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Timing-specific patterns of cerebral activations during motor imagery: A case study of the expert brain signature

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17 **ABSTRACT**

18 Brain activations elicited during motor imagery (MI) in experts are typically reduced compared to
19 novices, which is interpreted as a neurophysiological correlate of increased neural efficiency. However,
20 the modulatory effects of MI speed on expertise-related differences in brain activation remains largely
21 unknown. In the present pilot study, we compared the magnetoencephalographic (MEG) correlates of
22 MI in an Olympic medallist and an amateur athlete under conditions of slow, real-time and fast MI. Data
23 revealed event-related changes in the time course of alpha (8-12 Hz) power of MEG oscillations, for all
24 timing conditions. We found that slow MI was associated with a corollary increase in neural
25 synchronization, in both participants. Sensor-level and source-level analyses however disclosed
26 differences between the two expertise levels. The Olympic medallist achieved greater activation of
27 cortical sensorimotor networks than the amateur athlete, particularly during fast MI. Fast MI elicited the
28 strongest event-related desynchronization of alpha oscillations, which was generated from cortical
29 sensorimotor sources in the Olympic medallist, but not in the amateur athlete. Taken together, data
30 suggest that fast MI is a particularly demanding form of motor cognition, putting a specific emphasis on
31 cortical sensorimotor networks to achieve the formation of accurate motor representations under
32 demanding timing constraints.

33

34 **Keywords:** Mental practice; Neuroplasticity; Imagery speed; Motor performance.

35

36 1. INTRODUCTION

37 The theory of motor simulation by Jeannerod (2006) postulates that cognitive motor processes involve
38 the subliminal activation of the motor system. Within this action-related cognitive state framework,
39 motor imagery (MI – the mental representation of a movement without engaging its actual execution)
40 represents one of the most remarkable capacities of the human mind (Moran, Guillot et al., 2012). The
41 subjective experience of action simulation can be generated in the absence of sensory input (Munzert et
42 al., 2009), hence representing a top-down construct derived from sensorimotor memories with an
43 emphasis on specific sensory modalities (for review, see Guillot, 2020). Investigating the neural
44 underpinnings of imagined goal-directed actions has been an overarching aim of cognitive brain
45 research. Although the neural networks mediating MI and motor performance are not strictly similar,
46 there is now compelling evidence supporting that these two forms of practice engage overlapping
47 cerebral substrates (Hardwick et al., 2018; Guillot et al., 2014; Héту et al., 2013), including the premotor
48 cortex, the supplementary motor area, the basal ganglia and the cerebellum, as well as inferior and
49 superior parietal lobules (Decety et al., 1994; Guillot et al., 2009; Lotze et al., 1999). MI has also been
50 shown to involve the primary motor cortex, particularly when the functional brain imaging methodology
51 allows a high temporal resolution (Grèzes and Decety, 2001; Lotze and Haslband, 2006). As a limitation,
52 the neurofunctional equivalence hypothesis mostly emerged from research carried on simple movement
53 of the upper limbs, performed in non-ecological contexts.

54 Due to the similarities in cerebral recruitment profiles, MI has been used as a window to study functional
55 reorganizations associated with the sporting expertise across a variety of disciplines (for review, see Di
56 Rienzo et al., 2016). Lower cortical activations were usually observed in the neural networks mediating
57 MI in expert athletes (Ross et al., 2003; Milton et al., 2007, 2008; Chang et al. 2011). Notwithstanding
58 this, greater and more focused activity in motor-related, as well as increased involvement of the basal
59 ganglia, were also correlated to expertise (Baeck et al., 2012; Mizuguchi and Kanosue, 2017, Zhang et
60 al., 2018). More focused activation patterns were finally reported in prefrontal areas of expert athletes
61 (Wei and Luo, 2010), hence supporting that expertise contributes to refined action representation
62 processes (Orlandi et al., 2020). Overall, data revealed a more refined and circumscribed pattern of brain

63 activations in expert/high imagers compared to novice/poor imagers, indicative of structural and
64 functional neuroplasticity as a result of long-term online and offline learning processes elicited by
65 training (Di Rienzo et al., 2016). This pattern of results across experiments supports the postulates of
66 the neural efficiency theory of expertise (Li and Smith, 2021). The theory posits that reduced neural
67 activation in experts stems from neural specialization at the network-level. This is due to experience-
68 based neuroplasticity as a result of long-term training practice, yielding more efficient management of
69 energy resources along with motor skills performance (Li and Smith, 2021; Yang, 2015). Interestingly,
70 different patterns of brain activations were further reported in regards to imagery type and imagery
71 intensity. Data revealed that first-person and kinaesthetic imagery were more tightly coupled to the
72 sensory-motor system, while third-person visual imagery predominantly recruited visual pathways
73 (Jackson et al., 2006; Jiang et al., 2015; Lorey et al., 2009; Seiler et al., 2015, 2022; Guillot et al., 2009;
74 Solodkin et al., 2004). Mizuguchi et al. (2014) further investigated brain activations during MI of
75 muscular contractions performed at different intensities. They found that the pattern of frontoparietal
76 activations increased along with the intensity of imagined contractions, hence supporting a selective
77 neural signature of the imagined movement.

78 Questioning the selective effects of imagery speed and its corresponding neural correlates has received
79 far less attention. In a pioneering study, Sauvage et al. (2013) showed that slow movements mainly
80 activated a motor cortico-striato-cortical loop and cortical associative areas, whereas fast movements
81 recruited (pre-)motor cortico-cerebellar regions. These findings provided first neuroanatomical evidence
82 of how/why modulating imagery speed is likely to harmfully affect actual movement speed (Louis et
83 al., 2008). While promising, whether timing specific differences exist along the expertise continuum
84 remains unknown. In particular, experimental research contrasting the patterns of active brain regions
85 in top world-class athletes and novices remain sparse. The present pilot case-study was therefore
86 designed to compare the selective neural networks mediating MI performed with different timing
87 instructions in an Olympic medallist and an amateur athlete.

88

89 **2. METHOD**

90 2.1 Participants

91 A 42 active year-old Olympic medallist of discus throw, selected for 6th participation in the Olympic
92 Games in 2021 in Tokyo, and a 36 years-old amateur athlete competing at a regional level took part
93 voluntarily in the experiment. Both were regularly engaged in competitive track and field events, and
94 were free of any recent injury, with a normal vision. Ethical approval was granted by the local ethics
95 committee, and participants signed a written informed consent in agreement with the statements of the
96 Declaration of Helsinki (2013).

97 2.2 Experimental design

98 A familiarization session was scheduled before the magnetoencephalography (MEG) recording session
99 to control the ability of the participants to perform different imagery types and manipulate their imagery
100 speed. We first administered the French version of the Movement Imagery Questionnaire 3 (MIQ-3f),
101 which provides an index of the ease/difficulty experienced while engaging in MI across different
102 modalities (Robin et al., 2021). Second, participants engaged in a mental chronometry paradigm where
103 they were requested to imagine their discus throw *i*) 100% faster as their actual performance (i.e. twice
104 faster), *ii*) at normal speed, and *iii*) 100% slower as their actual performance (i.e. twice slower), across
105 trials of 30s. Each 30s trial thus consisted in continuous mental rehearsal of the skill, at the instructed
106 timing level. They completed 4 trials for each condition, administered in a randomized order. The MEG
107 recording session then consisted in imagining the movement at these same distinct speeds: twice faster
108 (MI_{FAST}), same speed as the actual performance (MI_{NORMAL}), and twice slower (MI_{SLOW}). Experimental
109 conditions were randomly administered for both participants. A Total of 30 blocks of 30s (10 blocks per
110 MI condition) were performed and separated by rest-periods of 15s.

111 2.3 MEG analysis

112 2.3.1 Apparatus and preprocessing

113 MEG recordings were performed using a whole-head CTF(r)-MEG system (CERMEP), with 275 radial
114 gradiometers over the scalp and 33 reference channels for ambient field correction. Signals were
115 digitalized at a sampling rate of 600 Hz and recorded continuously using a low-pass filter (0-150 Hz).

116 Participants' head position were continuously recorded using head coils placed on the nasion and pre-
117 auricular points prior to scanning. Extraction and projection of the individual cortical anatomy in the
118 Montreal Neurologic Institute (MNI) template were respectively performed using Freesurfer
119 (<http://freesurfer.net/>) and Brainstorm, which is documented and freely available for download online
120 under the GNU general public license (<http://neuroimage.usc.edu/brainstorm>). Brainstorm algorithms
121 were applied to detect eye blinks and heart activity. These artifact were removed using Signal-Space
122 Projectors (Tesche et al., 1995; Uusitalo and Ilmoniemi, 1997). Signal portions containing muscle
123 activity (identified from visual inspection) were removed to complete the artifact rejection procedure.
124 Continuous MEG sensors signals were then band-pass filtered (0.5-70 Hz) and epoched into -15 s to
125 +30 s time windows relative to the onset of each trial.

126 *2.3.2 Data analysis*

127 Time-frequency power distributions from MEG sensors signals were calculated (0-60 Hz, Morelet
128 wavelets) and normalized with reference to the 15 s baseline preceding the onset of each trial (Z-score
129 normalization). Normalized time–frequency power distributions were then averaged across all sensors
130 and trials for each MI condition. This yielded the normalized frequency power distributions, for each
131 participant and MI condition. This revealed frequency domains exhibiting event-related
132 desynchronizations (ERD) and event-related synchronizations (ERS) patterns indicative of task-related
133 changes against the baseline. The alpha (8-12 Hz) exhibited the highest contrast values against the
134 baseline throughout the 30 s allocated to the completion of the MI conditions, for both participants. We
135 thus used these time-frequency parameters to perform the source reconstruction. This data-driven
136 approach enabled to control for by-condition bias in the source reconstruction step of MEG data analysis.
137 Source reconstruction was then obtained by applying a minimum-norm inverse solution to MEG signals
138 with constrained dipole orientation. This yielded [-15, 30] s of ongoing cerebral activations for each
139 trial, at each of the 2000 nodes of the participants' tessellation. To index neural
140 synchronization/desynchronization amplitudes, we calculated for each node the alpha power (8-12 Hz)
141 throughout the [-15, 30] s time window, and applied a Z-score normalization against the [-15, 0] s
142 baseline.

143

144 3. RESULTS

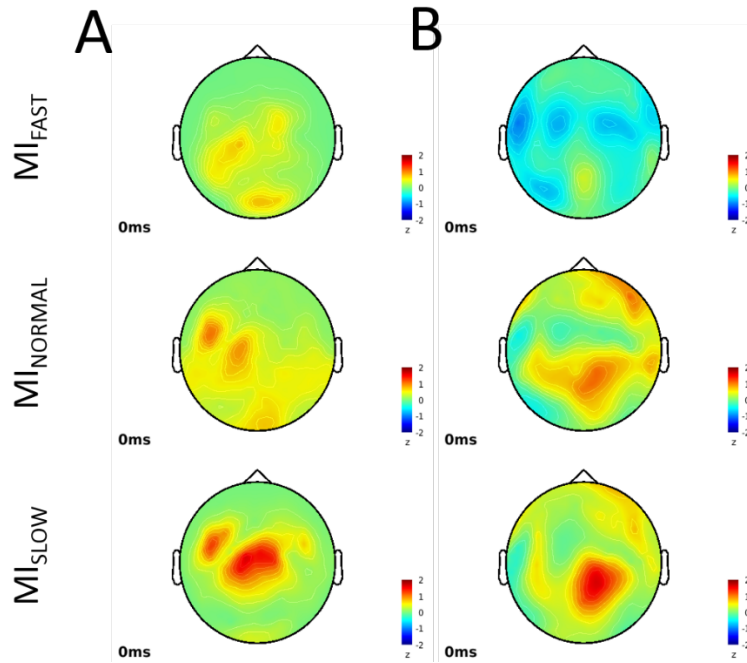
145 3.1 Psychometric and behavioural measures of MI ability

146 Unexpectedly, the MIQ-3f scores revealed a greater imagery ability in the amateur athlete (MIQ-3f score
147 = 22) than in the Olympic athlete (MIQ-3f score = 17). This difference was mainly due to a low score
148 reported by the Olympic athlete for kinaesthetic imagery (respective mean MIQ-3f scores for internal
149 visual, external visual and kinaesthetic imagery being 26, 25 and 25 in the amateur, and 20, 20, and 11
150 in the Olympic athlete).

151 We further checked that both athletes was able to respect the required imagery speed in each
152 experimental condition. In average (SD), the amateur athlete mentally performed 5.5 (0.57) movement
153 sequences during slow imagery, 7.5 (0.58) sequences during real-time imagery, and 9.25 (0.5) sequences
154 during fast imagery. The Olympic athlete respectively performed 7.25 (0.96), 12.75 (0.96), and 18 (0.82)
155 MI trials during slow, real-time and fast imagery. Taken together, these data supported that both athletes
156 were able to modulate the imagery speed as expected during each experimental condition.

157 3.2 Distribution of alpha power in the sensors-space

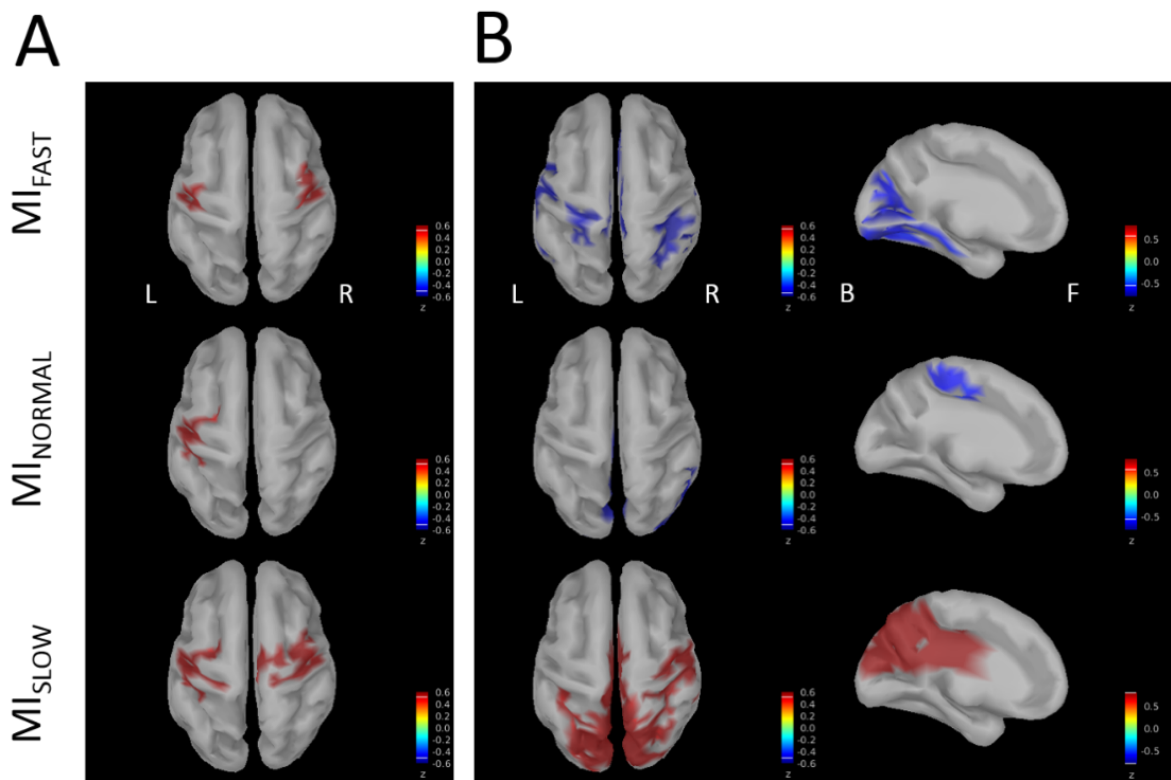
158 We first examined the topographical distributions of alpha power in the sensors-space (8-12 Hz). The
159 alpha rhythm is typically associated with ongoing sensorimotor processes, particularly during MI tasks
160 (Pfurtscheller, 2000; Pfurtscheller et al., 2006). Increased synchronization of neural oscillations emerged
161 along with the of MI durations (Figure 1). Noteworthy, only MI_{FAST} yielded a neural desynchronization
162 pattern in the Olympic medallist, while MI_{SLOW} elicited neural synchronization of alpha oscillations
163 recorded from central MEG sensors in both participants.



164

165 Figure 1. Topographical distributions of alpha power (8-12 Hz) in the sensors-space, averaged across
 166 trials in the regional (A) and Olympic athlete (B), for all experimental conditions.

167 Examining the spatial distribution of the generators of the alpha rhythm in the sources space revealed
 168 distinct patterns in the amateur and Olympic medallist for the different MI conditions (Figure 2). MI_{SLOW}
 169 elicited neural synchronization in a sensorimotor network of brain sources located within central and
 170 pre-central cortical regions in the amateur athlete, whereas the generators of alpha synchronization
 171 originated from occipital sources in the Olympic medallist. The generators of MEG alpha oscillations
 172 during MI_{NORMAL} and MI_{FAST} exhibited a neural synchronization pattern that originated from
 173 sensorimotor cortical structures in the amateur athlete. However, in the Olympic medallist, the
 174 generators of MEG oscillations involved the desynchronization of alpha oscillations within premotor
 175 and primary sensorimotor cortical sources along with faster MI speed.



176

177 Figure 2. Spatial distribution of the generators of the alpha rhythm (8-12 Hz) in the regional (A) and
 178 Olympic (B) athletes.

179

180 4. DISCUSSION

181 The present study sought to expand current knowledge regarding expertise-related differences in brain
 182 activation during MI of sporting skills. We specifically addressed whether influencing the *timing* of MI
 183 would magnify differences between the two extrema of the expertise continuum. Present MEG data
 184 emphasized differences in both the sensors and source-space between the two athletes, particularly a
 185 greater cortical sensorimotor recruitment during fast MI in the expert athlete. Such differences cannot
 186 be attributed to general differences in the capacity to reproduce the temporal organization of the
 187 movement during MI, as preliminary mental chronometry recordings confirmed that they were both able
 188 to adjust the speed of MI.

189 *Topographies of MEG neural oscillations power in the sensors-space*

190 Comparing oscillatory brain activity between amateur and Olympic athletes in a single-case
191 experimental design represents a novelty. In the sensors-space, both participants exhibited a diffuse
192 neural synchronization pattern that gravitated around central sensors during MI at normal speed, i.e.
193 similar as physical practice, but also during slow MI. It is noteworthy that the synchronization levels
194 were largely comparable in the two participants under these two MI timing conditions. We expected a
195 desynchronization of alpha oscillations during MI, since desynchronization of alpha rhythms is typically
196 associated with neural activation due to central processing of sensorimotor information (Pfurtscheller,
197 2000; Neuper et al., 2006). The synchronization pattern obtained in the sensors-space however
198 challenged this prediction. This could be due to the complexity of the skill that was rehearsed. Typically,
199 alpha desynchronization has been described in functional brain imaging experiments requiring
200 participants to engage in MI of simple and non-goal directed upper limb movements (e.g., finger or wrist
201 movements), in non-ecological contexts. The generators of alpha desynchronization during simple
202 movements are typically located in the neocortical layer of the brain, within pre-central and central
203 regions (Pfurtscheller and Neuper, 1997; Pfurtscheller, 2000; Miller et al., 2010). Possibly, closed but
204 complex motor skills of short duration, that are highly automated through repetition (even in novice
205 athletes who train regularly), may be controlled by subcortical and cerebellar sources, which were not
206 accounted in our present source reconstruction model. Detecting activity from these structures using
207 MEG would require additional steps of anatomical segmentation and a large number of trials, exposing
208 to the risk of degraded MI ability due to the occurrence of mental fatigue (Rozand et al., 2016;
209 Nakashima et al., 2022). An alternative approach would be to use spatial filtering of MEG alpha
210 oscillations across a voxel grid encompassing cortical, subcortical and cerebellar structures. Yet, a neural
211 desynchronization pattern was observed only in the Olympic medallist, during fast MI. This suggests
212 that increasing MI speed may be more discriminative for expertise-related differences in neural
213 activation than slowing imagined movements. Overall, examining the topographical distribution of
214 alpha power density in the sensors-space revealed a neural synchronisation gradient along with MI
215 duration of the discus throw. In both the amateur and Olympic athletes, greater neural synchronization
216 was obtained during slow MI compared to fast MI. It is suggested that extending the duration of MI
217 requires active inhibition yielding synchronization of brain rhythms, which are associated to “idling”

218 neural structures (Pfurtscheller et al., 1996; van Wijk et al., 2012). The generation of motor
219 representation within a shorter period of time might trigger additional demands on executive motor
220 systems, hence being facilitated in the expert athlete through enhanced neural desynchronization (Di
221 nota et al., 2017; Zabielska-Mendyk et al., 2018).

222 *Spatial distribution of alpha generators in the source space*

223 Differences between the amateur and the Olympic medallist were more pronounced in the sources-space
224 than in the sensors-space. First, brain activations departed between the two athletes during slow MI. The
225 generators of the neural synchronization of alpha oscillation involved primary sensorimotor cortical
226 sources in the amateur athlete but occipital sources in the Olympic medallist. This could be indicative
227 of distinct sites of neural inhibition associated with the downregulation of MI speed. In the amateur
228 athlete, it is suggested that longer MI durations are mediated by the slowing of the action simulation
229 process, whereas in the Olympic medallist, slow MI was the only condition that did not elicit activation
230 of cortical sensorimotor sources. Although speculative, slow MI possibly yielded a disembodied form
231 of MI, i.e. a mental representation of the skill without engaging motor simulation. The timing
232 requirements under the slow MI condition were particularly inconsistent with the demands of actual
233 practice for the Olympic medallist. Slow MI indeed contradicts the purpose of discus throw, where
234 athletes intentionally attempt to reach the highest execution velocities. The source analysis further
235 confirmed the recruitment of cortical motor networks in the Olympic medallist compared to the amateur
236 athlete, during both real-time and fast MI. Fast MI, particularly, reproduced task demands faced by
237 expert athletes, whereas novices may have paid greater attention to technical components of the
238 coordination due to a lesser degree of automation. While greater cortical sensorimotor activation was
239 observed during real-time MI, differences were particularly pronounced during fast MI. This confirms
240 the sensor-level analysis, and supports that performing MI of a sporting skill in an ecological context
241 with greater time constraints emphasizes brain motor networks recruitment to achieve the formation of
242 accurate motor representations. This is in keeping with both the motor simulation theory and
243 computational approaches of motor simulation, particularly internal models theory which accounts for
244 the facilitatory effects of motor expertise (Lebon et al., 2013; MacIntyre et al., 2013; Ridderinkhof and

245 Brass, 2015). Fast MI appeared particularly discriminant to disclose source-level differences related the
246 motor expertise. This adds to previous findings by Sauvage et al. (2013) for foot movements, who
247 emphasized the increased recruitment of the sensorimotor cerebral cortex during fast MI. We provide
248 additional data pointing at the modulatory role of motor expertise in timing-dependent involvement of
249 cortical structures during the voluntary process of action simulation.

250 *Modulatory effects of expertise on brain activation across different timings of MI*

251 Previous experimental studies sought to determine the beneficial/detrimental effects of performing MI
252 at different speeds (Louis et al., 2008; O and Munroe-Chandler, 2008; Debarnot et al., 2011; Forlenza
253 et al., 2013; Shirazipour et al., 2016), while other carefully questioned the reasons why athletes
254 deliberately manipulate the speed of their mental representations. Using a quantitative analysis in a large
255 sample of athletes, O and Hall (2009) reported that slow, real-time and fast MI were successively
256 performed at each stage of learning, with slow MI being preferred for learning and developing a motor
257 skill, and fast MI being most often used once skills have been mastered. O and Hall (2013) extended
258 these results and concluded that different imagery speeds might serve specific purposes and that athletes
259 are likely to consciously and purposefully select the speed of their MI. In particular, slow MI may help
260 to promote development or refinement of motor skills, while fast MI may primarily be useful to elaborate
261 strategy planning, improve confidence and energize athletes. In-between these two extremes, real-time
262 MI would contribute to rehearse motor skills by controlling movement tempo and relative timing.
263 Interestingly, these authors also argued that novice athletes might encounter greater difficulties to
264 manipulate their imagery speed. Present neuroimaging results support this assumption, as revealed by
265 the greater and more consistent involvement of cortical motor networks in the Olympic athlete, during
266 both real-time and fast MI. Data further confirm that these two MI speeds might be more easily and
267 often employed when the skill is mastered, as the Olympic athlete found very difficult to downregulate
268 MI speed of the rapid and ballistic motor skill.

269 *Limitations and perspectives*

270 The present pilot study expectedly suffers from sample size limitations inherent to single case designs,
271 but the comprehensive understanding of skill acquisition is important (e.g., Hodge et al., 2014), and
272 investigating the neural correlates of an elite expert athlete provides fruitful information on his/her
273 uniqueness that cannot be collected from novices or confirmed athletes (Budnik-Przybylska et al., 2021).
274 While it is inappropriate to offer definitive recommendations, case-studies therefore provide helpful
275 insights for the understanding of the neurophysiological processes mediating mental practice and the
276 study of excellence in sport. Case-studies also contribute to set the stages for future experimental studies.
277 We believe that present preliminary MEG recordings enable to generate several hypotheses. MEG data
278 revealed differences in brain activity between two extreme levels of expertise, primarily in the source-
279 space. First, the topographical distribution of the generators of alpha rhythm in the sensors-space during
280 MI of sporting skills at normal or slow speed appeared quite similar between the amateur and the
281 Olympic athletes. The spatial distribution of the generators in the source space, however, differed
282 between the two expertise levels. Differences were magnified as athletes were instructed to perform fast
283 MI, particularly regarding the involvement of cortical motor networks. Our data support the hypothesis
284 that motor expertise comes along with an enhanced cognitive ability to maintain an embodied motor
285 representation of sporting skills under higher time constraints. This hypothesis should now be tested in
286 more robust experimental designs including larger samples of athletes with different levels of expertise.
287 Another limit is that the assessment of the imagery ability revealed discrepancies between both athletes.
288 While the amateur athlete reported slight experience in imagery use during practice of another skill
289 earlier in this career, the Olympic athlete reported having encountered difficulties to imagine single-
290 joint movements unrelated to sporting contexts while completing the items of the MIQ-3 questionnaire,
291 compared to imagining the discus throw during her training practice. Henceforth, we cannot rule out a
292 negative bias during the subjective evaluation of imagery ability in the Olympic athlete, due to high
293 standards and expectations related to her past imagery experience in her sporting discipline. Replicating
294 this experiment with athletes presenting a similar level of imagery, but with different sport experiences,
295 might help to extend our understanding of the MI expert brain signature. Practically, present data may
296 find relevant applications in the fields of neural training, for instance to develop neurofeedback systems
297 designed to facilitate motor expertise in sport training and rehabilitation.

298

299 **DISCLOSURE STATEMENT**

300 There exists no conflict of interest among the authors.

301

302 **DATA AVAILABILITY STATEMENT**

303 The datasets analysed in the present investigation could be available from the corresponding author
304 on request.

305

306 **REFERENCES**

- 307 Baeck, J.S., Kim, Y.T., Seo, J.Y., Ryeom H.K., Lee, J., Choi, S.M., Woo, M., Kim, W., Kim, J.G.,
308 Chang, Y., 2012. *Brain activation patterns of motor imagery reflect plastic changes associated with*
309 *intensive shooting training*. Behav. Brain Res. 234, 26-32.
- 310 Budnik-Przybylska, D., Kastrau, A., Jasik, P., KaKzmierniczak, M., Dolinski, L., Syty, P., Labuda, M.,
311 Przybylski, J., di Fronso, S., Bertollo, M., 2021. *Neural oscillation during mental imagery in sport:*
312 *an olympic sailor case study*. Front. Hum. Neurosci. 15, 669422.
- 313 Chang, Y., Lee, J.J., Seo, J.H., Song, H.J., Kim, Y.T., Lee, H.J., Kim, H.J., Lee, J., Kim W., Woo, M.,
314 Kim, J.G., 2011. *Neural correlates of motor imagery for elite archers*. NMR Biomed. 24, 366-372.
- 315 Debarnot, U., Louis, M., Collet, C., Guillot, A., 2011. *How does motor imagery speed affect motor*
316 *performance times? Evaluating the effects of task specificity*. Appl. Cogn. Psychol. 25, 536-540.
- 317 Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R.P., Mazziotta, J.C., Fazio,
318 F., 1994. *Mapping motor representations with positron emission tomography*. Nature 371, 600-602.
- 319 Di Nota, P.M., Chartrand, J.M., Levkov, G.R., Montefusco-Siegmund, R., DeSouza, J.F., 2017.
320 *Experience-dependent modulation of alpha and beta during action observation and motor imagery*.
321 BMC Neurosci. 18, 1-14.

322 Di Rienzo, F., Debarnot, U., Daligault, D., Saruco, E., Delpuech, C., Doyon, J., Collet, C., Guillot, A.,
323 2016. *Online and offline performance gains following motor imagery: A comprehensive review of*
324 *behavioral and neuroimaging studies*. Front. Hum. Neurosci. 10, 315.

325 Forlenza, S.T., Weinberg, R.S., Horn, T.S., 2013. *Imagery Speed and Self-Efficacy: How Fast (or Slow)*
326 *To Go?* Int. J. Golf Sci. 2, 126-141.

327 Grèzes, J., Decety, J., 2001. *Functional anatomy of execution, mental simulation, observation, and verb*
328 *generation of actions: a meta-analysis*. Hum. Brain Map. 12, 1-19.

329 Guillot, A., 2020. *Neurophysiological foundations and practical applications of motor imagery*. In:
330 Abraham, A. (Eds.), *Cambridge handbook of the imagination*, Cambridge University Press, pp. 207-
331 226.

332 Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., Doyon, J., 2009. *Brain activity during*
333 *visual versus kinesthetic imagery: an fMRI study*. Hum. Brain Map. 30, 2157-2172.

334 Guillot, A., Di Rienzo, F., Collet, C., 2014. *The neurofunctional architecture of motor imagery*. In:
335 Papageorgiou, T.D., Christopoulos, G., Smirnakis, S. (Eds.), *Advanced brain neuroimaging topics*
336 *in health and disease - Methods and Applications*. IntechOpen.

337 Hardwick, R.M., Caspers, S., Eickhoff, S.B., Swinnen, S.P., 2018. *Neural correlates of action:*
338 *Comparing meta-analyses of imagery, observation, and execution*. Neurosci. Biobehav. Rev. 94, 31-
339 44.

340 Héту, S., Grégoire, M., Saimpont, A., Coll, M.P., Eugène, F., Michon, P.E., Jackson, P.L., 2013. *The*
341 *neural network of motor imagery: an ALE meta-analysis*. Neurosci. Biobehav. Rev. 37, 930-949.

342 Hodge, K., Henry, G., Smith, W., 2014. *A Case Study of Excellence in Elite Sport: Motivational Climate*
343 *in a World Champion Team*. Sport Psychol. 26, 60-74.

344 Jackson, P.L., Meltzoff, A.L., Decety, J., 2006. *Neural circuits involved in imitation and perspective-*
345 *taking*. NeuroImage 31, 429-439.

346 Jeannerod, M., 2006. *Motor cognition: What actions tell to the self*. New York: Oxford University Press.

347 Jiang, D., Edwards, M.G., Mullins, P., Callow, N., 2015. *The neural substrates for the different*
348 *modalities of movement imagery*. Brain Cogn. 97, 22-31.

349 Lebon, F., Gueugneau, N., Papaxanthis, C., 2013. *Modèles internes et imagerie motrice [Internal models*
350 *and motor imagery]*. Mov. Sport Sci. 82, 51-61.

351 Li, L., Smith, D.M., 2021. *Neural efficiency in athletes: a systematic review*. Front. Behav. Neurosci.
352 167.

353 Lorey, B., Bischoff, M., Pilgramm, S., Stark, R., Munzert, J., Zentgraf, K., 2009. *The embodied nature*
354 *of motor imagery: the influence of posture and perspective*. Exp. Brain Res. 194, 233-243.

355 Lotze, M., Halsband, U., 2006. *Motor imagery*. J. Physiol. (Paris) 99, 386-395.

356 Lotze, M., Montoya, P., Erb, M., Hulsmann, E., Flor, H., Klose, U., Birbaumer, N., Grodd, W., 1999.
357 *Activation of cortical and cerebellar motor areas during executed and imagined hand movements:*
358 *an fMRI study*. J. Cogn. Neurosci. 11, 491-501.

359 Louis, M., Guillot, A., Maton, S., Doyon, J., Collet, C., 2008. *Effect of imagined movement speed on*
360 *subsequent motor performance*. J. Mot Behav. 40, 117-132.

361 MacIntyre, T.E., Moran, A.P., Collet, C., Guillot, A., 2013. *An emerging paradigm: A strength-based*
362 *approach to exploring mental imagery*. Front. Hum. Neurosci. 7, 104.

363 Miller, K.J., Schalk, G., Fetz, E.E., Den Nijs, M., Ojemann, J.G., Rao, R.P., 2010. *Cortical activity*
364 *during motor execution, motor imagery, and imagery-based online feedback*. PNAS 107, 4430-4435.

365 Milton, J., Solodkin, A., Hlustik, P., Small, S.L., 2007. *The mind of expert motor performance is cool*
366 *and focused*. NeuroImage 35, 804-813.

367 Milton, J., Small, S.L., Solodkin, A., 2008. *Imaging motor imagery: methodological issues related to*
368 *expertise*. Methods 45, 336-41.

369 Mizuguchi, N., Kanosue, K., 2017. *Changes in brain activity during action observation and motor*
370 *imagery: Their relationship with motor learning*. Prog. Brain Res. 234, 189-204.

- 371 Mizuguchi, N., Nakata, H., Kanosue, K., 2014. *Activity of right premotor-parietal regions dependent*
372 *upon imagined force level: an fMRI study*. Front. Hum. Neurosci. 8, 810.
- 373 Moran, A., Guillot, A., MacIntyre, T., Collet, C., 2012. *Re-imagining mental imagery: Building bridges*
374 *between cognitive and sport psychology*. Br. J. Psychol. 103, 224-247.
- 375 Munzert, J., Lorey, B., Zentgraf, K., 2009. *Cognitive motor processes: the role of motor imagery in the*
376 *study of motor representations*. Brain Res. Rev. 60, 306-326.
- 377 Nakashima, A., Moriuchi, T., Matsuda, D., Nakamura, J., Fujiwara, K., Ikio, Y., Hasegawa, T.,
378 Mitunaga, W., Higashi, T., 2022. *Continuous repetition motor imagery training and physical*
379 *practice training exert the growth of fatigue and its effect on performance*. Brain Sci. 12, 1087.
- 380 Neuper, C., Wörtz, M., Pfurtscheller, G., 2006. *ERD/ERS patterns reflecting sensorimotor activation*
381 *and deactivation*. Prog. Brain Res. 159, 211-222.
- 382 O, J., Hall, C.R., 2009. *A quantitative analysis of athletes' voluntary use of slow motion, real-time, and*
383 *fast motion images*. J. Appl. Sport Psychol. 21, 15-30.
- 384 O, J., Hall, C.R., 2013. *A Qualitative Analysis of Athletes' Voluntary Image Speed Use*. J. Im. Res. Sport
385 Phys. Act. 8, 1-12.
- 386 O, J., Munroe-Chandler, K., 2008. *The effects of image speed on the performance of a soccer task*. Sport
387 Psychol. 22, 1-17.
- 388 Orlandi, A., Arno, E., Proverbio, A.M., 2000. *The effect of expertise on kinesthetic motor imagery of*
389 *complex actions*. Brain Top. 33, 238-254.
- 390 Pfurtscheller, G., 2000. *Spatiotemporal ERD/ERS patterns during voluntary movement and motor*
391 *imagery*. Sup. Clin. Neurophysiol. 53, 196-198.
- 392 Pfurtscheller, G., Brunner, C., Schlögl, A., Da Silva, F.L., 2006. *Mu rhythm (de) synchronization and*
393 *EEG single-trial classification of different motor imagery tasks*. NeuroImage 31, 153-159.

394 Pfurtscheller, G., Neuper, C., 1997. *Motor imagery activates primary sensorimotor area in humans.*
395 *Neurosci. Let.* 239, 65-68.

396 Pfurtscheller, G., Stancak Jr, A., Neuper, C., 1996. *Event-related synchronization (ERS) in the alpha*
397 *band—an electrophysiological correlate of cortical idling: a review.* *Int. J. Psychophysiol.* 24, 39-
398 46.

399 Ridderinkhof, K.R., Brass, M., 2015. *How kinesthetic motor imagery works: a predictive-processing*
400 *theory of visualization in sports and motor expertise.* *J. Physiol. (Paris)* 109, 53-63.

401 Robin, N., Coudevylle, G., Laurent, D., Rulleau, T., Champagne, R., Guillot, A., Toussaint, L., 2021.
402 *Translation and validation of the Movement Imagery Questionnaire-3 second french version (MIQ-*
403 *3Sf).* *J. Bod. Mov. Ther.* 28, 540-546.

404 Ross, J.S., Tkach, J., Ruggieri, P.M., Lieber, M., Lapresto, E., 2003. *The mind's eye: functional MR*
405 *imaging evaluation of golf motor imagery.* *Am. J. Neuroradiol.* 24, 1036-44.

406 Rozand, V., Lebon, F., Stapley, P.J., Papaxanthis, C., Lepers, R., 2016. *A prolonged motor imagery*
407 *session alter imagined and actual movement durations: Potential implications for*
408 *neurorehabilitation.* *Behav. Brain Res.* 297, 67-75.

409 Sauvage, C., Jissendi, P., Seignan S., Manto, M., Habas, C., 2013. *Brain areas involved in the control*
410 *of speed during a motor sequence of the foot: Real movement versus mental imagery.* *J. Neuroradiol.*
411 40, 267-280.

412 Seiler, B.D., Monsma, E.V., Newman-Norlund, R.D., 2015. *Biological evidence of imagery abilities:*
413 *intraindividual differences.* *J. Sport Exerc. Psychol.* 37, 421-435.

414 Seiler, B.D., Monsma, E.V., Newman-Norlund, R.D., Sacko, R., 2022. *Neural activity during imagery*
415 *supports three imagery abilities as measured by the Movement Imagery Questionnaire-3.* *J. Sport*
416 *Exerc. Psychol.* 44, 344-358.

417 Shirazipour, C.H., Munroe-Chandler, K.J., Loughead, T.M., Vander Laan, A.G., 2016. *The effect of*
418 *image sped on novice golfers' performance in a putting task.* *J. Im. Res. Sport Phys. Act.* 11, 1-12.

419 Solodkin, A., Hlustik, P., Chen, E.E., Small, S.L., 2004. *Fine modulation in network activation during*
420 *motor execution and motor imagery*. Cereb. Cortex 14, 1246-1255.

421 Tesche, C.D., Uusitalo, M.A., Ilmoniemi, R.J., Huotilainen, M., Kajola, M., Salonen, O., 1995. *Signal-*
422 *space projections of MEG data characterize both distributed and well-localized neuronal sources*.
423 *Electroencephalogr. Clin. Neurophysiol.* 95, 189-200.

424 Uusitalo, M.A., Ilmoniemi, R.J., 1997. *Signal-space projection method for separating MEG or EEG*
425 *into components*. Med. Biol. Eng. Comp. 35, 135-40.

426 van Wijk, B.C., Beek, P.J., Daffertshofer, A., 2012. *Neural synchrony within the motor system: what*
427 *have we learned so far?* Front. Hum. Neurosci. 6, 252.

428 Wei, G., Luo, J., 2010. *Sport expert's motor imagery: functional imaging of professional motor skills*
429 *and simple motor skills*. Brain Res. 1341, 52-62.

430 Yang, J., 2015. *The influence of motor expertise on the brain activity of motor task performance: a meta-*
431 *analysis of functional magnetic resonance imaging studies*. Cogn. Affect. Behav. Neurosci. 15, 381-
432 394.

433 Zabielska-Mendyk, E., Francuz, P., Jaśkiewicz, M., Augustynowicz, P., 2018. *The effects of motor*
434 *expertise on sensorimotor rhythm desynchronization during execution and imagery of sequential*
435 *movements*. Neuroscience 384, 101-110.

436 Zhang, L., Pi, Y., Zhu, H., Shen, C., Zhang, J., Wu Y., 2018. *Motor experience with a sport-specific*
437 *implement affects motor imagery*. Peer J. 27, 6:e4687.