequency
510 within a predefined range. The individual target boxes could be "touched" by pressing a
511 corresponding key on a standard computer keyboard. Keys were chosen to match the hand
512 geometry of individual subjects to ensure pressing the keys was comfortable. The subjects
513 were instructed to track the oscillating cursors and to press the corresponding button once the
514 cursor was within its associated target box. If the button was pressed within this time window,
515 it counted as a correct press, if it was pressed outside it was counted as a false press. The
516 number of correct and false presses were summed over all fingers and accumulated over the
517 time of the trial.

518

519 The *performance* of the subjects was rated on their accuracy (correct presses/target count)
520 and error rate (false presses/all presses). The aim was to increase accuracy while decreasing
521 the error rate. At the beginning of each trial the target accuracy and the error rate threshold
522 was set according to the level (Supplementary Table 1); each level was defined by the
523 movement speed of the oscillating cursors and thresholds on the accuracy and the error rate.
524 Once the subject crossed both thresholds, the participant was expected to maintain their
525 performance above the accuracy and below the error threshold for 2 minutes, at which point
526 the trial would end and the level would be increased. For each subsequent level, the accuracy
527 threshold was set 10% higher and the error rate was set 10% lower. If the subject was able to
528 cross the 70% threshold for accuracy and go below the 30% threshold for the error rate the
529 oscillation frequency range was increased by 0.05 Hz. After increasing the oscillation
530 frequency, the accuracy threshold and error rate were set back to the original value of 50%.
531 See Supplementary Table 1 which highlights the parameter values associated with different
532 levels. If the subject was not able to reach the next level within seven minutes, the trial was
533 aborted and after a short break, the subject was asked to repeat the same level.

534 During each trial, the following additional visual feedback was presented to the subject. If no
535 key was pressed, the target boxes were displayed in white. Pressing a key while no cursor
536 was in the corresponding box, i.e. a false press, the target box turned red. Pressing a key
537 while a cursor was in the corresponding box, i.e. correct press, the target box turned blue.
538 Below the target boxes, two bars gave visual feedback about the subject's overall
539 performance. The upper bar reflected the accuracy and the lower bar the error rate. If the
540 accuracy of the subject increased, the accuracy bar filled up and vice versa. At the same time,
541 decreasing the error results in filling of the error bar, such that an error rate equal to 0 resulted
542 in an entirely filled bar, i.e. the value of 1-error rate was presented. Each bar was red until the
543 subject crossed the set threshold of the corresponding bar, at which point it turned green. The
544 threshold values were shown as gray markers on the bars. As soon as both bars turned green,
545 a red countdown of 120 seconds appeared in the lower centre of the screen. If one bar turned
546 red again before the time was expired, the countdown was reset to 120 seconds and
547 disappeared until both bars were green again. Furthermore, each cursor individually appeared
548 in red (if below) or green (if above) the performance threshold in relation to the individual
549 performance of the corresponding finger, so the subjects had an indication of which finger
550 required improvement.

551 The evolution of performance is shown in Fig. 3H. Subjects were tested for five consecutive
552 days as well as 10 days after. The subjects performed the task for 1 hour per day. The subjects
553 had to use two different finger combinations to press the keys; either all six fingers from the
554 right hand or the right hand but replaced the SF with the index finger of the left hand (Fig. 3H).

555

556 *Statistical analysis*

557 For comparing two independent samples we used the non-parametric, two-sided Wilcoxon
558 ranksum test and computed 95% confidence intervals on the effect size (i.e. the difference of
559 the population means) by using the two-sample pooled t-interval. For comparing two paired
560 samples we used the non-parametric, two-sided Wilcoxon signed rank test and computed 95%
561 confidence intervals on the effect size by using the paired t-interval. All reported confidence
562 intervals always reflect the mean for 5-fingered subjects subtracted from the mean for 6-
563 fingered subjects, i.e. positive values indicate larger values for 6-fingered subjects.

564 To assess the correlation between two variables we computed the Pearson correlation
565 coefficient. We did not assess the statistical significance of the Pearson correlation coefficient
566 as the samples across which correlations were computed were not independent.

567

568 **Data availability statement:** The data are not available due to them containing information
569 which could compromise research participant privacy and consent.

570

571

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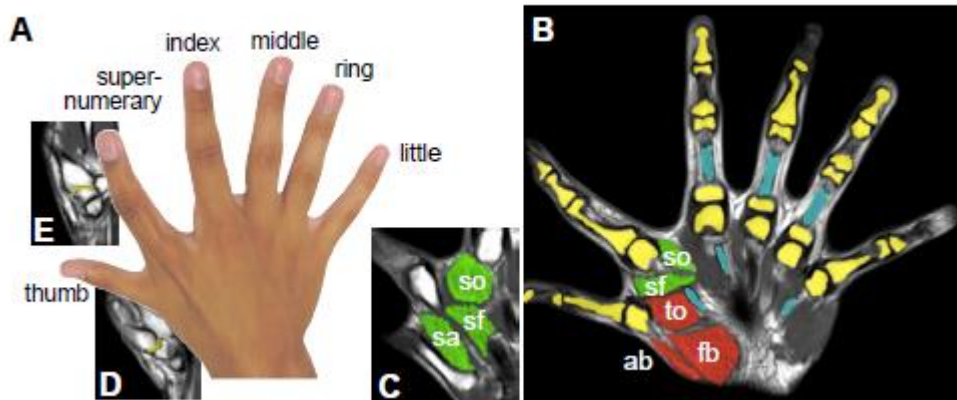
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656

657

658

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670 MOTION EP/NO29003/1.
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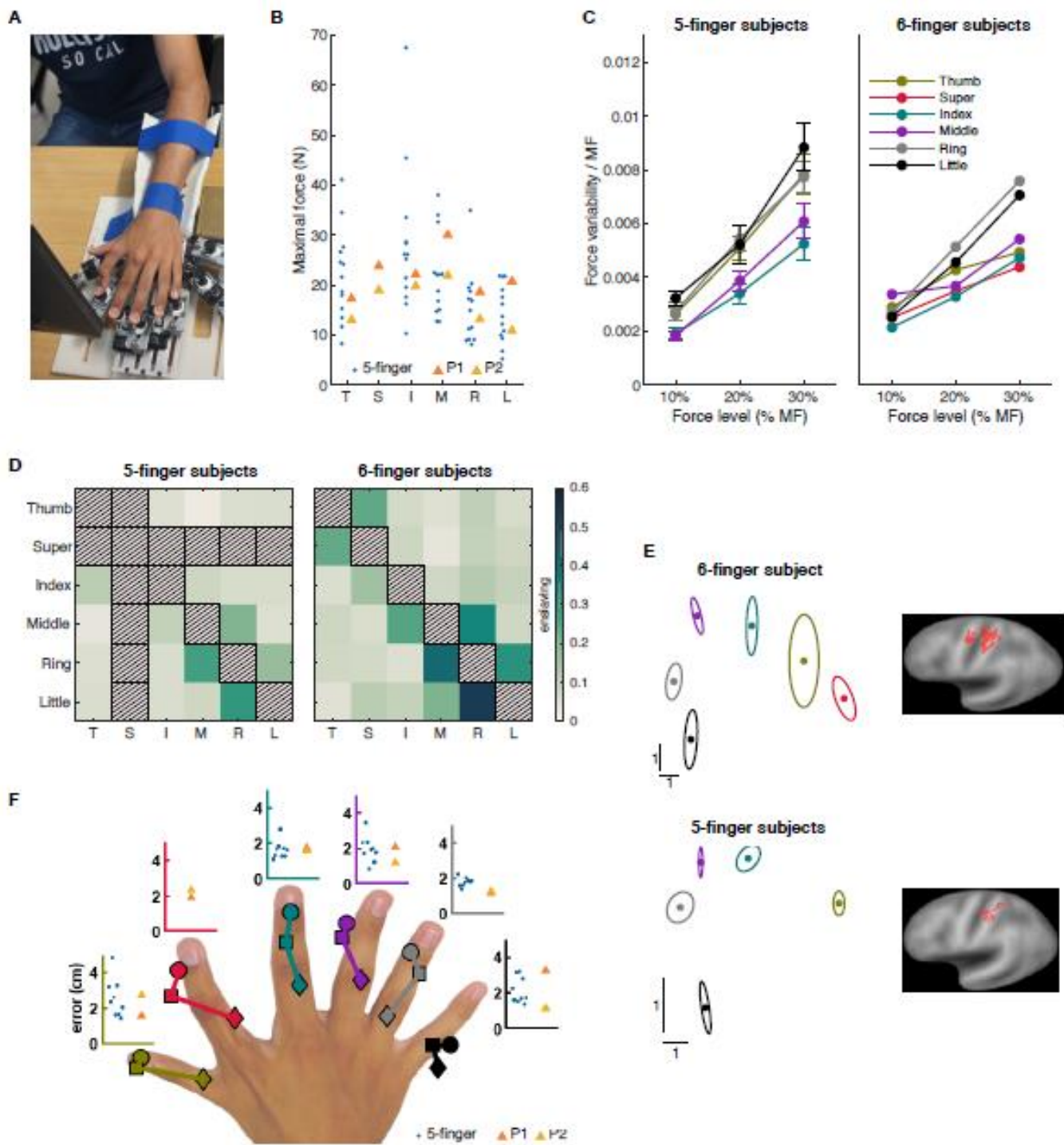


672

673 **Figure 1:** The right hand's anatomy of subject P1. A photo of the dominant right hand of one
 674 of the 6-fingered subjects (A). The joints of the wrist (radio-ulnar, radio-carpal and mid-carpal)
 675 are similar to that of a normal 5-fingered hand (B). Bones are in yellow, tendons in blue,
 676 muscles: so,sf,sa: supernumerary finger opponens, flexor, abductor; to: thumb opponens;
 677 abp: abductor pollicis brevis; fbp: flexor pollicis brevis. The four fingers from index to little have
 678 a similar skeleton, musculotendinous attachments and nerves as the corresponding fingers of
 679 a normal hand. The thumb resembles a normal thumb, with two phalanges. However, its
 680 carpometacarpal joint to the wrist (D) is of ball-and-socket type, with 3 degrees-of-freedom
 681 (dof) including torsion, while a normal thumb will have a saddle joint that does not allow torsion.
 682 The musculotendinous and neurovascular structures resemble the thumb of a normal hand
 683 (B,D). The sixth finger or supernumerary finger has three phalanges and a saddle
 684 carpometacarpal joint (E). It has two extrinsic flexor tendons and a normal extensor apparatus
 685 not dissimilar to that of a tri-phalangeal digit. Interestingly there are muscles whose origin is
 686 the second metacarpal and whose insertion is to the proximal phalanx of the finger (B,C),
 687 similar to the muscles of a normal thumb with spherical range of motion.

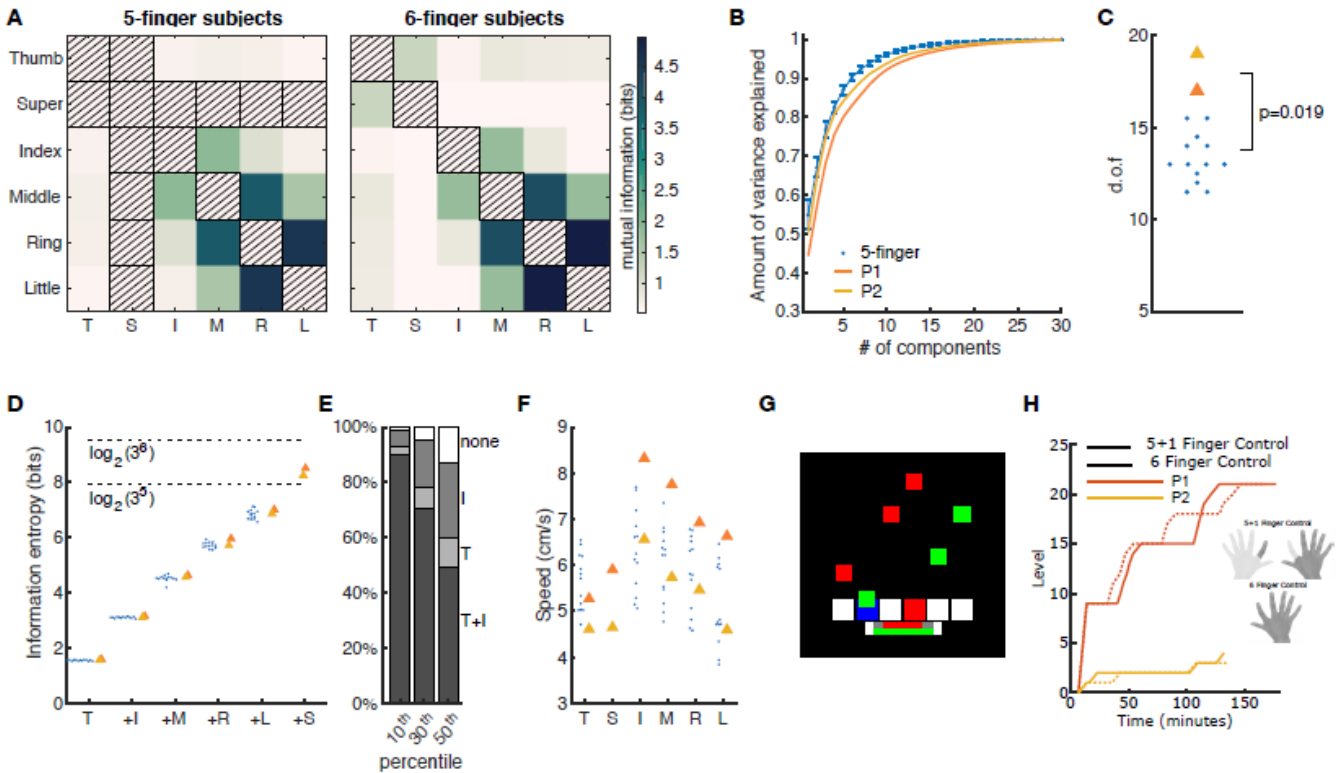
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689



690 **Figure 2:** Neuromechanics of the polydactyly hand. (A) Dedicated isometric interface to
 691 investigate the force capability of each finger in individuals with 5- and 6-fingered hands. The
 692 interface was used for the analyses presented in subplots (B),(C),(D). Subjects were initially
 693 asked to exert maximal force (MF) with a single finger. In a consecutive experiment subjects
 694 were asked to control 10%, 20%, or 30% of MF during 15s long trials. Two 6- and thirteen 5-
 695 fingered subjects carried out these experiments. (B) MF produced by individual fingers. The
 696 MF was similar for 5- and 6-fingered subjects for all regular fingers. (C) Force variability
 697 (standard deviation of the force) as a function of the magnitude of the produced force

698 expressed in percentage of the maximal force. Error bars depict SEMs across subjects. (D)
699 Enslaving shows the forces induced in other fingers when the subject is instructed to exert the
700 maximal force in one finger. Enslaving between finger i and j was computed as $e_{ij} = \frac{F_j(i)}{MF_j}$,
701 where F_j is the force produced by finger j when finger i was instructed to produce maximal
702 force. MF_j depicts the maximal force of finger j . In the matrix plot the instructed finger is shown
703 on the y-axis, hence, each row shows the induced force relative to the maximal force of the
704 corresponding finger, i.e. e_i . (E) Two-dimensional projection (multi-dimensional scaling,
705 MDS) of fMRI activation in sensorimotor cortex during individual finger movements in subject
706 P1 and the average across nine 5-fingered control subjects (left). Colors depict different fingers
707 as in (C). Ellipses show the standard error of the mean. The location of the activation cluster
708 of the supernumerary finger is separate from the activation clusters of the other fingers.
709 Selected voxels which were used for the MDS are shown on the right. (F) Mental
710 representation of 6-fingered hands. Blindfolded subjects pointed with the index finger of one
711 hand to a cued location (1st, 2nd knuckle or tip) on the other hand. Pointing errors were similar
712 in the two 6- and thirteen 5-fingered subjects and similar for the supernumerary as for other
713 fingers.



714 **Figure 3:** Hands with supernumerary fingers perform more complex movements. Subplots
 715 (A)-(F) report on analyses of hand movements recorded during manipulation of objects of
 716 various shapes. The movement task was carried out by two 6- and thirteen 5-fingered
 717 subjects. (A) Dependency between individual fingers quantified by the mutual information
 718 between the movements of pairs of fingers, with a value of 0 indicating complete
 719 independence between fingers and positive values an increasing dependency. Note that the
 720 mutual information is symmetric, i.e. $I(X, Y) = I(Y, X)$. (B) The cumulative amount of explained
 721 variance of hand movements as a function of an increasing number of principal components.
 722 Error bars depict SDs across subjects. (C) The number of effective dof (computed using the
 723 principle components, see Methods) was higher in 6-fingered than in 5-fingered subjects. (D)
 724 Information entropy of the discretized movements where each finger is either resting, flexing
 725 or extending. Entropy is shown for an increasing number of fingers, starting with thumb only
 726 ('T') and successively adding one finger (index 'I', middle 'M', ring 'R', little 'L' and
 727 supernumerary 'S'). Dotted lines indicate the theoretically maximum possible entropy for 5-
 728 and 6-fingered hands. (E) Percentage of times thumb and index finger ('T+I'), thumb only ('T'),
 729 index only ('I') were moving when the supernumerary finger moved. From left to right: different
 730 percentiles of the speed distribution were used as thresholds to separate rest from movement.
 731 (F) Median movement speed of individual fingers for 5- and 6-fingered subjects. Subplots (G)
 732 and (H) show results from the video game experiment. (G) Schematic of the task, subjects
 733 were required to press a button corresponding to the bottom white targets every time an
 734 oscillating cursor (green or red) entered the box. The target boxes flashed blue if a correctly

735 timed press occurred and displayed as red if an incorrectly timed press occurred. Horizontal
736 bars at the bottom of the screen displayed the fraction of correct key presses (top) and one
737 minus the fraction of missed (bottom) key presses. (H) Subjects' learning curve for the 5+1
738 (dotted) and 6 finger (solid) control. Digits used shown in the inset in dark gray.
739