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► **To cite this version:**

Josselin Baumard, Mathieu Lesourd, Chrystelle Remigereau, Charlène Lucas, Christophe Jarry, et al.. Imitation of meaningless gestures in normal aging. *Aging, Neuropsychology and Cognition*, 2019, pp.1-19. <10.1080/13825585.2019.1674773>. <hal-02392365>

HAL Id: hal-02392365

<https://hal.science/hal-02392365v1>

Submitted on 17 Mar 2023

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1 **IMITATION OF MEANINGLESS GESTURES IN NORMAL AGING**

2 Josselin Baumard¹, Mathieu Lesourd^{2,3}, Chrystelle Remigereau⁴, Charlène Lucas⁵,
3 Christophe Jarry⁵, François Osiurak^{4,6}, & Didier Le Gall^{5,7}

4 ¹ Normandie Univ, UNIROUEN, CRFDP (EA 7475), 76000 Rouen, France

5 ² Aix Marseille Univ, CNRS, LNC, Laboratoire de Neurosciences Cognitives, Marseille, France

6 ³ Aix Marseille Univ, CNRS, Fédération 3C, Marseille, France

7 ⁴ Laboratoire d'Etude des Mécanismes Cognitifs (EA 3082), Université de Lyon, France

8 ⁵ Laboratoire de Psychologie des Pays de la Loire (EA 4638), Université d'Angers, France

9 ⁶ Institut Universitaire de France, Paris, France

10 ⁷ Unité de Neuropsychologie, Département de Neurologie, Centre Hospitalier Universitaire d'Angers, France

11 **Corresponding author:**

12 Josselin Baumard

13 Normandie Univ, UNIROUEN, CRFDP, 76000 Rouen, France

14 Centre de Recherche sur les Fonctionnements et Dysfonctionnements Psychologiques (EA 7475)

15 Place Emile Blondel, Bât. Freinet, Bureau F113, 76821 MONT-SAINT-AIGNAN Cedex

16 Email: josselin.baumard@univ-rouen.fr

17 **Short title: Imitation in normal aging**

18 **Word count:** 7479 including title page, abstract, keywords; Figures: 1; Tables: 4

19 **Acknowledgments / Funding**

20 This work was supported by grants from ANR (Agence Nationale pour la Recherche;
21 Project Démences et Utilisation d'Outils/Dementia and Tool Use, N°ANR 2011 MALZ 006
22 03; D. Le Gall, F. Osiurak), and was performed within the framework of the LABEX
23 CORTEX (ANR-11-LABX-0042) of Université de Lyon, within the program
24 "Investissements d'Avenir" (ANR-11- IDEX-0007; F. Osiurak,) operated by the French
25 National Research Agency (ANR).

27 **DISCLOSURE STATEMENT**

28 We declare that we have no conflict of interest arising from this research or its applications.

29

30

31 **ABSTRACT**

32 While imitation of meaningless gestures is a gold standard in the assessment of apraxia
33 in patients with either stroke or neurodegenerative diseases, little is known about potential
34 age-related effects on this measure. A significant body of literature has indicated that different
35 mechanisms (i.e., executive functioning, visuospatial skills, sensory integration, body
36 knowledge, categorical apprehension) may underlie the performance depending on imitation
37 conditions (i.e., finger/hand, uni-/bimanual, symmetric/asymmetric, crossed/uncrossed
38 configurations). However, neither the effects of these conditions on performance, nor the
39 contribution of the abovementioned mechanisms to imitation have been explored in normal
40 aging. The aim of the present study was to fill this gap. To do so, healthy adults ($n = 103$)
41 aged 50 to 89 were asked to imitate 45 meaningless gestures. The authors controlled for
42 general cognitive function, motor function, visual-spatial skills, executive function, sensory
43 integration, body knowledge, and mechanical problem-solving skills. The results showed that
44 asymmetry, body-midline crossing and, to a lesser extent, bimanual activity added an
45 additional layer of difficulty to imitation tasks. After controlling for motor speed and
46 cognitive function, age had an effect on imitation skills after 70 years old. This may reflect a
47 decline in body knowledge, sensory integration, and executive functions. In contrast, the
48 visuospatial and mechanical problem-solving hypotheses were ruled out. An additional motor
49 simulation hypothesis is proposed. These findings may prove useful for clinicians working in
50 memory clinics by providing insights on how to interpret imitation deficits. Lower
51 performance after 70 years old should not be considered abnormal in a systematic manner.

52 *Keywords: imitation, apraxia, body schema, midline crossing, normal aging*

53

54 **1. INTRODUCTION**

55 1.1. AIMS OF THE STUDY

56 Apraxia is the inability to perform voluntary gestures in the absence of motor or sensory
57 deficit, incoordination, incomprehension of or inattention to commands (Rothi et al., 1997;
58 Signoret & North, 1979). The label “apraxia” encompasses a wide range of disorders (e.g.,
59 Wheaton & Hallett, 2007) that may be caused by parietal, temporal and/or frontal cortical
60 lesions (Buxbaum, 2017; Goldenberg, 2009; Osiurak, 2014). Imitation of meaningless
61 gestures has become a gold standard to assess apraxia because defective imitation of visually-
62 presented gestures (i.e., visuo-imitative apraxia) is due to cognitive rather than motor
63 impairments, at least in patients with left parietal lesions (Goldenberg, 1995). Despite an
64 extensive body of literature on imitation skills in neurological patients (e.g., Alzheimer’s
65 disease; Lesourd et al., 2013), there is no information concerning normal aging. It should
66 nonetheless be possible to depict specific age-related patterns of performance in older adults
67 given that this task calls for cognitive mechanisms. Furthermore, there is no study comparing
68 different types of meaningless gestures in healthy adults. So, the aim of this study was
69 threefold: (1) To compare different imitation tasks in healthy adults (i.e., finger/hand, uni-
70 /bimanual, symmetric/asymmetric, crossed/uncrossed); (2) To investigate the effect of aging
71 on imitation skills; (3) To test the relationships between imitation skills and other cognitive
72 functions (i.e., visuoconstructive skills, body knowledge, sensory integration, categorical
73 apprehension).

74 1.2. DIFFERENT TYPES OF MEANINGLESS GESTURES

75 In contrast with meaningful gestures (e.g., military salute) that are supposed to test a
76 “lexical route” composed of action lexicons and semantic memory (Rothi et al., 1991, 1997),
77 meaningless gestures have been proposed to test a “direct route” between visual inputs and

78 motor patterns (Goldenberg & Hagmann, 1997). Looking deeper into imitation tasks,
79 Goldenberg et al. deconstructed the direct route and showed that different meaningless
80 gestures (**Figure 1**) may call for different brain regions and cognitive mechanisms which are
81 not necessarily praxis-specific (e.g., visuospatial skills).

82 1.2.1. FINGER VERSUS HAND CONFIGURATIONS

83 The imitation of finger configurations is sensitive to both lesions in the right hemisphere
84 (Goldenberg, 1999) and visuospatial dysfunction (Goldenberg, Münsinger, & Karnath, 2009)
85 because fingers differ in their serial position rather than in their nature. This task is also
86 sensitive to lesions in the left inferior frontal gyrus (Goldenberg & Karnath, 2006),
87 presumably because the similarity between fingers calls for additional executive control. This
88 body of evidence led Lesourd et al. (2013) to consider this task as a visuoconstructive task
89 very similar to the “cubes” subtest from the WAIS (Wechsler, 1997) for the latter also calls for
90 spatial differentiation and executive planning of the response (i.e., the *visuoconstructive*
91 *hypothesis*, which can be divided into a *visuospatial hypothesis* and an *executive hypothesis*).

92 In contrast, the imitation of hand gestures toward the body is particularly sensitive to
93 lesions in the left hemisphere (Goldenberg, 1999). Importantly, these gestures are performed
94 without visual control (e.g., right hand on the right ear) hence they imply that participants
95 convert the visual model into a body-centered reference frame. Therefore, impairment in this
96 task may be caused by sensory integration and/or proprioceptive deficits (i.e., the *sensory*
97 *integration hypothesis*) which corresponds to a dysfunction of the “emergent body schema”
98 (Sirigu, Grafman, Bressler, & Sunderland, 1991). Body schema is an umbrella term
99 sometimes considered as synonymous with sensory integration which was itself defined as the
100 process of differentiating and combining sensations arising from different modalities and
101 body regions (Bonnier, 1905). In this view, multisensory integration should be necessary to
102 convert a visual hand configuration into a body-centered hand configuration. In normal aging,

103 atrophy in the somatosensory cortex may be related to increased reliance on visual feedback
104 (Seidler et al., 2010).

105 This hypothesis has been ruled out in patients with left brain lesions and apraxia, who
106 have difficulties in both imitating configurations and reproducing them on mannikins
107 (Goldenberg, 1995). Therefore, defective imitation of hand configurations directed toward the
108 body has been proposed to be caused by a loss of general knowledge on the visual structure of
109 the body (i.e., *the body knowledge hypothesis*; Goldenberg, 1995; see also Sirigu et al., 1991).

110 Finally, according to *the categorical apprehension hypothesis*, the role of the left
111 inferior parietal lobe is to unify different objects or multiple parts of objects into a coherent
112 spatial configuration, whether it concerns either mechanical relationships as in mechanical
113 problem-solving tasks and tool use (e.g., the hand, screwdriver and screw), or body part
114 coding (Goldenberg, 2009). For use of tools and objects, categorical apprehension encloses
115 the different parts of the biomechanical chain from the hand to the object (i.e., between the
116 hand and the tool; between the tool and the recipient object; between the recipient object and
117 other objects). For example, for a screwing action, the position of the hand on the screwdriver
118 and the alignment of the screwdriver with the screw's slot, as well as the orientation of the
119 screw relative to the wooden board, are categorical features forming a mechanical chain. For
120 imitation of gestures, categorical apprehension reduces the visual appearance of the
121 demonstrated gesture to a limited set of body parts forming a similar biomechanical chain
122 (e.g., the configuration of fingers, the anchor point of the hand on the head). It is called "body
123 part coding" in that it generates an abstract model of the body allowing to transpose the
124 examiner's model into a body-centered configuration, in spite of actual differences in body
125 features (e.g., in body size). In this framework, defective imitation of hand configurations
126 would be caused by a deficit of categorical apprehension. Since the latter is considered a

127 general function of the left parietal lobe, this hypothesis predicts positive correlations between
128 imitation skills and mechanical problem-solving skills.

129 1.2.2. UNIMANUAL VERSUS BIMANUAL CONFIGURATIONS

130 As emphasized by Lesourd et al. (2013), bimanual configurations are more difficult to
131 imitate than unimanual configurations for patients with Alzheimer's disease. However, this
132 work also pointed out the lack of comprehensive and systematic assessment of imitation skills
133 so that it is not possible to determine whether difficulty arises from bimanual activity *per se*
134 or from other sources of error. Although a recent meta-analysis confirmed that bimanual
135 activity is less accurate and slower in older than in younger adults (Krehbiel, Kang, &
136 Cauraugh, 2017), there is still a lack of data regarding imitation and normal aging, which
137 encourages the systematic comparison of uni-/ and bimanual performance.

138 1.2.3. CROSSED VERSUS UNCROSSED CONFIGURATIONS

139 Yamaguchi et al. (2010) proposed that crossing the body midline (e.g., the left hand
140 invading the contralateral space or conversely) is particularly difficult for patients with
141 Alzheimer's disease, an assertion that remains unsubstantiated until now. Noticeably, the
142 question remains whether complexity arises either from midline crossing *per se* or from
143 bimanual activity in itself. Mid-line crossing inhibition (i.e., hesitancy in reaching or stepping
144 across the midline of the body) is normal in young infants and disappears in normal
145 development around eight years of age when spatial orientation, body schema and bimanual
146 coordination become mature (Cermak, Quintero, & Cohen, 1980). This phenomenon re-
147 emerges after 65 years old (Lombardi, Surburg, Eklund, & Kocejka, 2000), but to our
148 knowledge, the implications for imitation skills have not been explored in older adults.

149 1.2.4. SYMMETRIC VERSUS ASYMMETRIC CONFIGURATIONS

150 The effect of symmetry on bimanual imitation (i.e., both hands have the same
151 configuration or position relative to the body) has not been addressed in healthy adults but
152 asymmetric configurations have been proposed to be particularly difficult for patients with
153 Alzheimer’s disease (Ajuriaguerra et al., 1966). Different developmental ages for symmetric
154 and asymmetric configurations (i.e., 6 and 9, respectively; Wallon & Lurçat, 1962) suggest
155 different levels of complexity, yet there is no available data in healthy older adults. So, the
156 aim of this study was to systematically assess imitation of meaningless configurations under
157 various conditions.

158 1.3. EXPECTED TASK EFFECTS

159 In summary, beyond the expected effects of age on imitation, the main expected task
160 effects were as follows. According to the visuoconstructive hypothesis, finger configurations
161 were expected to be more difficult than hand configurations, based on the literature on
162 neurological patients. This effect has been described in stroke patients with lesions in either
163 the left frontal (i.e., executive component) or right parietal (i.e., visuospatial component) brain
164 regions. In contrast, better performance with hand configurations than with finger
165 configurations – a pattern already documented in patients with lesions in the left parietal lobe
166 – would have been consistent with the sensory integration, body knowledge, and categorical
167 hypotheses (hence the need for further correlational analyses). In light of the literature on
168 normal aging and Alzheimer’s disease, bimanual, crossed or asymmetric configurations were
169 expected to be more difficult than unimanual, uncrossed or symmetric configurations
170 (respectively).

171 **2. METHOD**

172 2.1. PARTICIPANTS

173 A total of 104 healthy, native French-speaker adults took part in this study. All of them
174 lived at home and were recruited either in senior clubs or through a clinical research center.
175 They had normal or corrected-to-normal vision. Exclusion criteria were as follows: Loss of
176 autonomy documented by clinical interview (i.e., home care services, living in a nursing
177 home); presence of cognitive complaints; previous history of neurological or psychiatric
178 illnesses; rheumatologic condition, mood disorders, medical treatment or cognitive state
179 preventing clinical assessment. In order to control for general cognitive functioning,
180 participants completed a short neuropsychological testing session with the MMSE (Folstein,
181 Folstein, & McHugh, 1975) and a French gold standard cognitive battery (i.e., the BEC 96
182 questionnaire; Signoret et al., 1989). The latter assessed working memory (i.e., saying the
183 days of the week in reverse order), naming, verbal fluency (i.e., saying as many animal names
184 as possible in 2 min), verbal reasoning (i.e., arithmetic problem-solving, word categorization,
185 proverb comprehension), orientation, visual memory (i.e., 10-min recall and recognition of six
186 black-and-white pictures), verbal learning (i.e., three successive immediate recalls of eight
187 words), and visuoconstructive skills (i.e., copying two 3D and 2D geometrical drawings). The
188 maximum score was 12 for each of the eight subtests (maximum score = 96).

189 The mean MMSE score was 28.0 (standard deviation = 1.7, range = 23-30, cut-off =
190 24). The mean BEC score was 90.3 (standard deviation = 4.3, range = 73-96, French cut-off =
191 80). Four participants performed below the cut-off score in either the MMSE (one participant,
192 score = 23/30) or the BEC battery (three participants, scores = 79, 79, 77). These scores were
193 accepted as normal – as recommended in French normative studies (Kalafat, Hugonot-Diener,
194 & Poitrenaud, 2003) – because the age and years of education of these participants were in the
195 highest (Q3-Q4) and lowest quartiles (Q1), respectively. Low cognitive scores are indeed
196 normal in healthy older adults (e.g., Ishizaki et al., 1998; Piccinin et al., 2013) and
197 participants with low educational level (Kalafat et al., 2003). One participant was excluded

198 from the sample because she had the lowest BEC score (73/96), but almost the highest
199 educational level (16 years of education). Accordingly, the final sample included 64 women
200 and 39 men. The mean age was 66.6 years (standard deviation = 7.9, range = 50-89) and the
201 mean years of education were 12.5 years (standard deviation = 3.7, range = 5-20). There were
202 90 right-handed, 11 left-handed, and 2 ambidextrous participants. The study was conducted in
203 accordance with the Declaration of Helsinki and approved by local ethic committee (Western
204 Protection to Persons Committee II, n° 2012/32).

205 2.2. IMITATION OF MEANINGLESS GESTURES

206 Participants sat at a desk in front of the examiner, who asked them to (concurrently)
207 imitate 45 meaningless configurations “as in a mirror” with their dominant hand, in the
208 following order (**Figure 1**; the complete materials are available in **Supplementary Figure 1**):
209 (1) Unimanual finger configurations ($n = 10$); (2) Bimanual asymmetric finger configurations
210 ($n = 5$); (3) Bimanual symmetric finger configurations ($n = 5$); (4) Unimanual hand
211 configurations ($n = 10$); (5) Bimanual asymmetric, crossed hand configurations ($n = 5$); (6)
212 Bimanual symmetric, crossed hand configurations ($n = 5$); (7) Bimanual symmetric,
213 uncrossed hand configurations ($n = 5$). In crossed configurations either one or both hands
214 invaded the contralateral space of the body. Symmetric and asymmetric configurations were
215 equivalent as regarded the nature and relative position of body parts. As in previous works
216 (e.g., Goldenberg, 1999), hand configurations were directed toward the head or neck so that
217 participants could see the model performed by the examiner but not their own performance. In
218 contrast, finger configurations were performed under visual control so that participants could
219 see both the model and their own hand. Pre-tests indicated that bimanual configurations were
220 more difficult to imitate than unimanual configurations. Therefore, the item time limit was set
221 to 10 seconds for unimanual finger configurations and unimanual hand configurations, and to
222 20 seconds for bimanual asymmetric finger configurations, bimanual symmetric finger

223 configurations, bimanual asymmetric crossed hand configurations, bimanual symmetric
224 crossed hand configurations, and bimanual symmetric uncrossed hand configurations. For the
225 same reason, bimanual blocks were preceded by two training items (i.e., one finger and one
226 hand configuration, both being symmetric).

227 <-----Insert Figure 1 about here----->

228 2.3. SCORING SYSTEM

229 Performance was coded on a 2-point efficiency scale: (2) The participant imitated
230 perfectly the configuration within the time limit; (1) The participant imitated the configuration
231 within the time limit but the result was approximate (e.g., some of the fingers were not
232 straight; the hand was appropriately anchored on the body but its orientation was incorrect);
233 (0) The participant did not imitate the configuration within the time limit and/or he/she was
234 satisfied with a configuration that was too different from the model. Hesitations, trial and
235 error strategies and self-corrections were frequent and hence accepted as normal. In finger
236 items, the coding system focused on the selection and relative positions of fingers while the
237 position and orientation of the hand relative to the body were not considered. In hand items,
238 the coding system focused on the position and orientation of the hand relative to the body,
239 irrespective of the selection of fingers.

240 Ceiling effects are frequent with praxis tests and may lead to underestimate group
241 differences (Lesourd et al., 2013) so a data conversion method was applied, similar to the one
242 used in the Wechsler Adults Intelligence Scale (Wechsler, 1997; see also Lesourd, Baumard,
243 Jarry, Le Gall, & Osiurak, 2017). Completion time was measured for each item that was worth
244 2 points, then four centiles were computed on the whole distribution of completion times (i.e.,
245 C5, C25, C50, C75 and C95). On this ground, additional points rewarded fast performances:
246 The faster the performance, the greater the composite score. The maximum composite score
247 was 450 (i.e., 45 items x 10 points).

248 Two coders discussed and tested this scoring system on ten videos (i.e., 9.6% of total
249 videos) separately. The mean percentage of agreement was 93% for raw scores ($r = 0.92, p <$
250 $.001$) and 73% for time ($r = 0.95, p < .001$).

251 2.4. MOTOR SPEED TASK

252 Processing speed was controlled using a paper-and-pencil tracking task (i.e., the motor
253 task from Baddeley's dual task; Baddeley, 1996). Participants were asked to draw crosses in a
254 chain of 0.5-cm² boxes, as rapidly as possible. The score was the number of crosses made
255 within 2 minutes.

256 2.5. ADDITIONAL VARIABLES

257 Additional tests were available in a subsample of $n = 49$ participants, that assessed
258 executive functioning, visuospatial skills, sensory integration, body knowledge and
259 categorical apprehension.

260 2.5.1. EXECUTIVE FUNCTIONING

261 Executive functioning was tested with a short version of the Tower of London test (Jarry
262 et al., 2013). Participants were presented with two identical devices made of three vertical
263 sticks and three color beads each. The examiner arranged the beads on his own device and
264 asked the participant to replicate the model with the constraint of moving one bead at a time
265 and doing as few moves as possible. There were two practice items and six experimental
266 items requiring two to seven moves to be solved. The time limit was set to two minutes per
267 item. The performance was scored on a 4-point scale ranging from 0 to 3 as a function of the
268 number of moves. The maximum score was 18 (i.e., 6 items x 3 points).

269 2.5.2. VISUOSPATIAL SKILLS

270 Visuospatial skills were assessed with incomplete figures from the Developmental Test
271 of Visual Perception (DTVP-2; Hammill, Pearson, & Voress, 1993; **Supplementary Figure**

272 **2)**. This test was selected because it is a quick and reliable method to assess complex visual
273 integration, a process that is known to decline with age (Danziger & Salthouse, 1978). Items
274 are also meaningless and hence they can specifically assess visuospatial skills while
275 controlling for semantic access requirements. Participants were presented with a complete
276 figure and three to five incomplete figures – depending on items. They were instructed to
277 select the incomplete figure that was identical to the model (i.e., same identity and same
278 orientation).. The time limit was set to 20 seconds. The maximum score was 20 (i.e., 20 items
279 x 1 point per correct answer given within the time limit).

280 2.5.3. SENSORY INTEGRATION

281 Participants underwent extensive neurological testing: **(1)** Elementary sensitivity:
282 Detection of simple tactile (i.e., light touch with a pen on the hand or forearm, $n = 10$ items),
283 visual (i.e., the examiner moves the index finger in one of the visual spaces, $n = 10$ items) and
284 proprioceptive stimuli (i.e., passive mobilization of either the thumb or index fingers, $n = 20$
285 items); **(2)** Unimodal sensory integration: Localization of multiple tactile ($n = 10$ items) and
286 visual stimuli ($n = 10$ items); **(3)** Multimodal sensory integration: Graphesthesia (i.e., visual
287 recognition of tactile stimuli like numbers and drawings, $n = 20$ items scored on a 2-point
288 scale: 2 points for an immediate correct answer, 1 point if a second stimulation is needed),
289 stereognosia (i.e., visual recognition of objects explored in the tactile modality, $n = 20$ items).
290 The maximum score was 120 (i.e., 80 items x 1 point per correct answer, plus 20 items scored
291 on a 2-point scale) and reflected the integrity of the somesthetic function.

292 2.5.4. BODY KNOWLEDGE

293 Participants were presented with 34 photographs of persons adopting either possible or
294 impossible, digitally retouched body postures (**Supplementary Figure 3**). They were asked
295 whether the posture was either possible or impossible. The maximum score was 34 (i.e., 34
296 items x 1 point per correct answer).

297 2.5.5. CATEGORICAL APPREHENSION

298 Participants were asked to solve mechanical problems already presented in previous
299 studies (Baumard et al., 2016, 2018; Lesourd et al., 2016, 2017; **Supplementary Figure 4**).
300 The goal of the task was to extract a small wooden cube from three transparent boxes using
301 different rods varying on length, diameter and material. The participants solved the same
302 problems twice: Once in a “choice” condition (i.e., they had to select one of eight novel tools)
303 and once in a “no-choice” condition (i.e., they were given one appropriate tool). The
304 performance was coded on a 3-point scale depending on the progress toward a solution (e.g.,
305 3 points if the problem is solved; 2 points if the participant reaches the first step of the
306 solution; 1 point if the participant merely reaches the target with a tool; 0 point otherwise).
307 The maximum score was 18 (i.e., 6 problems x 3 points).

308 2.6. STATISTICS

309 Although the time-based scores improved the distribution of data and avoided ceiling
310 effects, Lilliefors tests revealed that the “unimanual finger” ($p = .002$), “unimanual hand” ($p <$
311 $.001$), “bimanual asymmetric finger” ($p = .04$) and “bimanual symmetric uncrossed hand” (p
312 $< .001$) scores did not follow a normal distribution. Therefore, non-parametric statistics were
313 preferred. Between-group and within-group differences were tested with Mann-Whitney U
314 tests and Wilcoxon tests, respectively. The correlational structure of data was explored with
315 Spearman rank order correlations. In order to infer the cognitive factors underlying imitation
316 skills we conducted a principal component analysis in a subsample of $n = 49$ participants. The
317 active variables used to infer components were the scores in the Tower of London, Visuo-
318 Spatial, Body Knowledge, Sensory Integration, and Mechanical Problem Solving tests. The
319 additional quantitative variables were the total scores in the “Unimanual Finger”, “Unimanual
320 Hand”, “Bimanual Finger”, and “Bimanual Hand” tests. The data of interest were the
321 correlations between dimensions and each of the abovementioned variables. The analyses

322 were performed with R statistical software. P-values were adjusted with Holm's correction for
323 multiple tests.

324 **3. RESULTS**

325 **3.1. BETWEEN-TASK COMPARISONS**

326 As displayed in **Table 1 and Table 2**, different levels of performance were found across
327 tasks. Participants performed better on symmetric than on asymmetric configurations, whether
328 for hand or finger subtests. Likewise, participants performed better on the bimanual hand
329 configurations that did not require body midline crossing.

330 <-----Insert Table 1 and Tale 2 about here----->

331 Unimanual finger configurations (mean score = 83.9%, SD = 13.4%) were slightly more
332 difficult than unimanual hand configurations (mean score = 89.2%, SD = 12.5%; $W = 850.5$,
333 $p < .001$, Cliff's delta = -0.26, small). Bimanual finger symmetric configurations (mean score
334 = 55.8%, SD = 17.1%) were more difficult than bimanual hand symmetric uncrossed
335 configurations (mean score = 83.2%, SD = 16.6%; $W = 48.0$, $p < .001$, Cliff's delta = - 0.74,
336 large).

337 The "Unimanual finger" score (mean score = 83.9%, SD = 13.4%) was significantly
338 higher than the "bimanual symmetric finger" score (mean score = 55.8%, SD = 17.1%; $W =$
339 5317.0 , $p < .001$, Cliff's delta = 0.80, large). The same was found (although with smaller
340 effect size) between unimanual hand configurations (mean score = 89.2%, SD = 12.5%) and
341 bimanual symmetric uncrossed hand configurations (mean score = 83.2%, 16.6%; $W =$
342 2765.0 , $p < .001$, Cliff's delta = 0.22, small).

343 **3.2. EFFECT OF AGE ON IMITATION SKILLS**

344 Performance was similar in women ($n = 64$) and men ($n = 39$; all $ps > .22$). Participants
345 were pooled into two subgroups based on the median years of education (i.e., $m = 12$):
346 Subgroup 1 (Range = [5-12], $n = 55$) and subgroup 2 (Range = [13-20], $n = 48$). Imitation
347 scores were virtually the same in both groups (all $ps > .18$) and no correlation was found
348 between education and imitation scores (all $ps > .31$). As shown in **Table 3**, partial
349 correlations controlling for cognitive functioning and motor speed were found between age
350 and imitation tasks. Motor speed appeared to have little influence on the value of correlations.
351 Participants were pooled into four subgroups corresponding to ten-year periods from 50 to 89
352 years old. There was an effect of age on imitation scores mainly after 70 years old (**Table 4**).
353 As sample sizes were low in the youngest and oldest age groups (i.e., $n = 12$ and $n = 8$,
354 respectively), participants were grouped into two subgroups aged 50-69 ($n = 75$) and 70-89 (n
355 = 28). The decline in performance was confirmed for the unimanual finger, unimanual hand,
356 and bimanual hand configurations (all $ps < .001$, $d = 0.46$ to 0.58 , medium to large effect
357 sizes). There was no effect regarding the bimanual finger configurations (both $ps > .08$),
358 presumably because those were the most difficult configurations even for younger adults
359 (**Table 2, Table 4**).

360 <-----Insert Table 3 and Table 4 about here----->

361 3.3. ADDITIONAL VARIABLES

362 Since sections 3.1 and 3.2 showed a significant effect of age (mainly after 70 years old)
363 on imitation tasks in general and on hand configurations in particular, the influence of
364 additional variables on the imitation of hand configurations was further explored. Two
365 subgroups were formed aged 50-69 (Subgroup 1, $n = 39$) and 70-89 (Subgroup 2, $n = 11$). A
366 significant effect of group was found on the total sensory integration score (Subgroup 1: mean
367 = 107.6, $SD = 5.1$; Subgroup 2: mean = 101.6, $SD = 7.4$; $U = 315.0$, $p = .037$, Cliff's delta = -
368 0.45, medium) as well as the body knowledge task (Subgroup 1: mean = 32.4, $SD = 1.1$;

369 Subgroup 2: mean = 31.4, SD = 1.0; $U = 320.0$, $p = .018$, Cliff's delta = - 0.43, medium). The
370 difference was not significant with regards to the mechanical problem-solving task (Subgroup
371 1: mean = 16.9, SD = 2.6; Subgroup 2: mean = 16.4, SD = 2.1; $U = 1292.0$, $p = .127$), the
372 visuospatial task (Subgroup 1: mean = 17.2, SD = 1.7; Subgroup 2: mean = 15.4, SD = 4.0; U
373 = 243.5, $p = .326$) and the Tower of London test (Subgroup 1: mean = 14.8, SD = 1.8;
374 Subgroup 2: mean = 14.4, SD = 1.7; $U = 241.0$, $p = .35$).

375 Significant partial correlations (controlling for both the BEC score and motor speed)
376 were found between age and sensory integration ($r = -0.45$, $p < .001$), age and body
377 knowledge ($r = -0.55$, $p < .001$), age and visuospatial skills ($r = -0.29$, $p < .001$), but not
378 between age and either executive functioning ($r = -0.05$, $p = 1$) or mechanical problem-
379 solving skills ($r = -0.02$, $p = 1$). Sensory integration scores significantly correlated with
380 performance in the body knowledge task ($r = 0.44$, $p < .001$).

381 We conducted a principal component analysis in order to infer the influence of cognitive
382 dimensions on imitation tasks (see section 2.6). Three components were found (eigenvalues =
383 2.58, 0.72, 0.44). The first component (interpreted as the overall performance in imitation
384 tests) explained 64.6% of variance. It was correlated with all of the four imitation scores ($r =$
385 0.71 to 0.86, all $ps < .001$) as well as with the "Body knowledge" ($r = 0.44$, $p < .001$),
386 "Mechanical problem-solving" ($r = 0.37$, $p < .001$) and "Sensory integration" ($r = 0.36$, $p <$
387 $.001$) scores while no correlation was found with the Tower of London and Visuospatial
388 scores. The second component explained 18.1% of data dispersion. It was positively
389 correlated with the Bimanual Finger score on the one hand, but negatively with the
390 Unimanual Hand and Unimanual Finger scores on the other hand. The third component
391 explained 11.1% of variance. It was positively correlated with the Tower of London score ($r =$
392 0.46, $p < .001$), the Sensory integration score ($r = 0.30$, $p = .03$) and with the Unimanual
393 Finger and Bimanual Finger scores ($r = 0.40$ and 0.29 , $p = .003$ and $.04$, respectively). It was

394 also negatively correlated with the Bimanual Hand score ($r = -0.35, p = .012$). To sum up, the
395 sensory integration, body knowledge and categorical apprehension scores seemed to predict
396 the overall imitation performance; the executive score specifically predicted the performance
397 in the “Finger” subtests; and the visuospatial score was not a significant predictor.

398 **IV. DISCUSSION**

399 **4.1. LEVELS OF DIFFICULTY**

400 Significant differences were found in healthy adults between different imitation
401 conditions. Levels of performance seemed to depend on the intrinsic complexity of
402 meaningless gestures as defined by the following dimensions.

403 **4.1.1. FINGER VERSUS HAND CONFIGURATIONS**

404 Finger configurations were intrinsically more difficult than hand configurations. Since
405 this study involved healthy adults only, this effect was interpreted in terms of complexity. The
406 question is, therefore, what was the source of this complexity? As proposed in the
407 introduction, the imitation of finger configurations resembles a visuoconstruction test
408 (Lesourd et al., 2013) in that impairment in this task has been found to result from either
409 visuospatial impairments (Goldenberg et al., 2009), or executive dysfunction (Goldenberg &
410 Karnath, 2006). Accordingly, the influence of cognitive scores on the correlational analysis
411 may have reflected the influence of executive and visuospatial functions since the BEC 96
412 questionnaire contained both executive and visuospatial subtests. For instance, a positive
413 correlation was found between unimanual finger imitation and a subtest of the BEC 96
414 questionnaire assessing verbal problem-solving skills ($r = 0.23, p = .025$). Furthermore, the
415 finger configurations presumably put high demands on executive functioning and selective
416 attention. In support of this hypothesis, the Finger/Hand effect was mainly observed with two

417 hands and with asymmetric configurations. That is, when visual complexity – intrinsically
418 higher in these conditions – increased, performance decreased. Said differently, increasing the
419 number and the asymmetry of visual elements added complexity to the task, as is the case in
420 visuoconstructive tests, and this was relatively specific to finger configurations. Finally, the
421 principal component analysis revealed a common component for the Tower of London score
422 and the imitation of finger configurations. So, the Finger/Hand effect was consistent with the
423 idea that executive functioning and selective visual attention are critical to the imitation of
424 finger configurations.

425 Another, less cognitive explanation for the finger/hand effect lied in the potential influ-
426 ence of sensory feedbacks. Indeed, one could have expected finger configurations to be easier
427 because participants had visual control of their own performance, and because age-related
428 atrophy in the somatosensory cortex has been related to increased reliance on visual control
429 (Seidler et al., 2010). Our findings were not in line with these expectations, and might rather
430 suggest that participants benefited from the tactile feedback that occurred after performing the
431 movement (e.g., touching the hand to the ear). This is rather unlikely however, because hu-
432 mans prioritize vision, and yet, visually-controlled tasks were the most difficult ones. This
433 suggests that sensory feedbacks were not the only determinants of imitation scores. Further-
434 more, imitation was quite easy and straightforward in the unimanual, hand items (mean com-
435 pletion time = 1.3 seconds, SD = 0.39), meaning that participants performed well even before
436 touching the head. The role of tactile feedback could nonetheless be considered as regards
437 bimanual, hand items (mean completion time = 2.9, SD = 0.96). Indeed, our coding system
438 accepted hesitations and self-corrections as normal so participants could broadly reach the
439 head with the hand before correcting their movement based on tactile inputs. Future works
440 might investigate the effect of age-related, modality-specific sensory decline on imitation
441 skills.

442 4.1.2. UNIMANUAL VERSUS BIMANUAL CONFIGURATIONS

443 The results suggested that the Uni-/Bimanual difference emphasized elsewhere in
444 patients with Alzheimer's disease (Lesourd et al., 2013) is already present in healthy adults,
445 and larger with finger than with hand configurations. Indeed, the difference was small with
446 hand configurations: Levels of performance were similar across the unimanual condition and
447 the easiest bimanual condition (i.e., symmetric uncrossed configurations). Therefore, using
448 both hands did not dramatically increase the difficulty of imitation tasks. Instead, difficulty
449 arised from other aspects of the task like the type of gesture (i.e., Finger/Hand
450 configurations). Although one could have expected the Uni-/Bimanual effect to be higher with
451 hand configurations (for these are performed in the absence of visual control), the reverse
452 pattern was observed. This was consistent with the hypothesis that hand configurations call
453 for specific cognitive functions (e.g., body knowledge; Goldenberg, 1995).

454 4.1.3. SYMMETRIC VERSUS ASYMMETRIC CONFIGURATIONS

455 Why were symmetric configurations consistently easier to imitate than asymmetric
456 ones? On this point, the old-fashioned *gestalt* theory (Köhler, 1947) can be invoked. This
457 theory posits that any visual stimulus is immediately organized through both differentiation
458 and combination of visual elements, which operates under different laws (e.g., close, similar
459 or familiar elements tend to be grouped). In monkeys, exposure to drawings meeting these
460 criteria has been found to elicit more activations than other drawings in the primary visual
461 cortex (Wannig, Stanisor, & Roelfsema, 2011). This intrinsic property of vision may explain
462 why both healthy humans and animals appear to have a preference for symmetric patterns
463 (Evans et al., 2012). Furthermore, the same theory may apply to non-visual sensory
464 modalities like touch and proprioception (Le Gall, 1998). In this view, the parts would be the
465 process of differentiating and combining tactile and proprioceptive inputs while the whole
466 would be the immediate knowledge on the relative positions of limbs and the orientation of

467 joints. This process may depend on the activity of the parietal lobe (Goldenberg, 2009) and of
468 the entorhinal and hippocampal cortex (Wiener, 1996). Seeing the diversity of brain regions
469 potentially involved, one could also consider it a general property of the brain – reflecting
470 synaptic collateral inhibition/activation – applying to any sensory or motor information. If this
471 “bodily gestalt” obeys the same laws as the visual one, then a preference for symmetry should
472 be observed in any modality. In the current study, the better performance with symmetric
473 configurations in both hand and finger conditions fitted well with this prediction.

474 Interestingly, this preference for symmetry has also been demonstrated in studies on
475 bimanual motor control (Huhn, Schimpf, & van der Wel, 2012; Kelso, Southard, & Goodman,
476 1979). At the neurophysiological level, the corpus callosum probably plays a key role in this
477 phenomenon by generating mirror activations in both hemispheres (Kinsbourne, 2003). In the
478 current study, the left and right motor parameters were very similar in terms of both spatial
479 and timing components in the bimanual symmetric items (e.g., left hand on the right ear, right
480 hand on the left ear), whereas they differed in the bimanual asymmetric items (e.g., left hand
481 on the right ear, right hand on top of the head). This difference induced different levels of
482 performance, presumably because asymmetry generated competition between both
483 hemispheres and ran counter to a natural preference for bodily and action symmetry. Perhaps
484 the need for conscious temporal coordination did not arise from bimanual activity *per se* but
485 rather from the asymmetry of motor control. It is true that participants tended to reproduce
486 asymmetric configurations one hand after the other but symmetric ones with both hands
487 simultaneously.

488 4.1.4. CROSSED VERSUS UNCROSSED CONFIGURATIONS

489 One of the aims of the present work was to disentangle the relative effects of bimanual
490 activity and body-midline crossing on imitation skills. In results, the uni-/bimanual effect was

491 moderate whereas the crossed/uncrossed effect was large. So, crossing the body midline
492 added an additional layer of difficulty to imitation tasks. How can this effect be explained?

493 Studies on cross-modal integration and bodily illusions are enlightening on this point. In
494 the famous rubber hand illusion, synchronous tactile stimulation applied to both a visible fake
495 hand and the participant's hidden hand results in illusory self-attribution of the rubber hand
496 (Botvinick & Cohen, 1998). This study and others confirmed the multisensory nature of the
497 body schema already proposed a century ago (Bonnier, 1905). Interestingly, crossing the
498 hands modulates bodily illusions (Pozeg, Rognini, Salomon, & Blanke, 2014) as well as
499 tactile discrimination (Yamamoto & Kitazawa, 2001) and spatial judgment (Furlanetto,
500 Gallace, Ansuini, & Becchio, 2014). These works suggested that body schema results from
501 the integration of both visual and somesthetic information (Röder, Rösler, & Spence, 2004),
502 and that individuals locate somesthetic stimuli in a spatial rather than purely somatotopic
503 reference frame, with the left and right hands being attributed to the left and right half-spaces,
504 respectively. In the same vein, developmental studies have demonstrated that midline-crossing
505 appears by 8 years of age, in consistency with the development of body schema, left-right
506 discrimination and bimanual coordination (Lombardi et al., 2000). This body of evidence has
507 suggested that bodily experience in early childhood contributes to the adjustment of
508 multisensory integration into a body schema defined as a spatial, body-centered (rather than
509 purely somatotopic) reference frame organized along a left-right axis. The higher difficulty of
510 crossed configurations in the present work could not be explained by the mere need to convert
511 visual information (i.e., the model) into body-centered information (i.e., the imitation)
512 because this was also necessary to imitate uncrossed configurations. In all likelihood,
513 overriding the left-right spatial organization (i.e., the allocation of the left hand to the left
514 half-space and conversely) generated conflict between different frames of reference (i.e.,

515 somatotopic maps, visual information, body-centered spatial information) hence the higher
516 difficulty of crossed configurations.

517 4.2. EFFECT OF AGE ON IMITATION SKILLS

518 The aim of the present study was to test the effect of demographic variables (i.e., age,
519 gender, education) on imitation skills. In our results, age, but not gender or education, had an
520 adverse influence on imitation scores after 70 years old, independently of motor speed. In
521 contrast, general cognitive functioning had an influence on imitation skills seeing changes in
522 correlation values with cognitive scores partialled out (**Table 3**). We shall now discuss these
523 effects regarding four hypotheses.

524 4.2.1. THE VISUOCONSTRUCTIVE HYPOTHESIS

525 According to the visuoconstructive hypothesis (Lesourd et al., 2013), imitating
526 meaningless configurations calls for both executive and visuospatial skills. Previous works
527 have demonstrated that age affects performance in tests assessing executive functioning
528 (Bugg, Zook, DeLosh, Davalos, & Davis, 2006). The executive functioning hypothesis
529 therefore predicted that the more complex the task, the more sensitive to age it should have
530 been. Results were not consistent with this prediction in that the most difficult imitation
531 condition (i.e., bimanual finger configurations) was not significantly affected by age, contrary
532 to other conditions. Likewise, no correlation was found between age and the Tower of London
533 score after controlling for general cognitive functioning and motor speed.

534 A recent meta-analysis (Techentin, Voyer, & Voyer, 2014) revealed that aging also has
535 an impact on visuospatial skills. In more details, perception is qualitatively normal but older
536 adults need more time than young adults to solve visuospatial tasks. This might have had an
537 effect on the time-based composite scores used in the design of the present work. However,
538 age-related changes in visuospatial processing should affect finger configurations more than
539 hand configurations, the former being more sensitive to visuospatial impairments than the

540 latter (Goldenberg, 1999). In fact, the reverse pattern was observed. In addition, age had an
541 effect on the visuospatial score but the latter did not predict the imitation score in the principal
542 component analysis. These findings suggested that the decline in imitation scores could not be
543 explained solely by a decline in visuospatial skills. Although aging has been associated with
544 changes in both executive and spatial processing, the latter were not likely to account for the
545 age-related differences observed in imitation tasks.

546 4.2.2. THE CATEGORICAL APPREHENSION HYPOTHESIS

547 The categorical apprehension hypothesis (Goldenberg, 2009) posited that both body part
548 coding and tool use would call for one and the same cognitive mechanism (i.e., differentiation
549 and combination of multi-part objects) and recruit overlapping left parietal brain regions. This
550 hypothesis predicted positive correlations between age and performance in both imitation
551 tasks and a mechanical problem-solving task. Results were not consistent with this prediction
552 and rather suggested that aging had only little influence on mechanical problem-solving skills.
553 Conversely, the present work ruled out a potential influence of these skills on imitation tasks
554 in normal aging.

555 4.2.3. THE SENSORY INTEGRATION HYPOTHESIS

556 The effect of age on imitation skills may have reflected changes in multisensory
557 integration. Consistent with this, the sensory integration score was affected by age and was a
558 significant predictor of performance in imitation tasks – especially with asymmetric hand
559 configurations. This hypothesis may thus explain why hand configurations, which required a
560 visual/proprioceptive conversion, were more affected by age than finger configurations which
561 required a visual/visual conversion. In line with this hypothesis, it is known that aging causes
562 sensitive and sensory loss in all modalities (Correia et al., 2016) of both central and peripheral
563 origin (Teasdale, Stelmach, Breunig, & Meeuwsen, 1991). Aside from elementary sensory
564 deprivation, aging also causes a decline in multimodal integration between sixty and ninety

565 years of age (Chan et al., 2011) but not between fifty and seventy years of age (Urbanowitsch
566 et al., 2015). This fits well with the results of the present study for age had an adverse
567 influence on imitation skills mainly after seventy years old.

568 4.2.4. THE BODY KNOWLEDGE HYPOTHESIS

569 According to the body knowledge hypothesis, the ability to imitate hand configurations
570 relies on general knowledge on the structure of the body. This hypothesis predicted both a
571 larger impact of age on hand rather than finger configurations, and positive correlations
572 between imitation tasks (hand configurations) and an additional task assessing body
573 knowledge. Both of these predictions were confirmed. This result can be interpreted using
574 either a cognitive or an embodied account of body image.

575 The cognitive account of body schema corresponds to the body knowledge hypothesis.
576 In this view, imitating the gestures required to convert the visual model into a proprioceptive
577 egocentric configuration, which was made possible by comparing the model with a standard
578 mental representation of a body (e.g., the knees can be bent only backward). On this ground,
579 our results may suggest a decline of general body knowledge after 70 years old that may
580 affect imitation skills (hand configurations). If this is correct, future studies may identify age-
581 related difficulties in both reproducing configurations on a mannikin (Goldenberg, 1995) and
582 designating body parts.

583 Before concluding, we would like to propose an alternative, more embodied account,
584 according to which both imitation of hand configurations and detecting possible/impossible
585 body configurations (as in the body knowledge task) called for motor simulation. Motor
586 simulation is a subtype of mental imagery that consists in the virtual rather than actual
587 execution of an action, with both activating overlapping cortical areas (for a review, see
588 Costello & Bloesch, 2017). It is necessary to perform posture imitation tasks (Lesourd et al.,
589 2016). Interestingly, aging has an adverse influence on motor imagery of unusual movements

590 in particular (Saimpont, Malouin, Tousignant, & Jackson, 2013). This may explain why age
591 had a larger impact on hand configurations performed without visual control (presumably
592 calling for motor imagery) than on finger configurations performed under visual control
593 (presumably calling for visual imagery). It turned out that age also influenced the body
594 knowledge score, perhaps because the latter task did not actually assess “knowledge” but
595 rather motor imagery. The fact that many participants tried to copy the presented body
596 configuration before answering (e.g., they tested on themselves the possible/impossible angles
597 of the wrist) was consistent with the above explanation. The positive correlation between the
598 sensory integration and body knowledge scores was also logical in that simulating a gesture in
599 the peripersonal space should imply the upstream construction of this peripersonal space
600 thanks to multisensory integration (Cardinali, Brozzoli, & Farnè, 2009).

601 **V. CONCLUSION**

602 While imitation of meaningless gestures is a gold standard in the assessment of apraxia
603 in patients with either stroke or neurodegenerative diseases, little was known about potential
604 age-related effects on this measure. Likewise, different imitation conditions had been tested in
605 literature on child development or neurological patients but they had never been tested in
606 normal aging, nor had they been directly compared. The present study filled this gap and
607 demonstrated that asymmetry and body-midline crossing – and to a lesser extent, bimanual
608 activity – added an additional layer of difficulty to imitation tasks. Another important result is
609 the effect of age on imitation skills after 70 years old, independently of motor speed and
610 cognitive measures. This evolution may reflect a decline in either body knowledge or sensory
611 integration while the categorical apprehension hypothesis was ruled out. Likewise, the
612 finger/hand effect was consistent with the visuoconstructive hypothesis but the latter failed to
613 account for the observed age-related changes in imitation skills. These findings may prove

614 useful for clinicians working in memory clinics by providing insights on how to interpret
615 imitation deficits. Lower performance after 70 years old should not be considered abnormal in
616 a systematic manner.

617 The repartition of women and men (i.e., $n = 64$ and $n = 39$, respectively) as well as the
618 small sample size in some age groups may hinder the generalizability of the conclusions. The
619 lack of data on the temporal fidelity of the imitation test was another limitation of the study.
620 To conclude, it should be mentioned that very recent studies on the neural substrates of finger
621 and hand imitation tests threw doubts on the body knowledge hypothesis (Achilles et al.,
622 2017). If this was to be confirmed it might lead to partially reinterpret the results of the
623 present work. An additional motor simulation hypothesis may also deserve further
624 substantiation in future works.

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781

782 **TABLE 1. PERFORMANCE OF 103 HEALTHY ADULTS IN**
783 **DIFFERENT IMITATION TASKS**

	Min.	C5	Q1	Q2	Q3	Max.
Unimanual Finger	46.0	60.0	76.0	86.0	96.0	100.0
Unimanual Hand	49.0	66.2	83.0	94.0	100.0	100.0
Bimanual Finger Asymmetric	4.0	10.2	29.5	40.0	52.0	76.0
Bimanual Finger Symmetric	12.0	28.2	44.0	56.0	68.0	88.0
Bimanual Hand Asymmetric Crossed	14.0	28.2	45.0	60.0	72.0	96.0
Bimanual Hand Symmetric Crossed	24.0	36.4	56.0	68.0	80.0	96.0
Bimanual Hand Symmetric Uncrossed	36.0	50.2	72.0	88.0	100.0	100.0

784 *Notes.* Scores have been converted into percentages for the sake of clarity. C5: Centile 5. Q: Quartile.

785

786 **TABLE 2. EFFECTS OF THE CHARACTERISTICS OF**
 787 **GESTURES ON IMITATION SCORES**

Tasks	Mean (SD)	<i>W</i>	<i>p</i>	Effect size (Cliff's delta)
Unimanual configurations ^a	86.5 (11.6)	4742.5	< .001	0.43.2 (medium)
Bimanual configurations ^a	60.6 (12.5)			
Finger configurations ^b	65.8 (12.0)	5355.0	< .001	- 0.85 (large)
Hand configurations ^b	77.2 (12.2)			
Finger symmetric	55.8 (17.1)	264.5	< .001	0.50 (large)
Finger asymmetric	39.7 (16.1)			
Hand symmetric crossed	66.1 (17.0)	1203.0	< .001	0.24.9 (small)
Hand asymmetric crossed	58.3 (17.4)			
Hand symmetric crossed	66.1 (17.0)	190.5	< .001	- 0.55 (large)
Hand symmetric uncrossed	83.2 (16.6)			

788 *Notes.* Scores have been converted into percentages of the maximum score for the sake of clarity. Values
 789 between brackets are standard deviations. *W*: Wilcoxon tests for paired samples. P-values were adjusted with
 790 Holm's corrections for multiple tests. Effect size: A positive value means that the first score is frequently higher
 791 than the second one, and conversely for negative values. ^a Finger and hand scores have been combined to test the
 792 main effect of uni- versus bimanual imitation. ^b Unimanual and bimanual scores have been combined to test the
 793 main effect of finger versus hand imitation.

794

795 **TABLE 3. CORRELATIONS AND PARTIAL CORRELATIONS**
 796 **OF CHRONOLOGICAL AGE WITH IMITATION TASKS,**
 797 **CONTROLLING FOR COGNITIVE FUNCTIONING (BEC) AND**
 798 **MOTOR SPEED (MS)**

Tasks	R ²	r	r (BEC partialled out)	r (MS partialled out) ^a	R (both BEC and MS partialled out) ^a
Unimanual Finger	0.20	- 0.44 ***	- 0.26 *	- 0.40 ***	- 0.38 ***
Unimanual Hand	0.16	- 0.40 **	- 0.23 *	- 0.30 **	- 0.29 ***
Bimanual Finger	0.05	- 0.22	- 0.02	- 0.18	- 0.14 *
Bimanual Hand	0.22	- 0.47 ***	- 0.23 *	- 0.28 **	- 0.29 ***

799 *Notes.* R²: Amount of variance explained by age. Spearman rank order correlations with Holm's correction for
 800 multiple tests: * p < .05; ** p < .01; *** p < .001. ^a: Missing MS value: n = 2. BEC: Cognitive efficiency battery;
 801 MS: Motor speed.

802

803

TABLE 4. EFFECT OF AGE ON IMITATION, COGNITION

804

AND MOTOR SPEED

	Maximum score	Efficiency score Mean (range)				p value ^a	
		G1 50-59 (n = 12)	G2 60-69 (n = 63)	G3 70-79 (n = 20)	G4 80-89 (n = 8)	Kruskal test	Post-hoc U tests
Unimanual	200	182.8 (14.3)	179.1 (20.3)	158.8 (20.6)	146.1 (29.7)	< .001	G1>G3,G4 G2>G3,G4
Finger	100	88.7 (9.8)	87.1 (12.0)	75.5 (14.5)	72.0 (11.9)	< .001	G1>G3,G4 G2>G3,G4
Hand	100	94.2 (7.5)	92.0 (10.6)	83.3 (11.4)	74.1 (19.5)	< .001	G1>G3,G4 G2>G3,G4
Bimanual	250	163.0 (19.2)	159.9 (27.4)	132.5 (34.6)	119.3 (26.6)	< .001	G1>G3,G4 G2>G3,G4
Bimanual Finger	100	49.8 (15.1)	49.6 (14.1)	44.2 (14.4)	39.8 (15.5)	.21	-
Asymmetric	50	23.2 (7.0)	20.5 (8.1)	17.8 (8.2)	15.4 (7.2)	.12	-
Symmetric	50	26.6 (9.7)	29.1 (8.2)	26.4 (8.5)	24.4 (10.0)	.47	-
Bimanual Hand	150	113.3 (11.2)	110.3 (17.4)	88.3 (24.0)	79.5 (15.0)	< .001	G1>G3,G4 G2>G3,G4
Asymmetric	50	30.7 (5.2)	31.3 (7.8)	23.9 (10.0)	23.5 (9.7)	.004	G2>G3
Symmetric	50	37.3 (6.2)	35.1 (7.8)	28.3 (8.2)	24.9 (6.0)	< .001	G1>G3,G4 G2>G3,G4
Uncrossed	50	45.3 (5.2)	43.9 (6.5)	36.1 (10.2)	31.1 (5.3)	< .001	G1>G3,G4 G2>G3,G4
Cognition (BEC)	96	93.6 (1.3)	91.0 (3.3)	89.7 (3.3)	84.6 (6.3)	< .001	G1>G2,G3,G4 G2>G4
Motor speed	-	136.3 (30.9)	134.5 (29.5)	110.6 (34.5)	94.0 (30.4)	.001	G1>G4 G2>G3,G4

805

Notes. Between-group comparisons performed with Kruskal-Wallis tests and post-hoc Mann-Whitney U tests

806

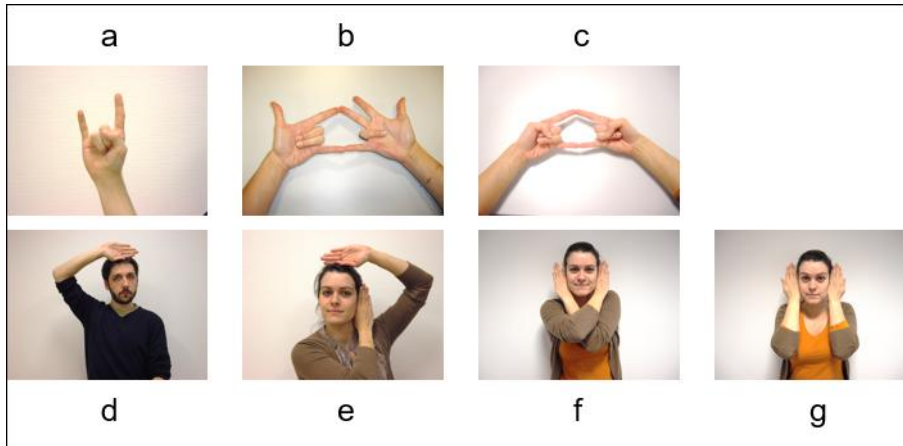
with Holm's correction for multiple tests. G1 to G4 correspond to four groups of age.

807

808

809

FIGURE 1



810

811 **Figure 1. Imitation of meaningless configurations.** *Notes.* (a) Unimanual finger
812 configurations; (b) Bimanual asymmetric finger configurations; (c) Bimanual symmetric
813 finger configurations; (d) Unimanual hand configurations; (e) Bimanual asymmetric, crossed
814 hand configurations; (f) Bimanual symmetric, crossed hand configurations; (g) Bimanual
815 symmetric, uncrossed hand configurations.

816