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Motor imagery of speech: the involvement of primary motor cortex in manual and articulatory motor imagery.

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33 **Abstract**

34

35 Motor imagery refers to the phenomenon of imagining performing an action without action
36 execution. Motor imagery and motor execution are assumed to share a similar underlying
37 neural system that involves primary motor cortex (M1). Previous studies have focused on
38 motor imagery of manual actions, but articulatory motor imagery has not been investigated. In
39 this study, transcranial magnetic stimulation (TMS) was used to elicit motor-evoked potentials
40 (MEPs) from the articulatory muscles (orbicularis oris) as well as from hand muscles (first
41 dorsal interosseous). Twenty participants were asked to execute or imagine performing a
42 simple squeezing task involving a pair of tweezers, which was comparable across both
43 effectors. MEPs were elicited at six timepoints (50, 150, 250, 350, 450, 550ms post-stimulus)
44 to track the time-course of M1 involvement in both lip and hand tasks. The results showed
45 increased MEP amplitudes for action execution compared to rest for both effectors at time
46 points 350, 450 and 550ms, but we found no evidence of increased cortical activation for motor
47 imagery. The results indicate that motor imagery does not involve M1 for simple tasks for
48 manual or articulatory muscles. The results have implications for models of mental imagery of
49 simple articulatory gestures, in that no evidence is found for somatotopic activation of lip
50 muscles in sub-phonemic contexts during motor imagery of such tasks, suggesting that motor
51 simulation of relatively simple actions does not involve M1.

52

53 1. Introduction

54 Motor imagery has been defined as “the mental rehearsal of simple or complex motor acts that
55 is not accompanied by overt movement” (Porro et al., 1996, p.7688). The concept of motor
56 imagery is inherently linked to that of motor execution, and the former is most easily
57 conceptualised as a covert form of - or subset of processes relating to - the latter (Jeannerod
58 2001). Fadiga et al. (1998) proposed that motor imagery includes aspects of motor execution
59 experience, on the basis that numerous biological parameters such as blood pressure and heart
60 rate, which increase during action execution, also correlate positively with action effort during
61 motor imagery. Likewise, the time course of motor imagery and motor execution of actions
62 has been found to be similar (Parsons, 1994). Functional imaging had by this time also shown
63 some overlapping activation for both types of processing (Porro et al., 1996; Roth et al., 1996).
64 Since such measures suggest a significant level of shared processing between the two
65 behaviours, the extent to which motor plans are used in motor imagery compared to motor
66 execution has been the subject of debate. Notably, Vogt, Di Rienzo, Collet, Collins, & Guillot
67 (2013) proposed a continuum from action observation to motor imagery, along which the extent
68 of the simulation of motor plans differs, though neither effect motor unit activation. Similarly,
69 Jeannerod (2001) proposed that covert and overt action stages also represent a continuum
70 where execution suggests the existence of a covert stage, but covert actions do not evolve into
71 the overt stage. In this sense, it can be said that a continuum of action processing, and so use
72 of motor plans for potential simulation of action, exists from action observation through covert
73 simulation of motor plans to overt execution of motor plans. Such models often implicate
74 primary motor cortex (M1) as an important element in simulation processing (Tian, Zarate, &
75 Poeppel, 2016), but the central question remains at what level, and to what degree, motor
76 imagery makes use of motor plans in the absence of overt action execution.

77
78 Early studies into motor imagery made use of mental rotation paradigms and investigated how
79 complexity can affect reaction time. Two well-known examples of this are the Shepard-Metzler
80 visual rotation task (Shepard & Metzler, 1971) and the hand laterality task (Parsons, 1994). In
81 the Shepard-Metzler task, participants are asked whether two three-dimensional shapes (on a
82 two-dimensional plane) are matching objects or not. The task involves the use of mental
83 rotation of this shape so as to try and decide whether two objects correspond or differ. Reaction
84 times tend to be positively correlated with the size of the angle that subjects are required to
85 rotate the object by mentally, so as to be able to provide a yes/no response. Similarly, the hand
86 laterality task presents an image of a left or right hand on-screen, with the participant deciding
87 which hand is shown. Reaction times here tend to be positively correlated with the angle
88 required to move the hand from its canonical position (achieved by lifting the hand in front of
89 the eyes) to that of the hand shown on-screen. Of particular note is that trials involving
90 uncommon angles or difficult flexion in real-world motor execution processes (e.g. right hand
91 rotated laterally rightward by $>45^\circ$, which requires distinctly more wrist and elbow motion
92 compared to internal leftward rotation of $>45^\circ$) are modulated to a similar degree in motor
93 imagery, even though no physical constraints exist. These tasks and other similar tasks have
94 been adapted for use with imaging methods such as positron emission tomography (PET)
95 (Deiber et al., 1998; Kosslyn, Digirolamo, Thompson, & Alpert, 1998) and functional magnetic
96 resonance imaging (fMRI) (Porro et al., 1996; Richter et al., 2000, see Munzert et al, 2009 for
97 review). Many of these imaging studies find activation in supplementary motor area (SMA)
98 and premotor areas (Kosslyn, Thompson, Wraga, & Alpert, 2001; Richter et al., 2000), while
99 some studies also find activation in M1 (Solodkin, Hlustik, Chen, & Small, 2004; Stippich,
100 Ochmann, & Sartor, 2002; again see Munzert et al, 2009, p. 308 for an extensive overview),
101 and especially early papers (see Porro et al., 1996) disagree on whether motor imagery activates
102 M1.

103
104 Several studies have examined the involvement of M1 in motor imagery, primarily in the hand
105 area of M1, using transcranial magnetic stimulation (TMS). For instance, Izumi et al. (1995)
106 asked participants to REST, THINK (motor imagery) or CONTRACT (motor execution) with
107 regard to index finger abduction, with electrodes measuring electrical activity at the *first dorsal*
108 *interosseous* (FDI – index finger abductor) (Izumi et al, 1995). A TMS pulse was administered
109 3-5 seconds after the instruction was given. Fifteen motor-evoked potentials (MEPs) were
110 collected per participant per condition. MEPs are responses induced in specific muscles by
111 administering a TMS pulse to the cortical site governing muscle activation on the M1, and
112 reflects the underlying excitability of the neurons at that cortical site and throughout the motor
113 pathway. An increase in MEP amplitude reflects an increased underlying activation of the
114 motor site and pathway, and is referred to as facilitation. Significant differences were found
115 between the positively modulated THINK and non-modulated REST conditions, as well as
116 between CONTRACT and THINK conditions and CONTRACT and REST conditions,
117 showing that M1 is active not only during motor execution, but also motor imagery. Further
118 studies investigating motor imagery effects find differences between motor imagery and rest
119 conditions in forearm (Yahagi et al., 1996) as well as biceps and thumb muscles (Fadiga et al.,
120 1998). With respect to other muscles, Tremblay, Tremblay, & Colcer (2001) similarly
121 examined leg muscle responses (quadriceps and thigh muscles) using MEPs and found similar
122 facilitation effects in M1 for imagery respective to non-facilitation during rest. In summary, a
123 number of TMS studies have shown that motor imagery increases the excitability of primary
124 motor cortex as measured by larger MEPs.

125
126 While the focus of the above papers is rightly on the increase in MEPs, there is little discussion
127 as to the fine-grained chronometry of motor imagery processes, as few studies included several
128 timepoints across which MEPs were compared. However, one such study by Hashimoto &
129 Rothwell (1999) made use of TMS to investigate a simple task with flexion and extension of
130 the wrist, measuring MEP amplitude at the *first dorsal interosseous* (thumb abductor, here used
131 as the control muscle), *flexor carpi radialis* and *extensor carpi radialis* (two muscles engaged
132 in radial abduction of the wrist). Nine participants were told to imagine performing repetitive
133 wrist movements at a rate of 1Hz, with TMS applied over the hand area of M1 at 0ms, 250ms,
134 500ms and 750ms after an auditory cue. Using averages of 8 MEPs, the authors found increases
135 in MEP amplitude over the time course 0ms - 250ms, with a plateauing and decrease of MEP
136 amplitude at 750ms in *flexor* and *extensor carpi radialis*. However the authors did not compare
137 activation in imagery condition with an execution condition. Given the simplicity of the task,
138 it should be possible to replicate such detailed chronometric results for the *first dorsal*
139 *interosseous* when it is the muscle of interest, as it is here.

140
141 Hyde et al. (2017) used the hand laterality task to measure the involvement of M1 in motor
142 imagery of simple and extensive manual rotation using TMS. Hyde et al. measured MEPs from
143 the hand (FDI) region in M1 to measure its involvement in motor imagery. Single-pulse TMS
144 was administered at latencies of 50ms, 400ms and 650ms post-stimulus presentation. The latter
145 two time-points (400 and 650ms) were included as previous studies (Ganis, Keenan, Kosslyn,
146 & Pascual-Leone, 2000; Tomasino, Borroni, Isaja, & Rumiati, 2005) showed increased
147 reaction times during the task when TMS was administered at these time points. The early
148 (50ms) timepoint was added as an early stimulation reference point. Twenty-two participants
149 were tested and subdivided into groups of ‘likely motor imagery users’ and ‘likely non-motor
150 imagery users’ on the basis of whether performance was better in case of simple biomechanical
151 actions (e.g. a 90° internal rotation) than of complex biomechanical action (e.g. a 90° external
152 rotation). Those likely to have used motor imagery were thought to use a strategy whereby they

153 mentally rotated their hand to fit the hand displayed, whereas those likely not to have used
154 motor imagery are thought to have used a strategy whereby they rotated the on-screen picture
155 to fit their hand rather than vice versa. If response times were not modulated on the basis of
156 physical difficulty, it was assumed that a strategy other than motor imagery was used, and
157 subjects were placed in the likely non-motor imagery group. In the likely motor imagery users
158 group, there was an increase in MEP at all three timepoints (vs. baseline), while this was not
159 the case for likely non-motor imagery users. This increase in MEP during motor imagery
160 presented evidence for increased cortical excitability of hand M1 during imagery of manual
161 movement.

162

163 The current study aimed to extend findings of previous work (Hyde et al., 2017; Hashimoto &
164 Rothwell, 1999) on motor imagery in hand muscles by studying the effects of motor imagery
165 for facial muscles, specifically the articulatory muscles, i.e. *orbicularis oris* (OO) in a sub-
166 phonemic context. The sub-phonemic quality of a simple lip task is on par with the non-
167 linguistic nature of a simple hand task – a task containing linguistic elements is eschewed in
168 favour of establishing the viability of basic imagery data collection from both effectors. While
169 motor imagery has been investigated using several hand muscles as well as leg muscles, there
170 is a lack of studies in other muscles – to our knowledge there has been no investigation into
171 articulatory muscles, such as lips or tongue, even though speech imagery is a well-known
172 phenomenon (Alderson-day & Fernyhough, 2015; McGuire et al., 1996; Oppenheim & Dell,
173 2008; Sokolov, 1972). Moreover, the effect of observation of speech on cortical excitability of
174 lip area is similar to observation of other motor sequences, e.g. manual sequences (Watkins,
175 Strafella, & Paus, 2003; Fadiga, Craighero, Buccino, & Rizzolatti 2002). Several studies have
176 examined motor imagery of speech actions using fMRI with motor tasks (Huang, Carr, & Cao,
177 2001; Shuster & Lemieux, 2005; Szenkovits, Peelle, Norris, & Davis, 2012; Tian, Zarate, &
178 Poeppel, 2016). For instance, Tian & Poeppel (2010; 2012) used fMRI and motor imagery
179 tasks to investigate the topography and time course of imagined speech actions and found that
180 such imagery actions are likely part of a simulation process. This simulation process is likely
181 a sub-process of an internal forward model used in prediction and online correction of
182 movement errors. Manual motor imagery has been investigated with neuroimaging and by
183 measuring MEPs, and motor imagery of speech has been investigated using neuroimaging
184 techniques only. No study so far has thus investigated cortical excitability as measured using
185 MEPs related to motor imagery for speech actions, and as far as we are aware, no study has
186 directly compared cortical excitability of hand and lip actions in a motor imagery context. Sub-
187 cortically, hand and lip MEPs arise via different efferent motor pathways: the corticospinal
188 pathway innervates the hand while the corticobulbar pathway innervates the lip muscles
189 (Adank, Kennedy-Higgins, Maegherman, Hannah, & Nuttall (2018). As a result, there are
190 differences between MEPs recorded from these sites. One difference concerns MEP latency,
191 which is longer in the hand due to the length of the corticospinal tract compared to the
192 corticobulbar tract, resulting in an MEP around 20ms post-pulse as opposed to 8-10ms post-
193 pulse in the lip. A second difference concerns MEP morphology, which is single-peaked in the
194 hand but often multi-peaked in the lip. As a result the MEP extraction method (area-under-the-
195 curve vs peak-to-peak) is critical and should be standardised across studies. Given these
196 differences which have not been addressed in the motor imagery literature, it is necessary to
197 evaluate the effects of motor imagery processes in corticobulbar-innervated muscles such as
198 *orbicularis oris*, and whether results from the hand literature can be generalised to such muscles
199 (at least with regard to simple actions).

200

201 We examined motor imagery in hand and lip muscles while participants performed a simple
202 motor imagery task. While a number of previous studies used a multi-finger tapping task

203 to investigate hand motor imagery, such a task is difficult to extend to the lip muscles due to
204 the smaller number of joints and muscles involved. We opted instead for an imagery task that
205 was simple and could be performed equally with both effectors using simple compression,
206 similar to joint flexion (Hashimoto & Rothwell, 1999). In the study, participants were asked to
207 either imagine pressing together a set of wooden tweezers between their lips (lip motor imagery
208 task), or between their thumb and index finger (hand motor imagery task), or to press together
209 the wooden tweezers between the lips (lip motor execution task), or fingers (hand motor
210 execution task), or to do nothing (remain at constant contraction - baseline). The squeezing
211 together of the lips in particular can be considered a sub-phonemic articulatory gesture, used
212 in the production of plosive sounds, such as /p/. In line with Hyde et al. (2017) and Hashimoto
213 & Rothwell (1999), we used a chronometric design and measured MEPs at various time points
214 from trial onset, including 50, 150, 250, 350, 450 and 550ms. A wide range of time points was
215 used as it is unclear to which extent motor imagery and motor execution of speech muscles
216 follow the same time course. By examining motor imagery and motor execution in speech and
217 hand muscles we aimed to clarify to which extent primary motor cortex for sub-phonemic
218 movement engages during motor imagery, as well as how this involvement develops over time.
219

220 2. Method

221 2.1 Participants

222 Twenty participants (11F, 9M, mean age = 22y 7m, SD = 3y 8m, age range = 19-34) took part
223 in the experiment. Handedness was established via the Edinburgh Handedness Inventory
224 (Oldfield, 1971), which found all participants to be right-handed. Participants reported no
225 history of neurological/ psychiatric disease, and none reported use of any long or short-term
226 medication. No medical conditions, relevant or otherwise, were reported, and neither was any
227 history of specific repetitive motor activity or muscle disorders. All subjects completed all
228 conditions on the same day in one session, and had a minimum high school-level education.
229 Experiments were undertaken with the understanding and written consent of each subject,
230 according to the University College London Research Ethics Committee (UREC). We
231 adhered to data collection and reporting conventions as established in Chipchase et al. (2012).
232

233 2.2 Materials

234 We used a tweezer-like tool to effect constant muscle contraction as well as to provide a tool
235 for the motor execution condition (Figure 1). Prompts were displayed on a 21.5" computer
236 monitor screen while participants sat approximately 70cm away. Prompts were a combination
237 of symbols (font size 24), with ‘%%’ representing hand use and ‘&&’ representing lip use.

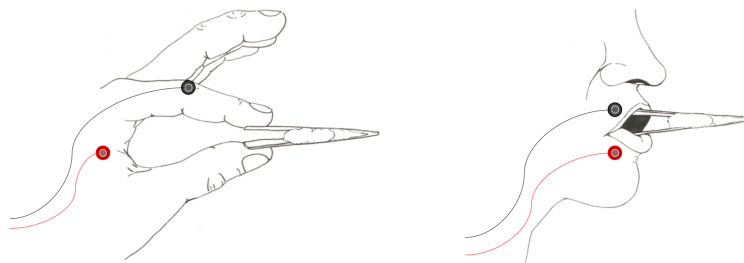


Figure 1: Examples of the tweezers as used in the hand (left panel) and lip (right panel) conditions. Participants were instructed to maintain a baseline level of activity as trained on in a pre-thresholding session. New tools were provided for each participant, with a white cotton filling acting as a spring to provide tension for muscle activation.

238 Colour was used to indicate whether the action should be imagined (blue) or overt (red), or
239 whether no action should be taken (black). Prompts were displayed on a light-grey background,
240 and were preceded by a white fixation cross.

241

242 2.3 Procedure

243 Each trial began by displaying a white fixation cross for 1000ms. The prompt was shown for
244 2000ms, with TMS pulses administered at 50ms, 150ms, 250ms, 350ms, 450ms, or 550ms
245 post-stimulus (counterbalanced). The screen was cleared of all prompts and remained clear for
246 at least 2000ms, but longer dependent on when the TMS pulse was given. The inter-pulse-
247 interval was kept constant at 6000ms. The next trial then began with a new fixation cross (see
248 fig. 2A). Blocks consisted of 25 trials presented in two minutes, with a break of one minute in
249 between each block. Each break was a minimum of one minute, after which the second tester
250 pressed a control key to continue, unless the participant requested more time for a break. Trials
251 were blocked by effector in separate blocks (first effector counterbalanced across participants),
252 with motor execution, motor imagery and baseline prompts as interleaved, mixed trials to avoid
253 potential muscle activation carry-over effects from one stimulus to the next. Each prompt was
254 presented 15 times so that 15 MEPs could be used to derive an average for each trial type at
255 each of the chronometric time points (see fig. 2A). The experiment consisted of 450 trials in
256 total (150 per task, 30 per time point). The experiment lasted 2 hours (45 mins of TMS).

257

258 Participants were recruited using the UCL online participant pool by advertising the study as a
259 session which examined the effects of attention on task processing without explicit reference
260 to MEPs, reaction time, grip strength, or imagery.

261

262 Upon arrival, the study was explained to the participant, and they were given information about
263 the TMS procedure. The participant was then shown what they were expected to do for each
264 symbol. A training session showed each trial type four times allowing the experimenter to make
265 comments on the actions performed. Training lasted 2 minutes and all participants were able
266 to successfully perform the actions.

267

268 Upon completion of the TMS section of the study, an audiometry test was completed (tested at
269 0.5, 1, 2, 4, and 8kHz, in accordance with guidelines from the British Society of Audiology
270 (2011), as was a Montreal Cognitive Inventory test (Nasreddine et al., 2005) to exclude any
271 abnormalities. Finally, participants completed the Varieties of Inner Speech Questionnaire
272 (VISQ, McCarthy-Jones & Fernyhough, 2011). The VISQ was included to test for a potentially
273 positive correlation between any VISQ factors (level of condensed inner speech, level of
274 dialogic inner speech, level of other people represented in inner speech and level of

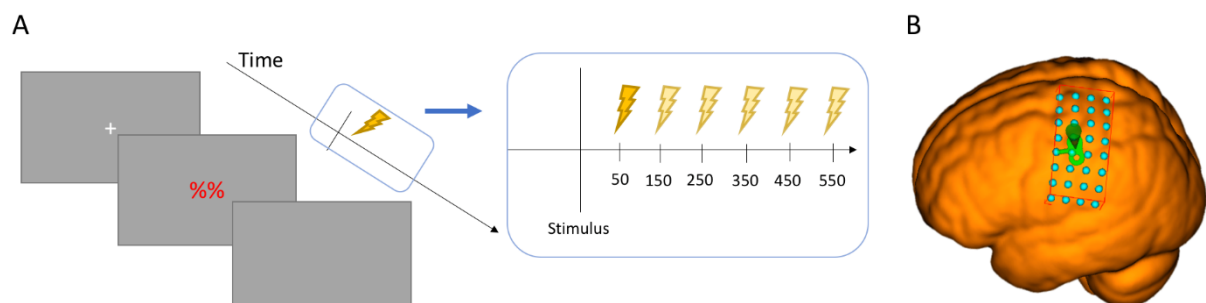


Figure 2: (A) Chronometric design of the study showing the six time points in relation to the stimulus; (B) the grid surface for the MNI brain used in thresholding.

275 motivational inner speech) and MEP area-under-the-curve (AUC), as it is expressly designed
276 to assess the nature of inner speech and the extent to which it is used on a per-subject level.
277 All MEPs were initially extracted from Spike² using custom-made scripts that allowed for the
278 extraction of the electromyography (EMG) signal for a time-frame between 1000ms pre-TMS
279 pulse and 40ms post-TMS pulse. The area-under-the-curve (AUC) of each MEP was then
280 calculated, with hand MEPs spanning the region 13-40ms post-TMS pulse, and lip MEPs
281 spanning the region 8-35ms post-TMS pulse due to their shorter onset time. An equally long
282 section of 27ms was extracted pre-pulse to allow post-hoc checks of equivalent baseline
283 contraction across conditions. The first MEP in each block was then removed as the first MEP
284 is non-representatively larger than those that follow, and this ensures stable neuronavigated
285 coil placement is in place. The mean and standard deviations for the data of each effector was
286 calculated and used to standardise the results and so enable cross-effector comparisons (z-
287 scores).

288 **2.4 Transcranial Magnetic Stimulation**

290 Following the successful conclusion of the training session, the electrodes (Ag/AgCl, \varnothing 10mm)
291 were attached to the FDI (tendon-belly montage) and the OO (belly-belly montage), and two
292 minutes were used for training to maintain baseline activity at 20% of maximum voluntary
293 contraction. This was intended to ensure consistent muscle activation maintained throughout
294 the experiment, except when responding in the action condition. The EMG signal was sampled
295 at 5000Hz, amplified by a factor of 1000 and band-pass filtered between 100-2000Hz using a
296 1902 amplifier, with digital-to-analog conversion using a Micro1401 unit (both Cambridge
297 Electronic Design, Cambridge, UK) connected to a Windows 7 PC. Frameless stereotaxy
298 (Brainsight, Rogue Resolutions, Montreal, Canada) was used to localise the area of stimulation
299 for each effector, making use of the built-in MNI-152 model. A virtual 8 x 4 grid was placed
300 over the motor cortex with the centre corresponding to MNI coordinates -64, -4, 39 (see fig.
301 2B). This was done to search for the hand and lip motor areas in a simple and consistent manner.
302 This system was also used to ensure correct coil location and stability were maintained
303 throughout. A figure-of-eight coil (\varnothing 70 mm) was placed at a 45° angle relative to the sagittal
304 plane, inducing a posterior-anterior current flow approximately perpendicular to the lateral
305 fissure. Once all grid points had been given a minimum of three TMS pulses, the MEPs were
306 extracted from Spike², averaged and visualized using a heatmap display command in
307 MATLAB, displaying the best area to stimulate for each effector. Thresholding was performed
308 using a standard thresholding procedure in which 5/10 MEPs must be elicited (Rossini et al.,
309 1994; Rossini et al., 2015; Watkins et al., 2003). An MEP was defined as a peak-to-peak
310 amplitude of 500 μ V for FDI and 200 μ V for OO. Once active motor threshold (aMT) was
311 established, testing threshold was set to 120% of aMT. This resulted in effector-specific motor
312 threshold and testing intensities as necessitated by the inherent differences between the motor
313 thresholds of facial and manual muscles (Groppa et al., 2012).

314 **2.5 Analysis**

317 We first performed a Repeated-Measures Analysis of Variance (ANOVA) on the combined lip
318 and hand data to establish the effect of the factors Effector (hand vs. lip), Condition (motor
319 execution, motor imagery, baseline) and Timepoint (50, 150, 250, 350, 450, 550ms) on the
320 areas-under-the-curve of MEPs. This overall ANOVA was followed up by two separate
321 ANOVAs for each effector separately to investigate the key interactions. Follow-up *t*-tests
322 were also performed. All results were Greenhouse-Geisser corrected where assumptions of
323 sphericity were violated. All significance values were corrected for multiple comparisons
324 (Bonferroni) where applicable. MEPs were removed from the analysis if they exceeded 3 SDs

325 from the effector-specific mean, which resulted in the removal of 64 MEPs (~0.7%). No subject
 326 scored <26 in the Montreal Cognitive Assessment, indicating normal cognitive function in all
 327 participants.

328
 329

330 3. Results

331 3.1 Overall data

332 Average MNI coordinates for hand were [-40, -15, 67] and average MNI coordinates for lip
 333 were [-59, -8, 46] (see supplementary table 1). Due to issues with the frameless stereotaxy
 334 system, we were able to extract localisation data from 13 out of 20 participants. A one-way
 335 ANOVA comparing baseline muscle contraction levels found no significant differences in
 336 baseline contraction across conditions in either the hand (motor imagery mean = 0.22mV/ms,
 337 SD = 0.10mV/ms; motor execution mean = 0.22mV/ms, SD = 0.10mV/ms; baseline mean =
 338 0.21mV/ms, SD = 0.10mV/ms; $F(2,357) = .058, p = .943$, n.s.) or lip (motor imagery mean =
 339 0.37mV/ms, SD = 0.19mV/ms; motor execution mean = 0.38mV/ms, SD = 0.19mV/ms;
 340 baseline mean = 0.37mV/ms, SD = 0.19mV/ms; $F(2,357) = .095, p = .910$, n.s.), showing that
 341 any difference in MEPs was not due to different levels of pre-pulse contraction.

342

343 We proceeded to use z-scores of the averaged data for a 2 x 3 x 6 omnibus ANOVA comparing
 344 Effector (hand vs. lip), Condition (motor execution, motor imagery, baseline) and Timepoint
 345 (50, 150, 250, 350, 450, 550). There was no significant main effect of Effector ($F(1,19) = .014$,
 346 $p = .906$, n.s.) as expected given our use of z-scores, but there was a significant main effect of
 347 Condition ($F(1.1, 20.9) = 54.202, p < .001, \eta_p^2 = .740$). Post-hoc comparisons show that motor
 348 execution MEPs ($Mean = .297, Standard Error = .097$) were significantly larger than motor
 349 imagery ($M = -.177, SE = .122, p < .001$) and baseline MEPs ($M = -.188, SE = .116, p < .001$),
 350 but that there was no difference between motor imagery and baseline MEPs ($p = 1$), see fig.
 351 3A. A second main effect was found for Timepoint ($F(2.6,49.4) = 22.273, p < .001, \eta_p^2 = .540$).
 352 Post-hoc comparisons showed a significant difference between the first timepoint and all
 353 subsequent timepoints (minimum $Mean Difference = -.166, SE = .036, p = .003$), except
 354 timepoint 150 ($MD = -.030, SE = .022, p = 1$), see fig. 3B. There was also a significant Condition

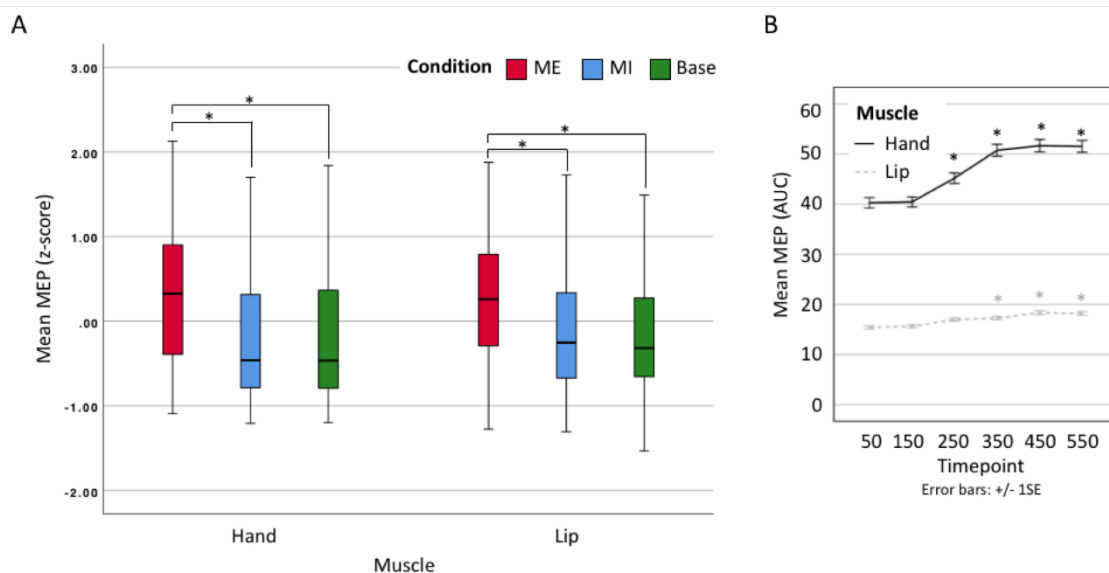


Figure 3: (A) Box plot showing z-scores for all data. Lip results appear as smaller due to their naturally smaller size. ME= Motor execution, MI = Motor imagery, Base = Baseline. (B) Line plot showing mean MEP AUC (raw) by timepoint. Error bars represent $\pm 1SE$, $\alpha = .001$.

355 × Timepoint interaction ($F(3.8, 71.4) = 24.651, p < .001, \eta_p^2 = .565$) with no other interactions
 356 found. Having shown that there is no difference between the effectors after standardisation
 357 around the mean (z-scores) we used the raw data in our per-effector analyses.

359 3.2 Lip

360 A 3 x 6 repeated-measures ANOVA comparing Condition (motor execution, motor imagery,
 361 baseline) and Timepoint (50, 150, 250, 350, 450, 550ms) was run on the lip data. The
 362 analysis of the lip MEPs showed a main effect of Condition ($F(1.2, 22.8) = 30.999, p < .001,$
 363 $\eta_p^2 = .620$), with contrasts revealing motor execution MEPs to be significantly larger than
 364 motor imagery MEPs ($MD = 3.512, SE = .582, p < .001$) and baseline MEPs ($MD = 3.583,$
 365 $SE = .647, p < .001$), but with no significant difference found between the motor imagery and
 366 baseline conditions ($MD = .070, SE = .233, p = 1$). There was also a main effect of Timepoint
 367 ($F(2.864, 54.422) = 10.893, p < .001, \eta_p^2 = .364$), with contrasts revealing MEPs at 50ms to be
 368 significantly smaller than at 350ms ($MD = -1.526, SE = .418, p = .025$), 450ms ($MD = -2.287,$
 369 $SE = .538, p = .006$) and 550ms ($MD = -2.234, SE = .478, p = .002$), see fig. 4. This main
 370 effect, however, was entirely driven by a significant interaction between Condition ×
 371 Timepoint ($F(3.883, 73.778) = 12.630, p < .001, \eta_p^2 = .399$). Specifically, the MEP size only
 372 increased with time in the motor execution condition but not in the motor imagery or baseline
 373 conditions (see fig 4b). Planned follow-up tests confirmed that while there were no
 374 differences across timepoints in the motor imagery and baseline conditions, there were
 375 significant differences across timepoints in the motor execution conditions, with MEPs at
 376 50ms significantly smaller than at 250ms ($t(19) = -3.894, p = .001$), 350ms ($t(19) = -4.543,$
 377 $p < .001$), 450ms ($t(19) = -5.466, p < .001$), and 550ms ($t(19) = -6.591, p < .001$), see
 378 supplementary table 3. In other words, MEP size only changed when participants actually
 379 squeezed the tweezers with their lips, and not when they only imagined doing so.

381 3.3 Hand

382 A 3 x 6 repeated-measures ANOVA comparing Condition (motor execution, motor imagery,
 383 baseline) and Timepoint (50, 150, 250, 350, 450, 550ms) was run on the hand data. There was
 384 a main effect of Condition ($F(1.120, 21.272) = 46.083, p < .001, \eta_p^2 = .708$), indicating that

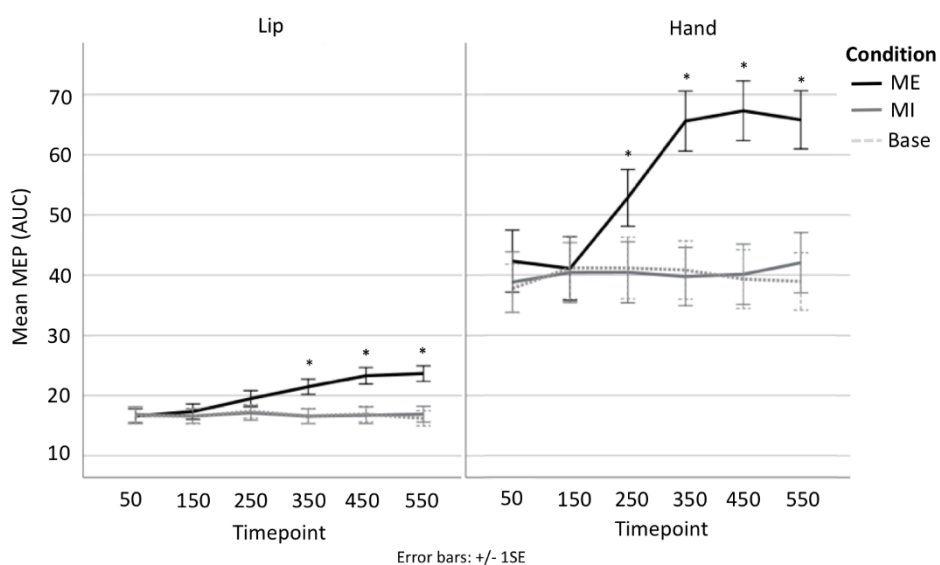


Figure 4: Line graph showing change in mean MEP AUC per time point and effects of condition. ME= Motor execution, MI = Motor imagery, Base = Baseline

385 motor execution MEPs were significantly larger than motor imagery MEPs ($MD = 15.549$, SE
386 $=2.285$, $p < .001$) and Baseline MEPs ($MD = 15.944$, $SE = 2.267$, $p < .001$), but with no
387 significant difference found between the motor imagery and baseline conditions ($MD = .396$,
388 $SE = .638$, $p = 1$), see fig. 3. There was also a main effect of Timepoint ($F(2.424, 46.062) =$
389 14.491 $p < .001$, $\eta_p^2 = .433$), with contrasts revealing MEPs at 50ms to be significantly smaller
390 than at 250ms ($MD = -5.186$, $SE = 1.116$, $p = .003$), 350ms ($MD = -9.089$, $SE = 1.421$, $p < .001$),
391 450ms ($MD = -9.282$, $SE = 1.702$, $p < .001$) and 550ms ($MD = -9.301$, $SE = 2.008$, $p = .003$),
392 see fig. 4. This was once again driven entirely by a significant interaction between Condition
393 \times Timepoint ($F(3.504, 66.572) = 15.162$, $p < .001$, $\eta_p^2 = .444$). Hand MEPs only increased with
394 time in the motor execution condition but not in the motor imagery or baseline conditions (see
395 fig. 4a). Follow-up tests confirmed that while there were no differences across timepoints in
396 the motor imagery and baseline conditions, there were significant differences across timepoints
397 in the motor execution conditions, with MEPs at timepoint 50 significantly smaller than at
398 250ms ($t(19) = -3.835$, $p = .001$), 350ms ($t(19) = -5.006$, $p < .001$), 450ms ($t(19) = -5.863$, $p <$
399 $.001$), and 550ms ($t(19) = -5.415$, $p < .001$), see supplementary table 2. In other words, MEP
400 size only changed when participants actually squeezed the tweezers by hand, and not when
401 they imagined doing so, as per the lip conditions.

402

403 **4. General discussion**

404 This study aimed to examine whether primary motor cortex was facilitated for speech motor
405 imagery by examining a simple motor imagery task in lip and hand muscles. A secondary aim
406 was to describe the time course of both motor imagery and motor execution in speech and hand
407 muscles. We conducted an experiment in which participants performed a speech or manual
408 action, imagined performing the action, or did nothing.

409

410 The results showed that primary motor cortex was facilitated during action execution for both
411 effectors, but we could not find evidence supporting the prediction that mental imagery
412 involves M1, therefore not replicating results from earlier studies (Hyde et al., 2017;
413 Hashimoto & Rothwell, 1999). The pattern of increasing MEPs in the results for lip and hand
414 during action execution followed a comparable time course, but differences in area-under-the-
415 curve of the MEPs were more pronounced for hand muscles.

416

417 The effect of action execution in both lip and hand muscles showed that MEPs successfully
418 captured M1 facilitation during execution of actions, with the time course showing the expected
419 increase between 150-350ms, plateauing thereafter. Compared to the lip, it might appear that
420 the hand showed changes in reaction times more quickly given that it was different to baseline
421 at an earlier timepoint, though this is likely to be a result of lip MEP changes being overall
422 smaller rather than a result of actual reaction time differences, as the hand action likely engages
423 a larger pool of motor units relative those engaged in lip.

424

425 The results showed no evidence of cortical facilitation for the imagery condition compared to
426 the baseline condition for either effector. This result was unexpected as previous studies
427 focusing on hand actions (Hyde et al., 2017; Hashimoto & Rothwell, 1999) reported cortical
428 facilitation during imagery. Both studies used tasks which are broadly comparable to the task
429 used in the present study, namely a mental rotation task and a mental flexion task. However, it
430 should be noted that Hyde et al. only reported an increase in MEP amplitudes for imagery
431 compared to baseline for a subset of their participants (namely the ones that were classified as
432 using motor imagery to a higher extent). We attempted a similar approach with our data and

433 split our participants into two groups depending on their VISQ scores using a medial split.
434 However, even for those showing higher VISQ scores, no increase in MEPs was found for the
435 hand data (or the lip data). Also, there was no evidence of a general positive correlation
436 between the VISQ scores and the MEP data across participants for either effector (or
437 condition). The lack of an increase in MEPs related to motor imagery in our results might be
438 attributable to task effects. Specifically, it could be the case that our task did not sufficiently
439 encourage participants to engage in motor imagery. The task was deliberately simplified to
440 allow for a direct comparison across hand and lip muscles. Studies that use a more complex
441 task tend to report larger increases in MEPs, for instance a study by Roosink & Zijdewind
442 (2010) did find such a modulation of MEPs. In this study, the authors measured the difference
443 in corticospinal excitability between action observation and motor imagery processes to infer
444 the usefulness of these processes in motor rehabilitation. The authors found significant
445 differences between active action observation and motor imagery conditions, with active action
446 observation showing greater MEPs than simple or complex motor imagery conditions (which
447 are not between them significantly different). As a result of their statistical analysis in which
448 the rest condition mean and SD was used to obtain z-scores for the experimental conditions,
449 the rest condition was not included in the multi-level analysis, and the authors did not claim
450 that the motor imagery conditions were significantly different to the rest condition. However
451 the authors did report significant differences between simple and complex actions. Based on
452 the results for a complex task reported in Roosink & Zijdewind and the lack of a clear result
453 for simple tasks reported in Hyde et al (2017) it seems possible that our task was too simple to
454 encourage participants to engage in motor imagery.

455
456 With respect to the time course results, it was expected that earlier timepoints would be
457 associated with smaller MEPs than any later timepoints. Data from both effectors showed the
458 expected pattern of increasing MEP amplitudes for later time points, which was likely due to
459 motor preparation and motor response. This addressed our secondary aim and clarified the time
460 points post-stimulus at which motor excitability was notably modulated during motor
461 processes. Follow-up analyses showed that this was a result of motor execution and very
462 different from motor imagery, which showed no difference to the baseline at any timepoint.

463
464 In sum, TMS can be used to measure changes in cortical excitability associated with overt
465 movement in simple tasks, but is perhaps not suitable for measuring motor imagery of
466 movement in simple tasks. There are several possible reasons for the lack of an increase in
467 MEPs associated with motor imagery compared to the baseline condition. The first could be
468 that MEP data can index larger changes in cortical activity for active movement, but not for
469 subtler changes, such as imagery of such movement. While certain studies are able to show
470 increases in blood flow to motor regions during imagery (see Munzert et al., 2009, p. 308),
471 including articulation imagery, direct measurement via TMS is more difficult to achieve and is
472 perhaps dependent on effort.

473
474 It could also be the case that participants did not engage in motor imagery as requested, which
475 would yield results similar to those above. A number of participants pointed out that while the
476 task was intuitive, imagery was not always attained without difficulty. Another reason could
477 be that while active muscle movement activates corresponding motor regions, imagery of
478 muscle movement does not. In this case, our results would contradict several imaging studies
479 that have found action imagery activates motor regions, but would fit with a number of TMS
480 studies that have found no increase in EMG in motor imagery using simple tasks, (e.g., Fadiga
481 et al., 1998; Tremblay et al. ,2001; and Yahagi et al., 1996). One final possibility is that the
482 premotor cortex and SMA actively inhibit primary motor cortex in motor imagery, but not

483 motor execution, precisely to ensure that no overt movement occurs. This may in turn cancel
484 out the activation of primary motor cortex as it is engaged in motor simulation. While this
485 process would affect MEP size negatively, the fMRI Blood-Oxygen-Level Dependent (BOLD)
486 signal would not dissociate between deactivation and activation, potentially explaining studies
487 that show premotor area activation (e.g. Deiber et al., 1998; Kasess et al., 2008). Additionally,
488 there may be inhibition further downstream (e.g. the brainstem or spinal column) which would
489 not be observable in the MEP.

490

491 The design of the study also presented certain limitations. As it is not feasible
492 to consistently obtain lip MEPs without muscle contraction (see Cattaneo & Pavesi, 2014),
493 participants were required to perform active isometric contraction throughout the task.
494 Therefore, as a result, our participants effectively performed two simultaneous tasks, the motor
495 execution and imagery task and the isometric contraction task. As a result, the EMG signal
496 could have masked underlying subthreshold voluntary activity. This issue needs to be
497 addressed in future studies, e.g., by attempting a replication of the hand task without voluntary
498 contraction, so that the consistency of task results between active and relaxed muscles can be
499 further examined. Another possibility is the use of a specialised population with regard to lip
500 muscles, e.g. wood and brass instrumentalists, to explore whether a lower threshold or indeed
501 the use of resting motor threshold is possible. In addition, this specialist population may already
502 routinely engage in motor imagery of lip movements through mental rehearsal, which could be
503 exploited in an imagery task.

504

505 This study explored the use of MEPs in measuring the excitability changes in M1 during
506 imagery of simple actions in hand and lip muscles. The use of MEPs to address these questions
507 specifically in lip muscles, using both execution and imagery conditions and recording the time
508 course of excitability changes, represents a combination of research techniques to deliver a
509 novel approach towards investigating motor imagery. Given the limited usability of MEPs (i.e.
510 they can be used to index M1 activation and nerve innervation along the motor pathway, but
511 not other cortical regions), this study does not impact on those models of motor simulation
512 which do not necessarily implicate the M1. Similarly, it should be noted that speech is a
513 complex use of muscle groups, rather than simple use of one single muscle – further research
514 should be conducted into phonemic-level tasks, both hand- and lip-related, to learn more about
515 how motor imagery may be used in higher-level articulatory performance.

516

517 In sum, this study aimed to establish whether motor imagery of simple tasks differed from a
518 baseline and action execution condition at the cortical level for hand and lip muscles, and to
519 assess the time course of cortical changes associated with each effector. The results showed
520 that while action execution of simple tasks could be indexed using TMS and MEPs, the same
521 was not found for motor imagery of these tasks. Similarly, while we found that it was possible
522 to record how excitability increased over the six time points for the action execution condition,
523 a similar increase was not recorded for the motor imagery condition. We conclude that the
524 involvement of motor cortex regions during motor imagery may be dependent on task
525 complexity, and may not be implicated in the simulation of simple tasks. Alternatively, motor
526 cortex involvement may be suppressed prior to the signal arriving at the muscle.

527

528 **Ethics statement**

529 This study was carried out in accordance with the recommendation of the UCL Research Ethics
530 Committee (UREC, #0599.001). All subjects gave written informed consent in accordance with
531 the Declaration of Helsinki and the General Data Protection Act 2018.

532

533 **Conflict of Interest**

534 *The authors declare that the research was conducted in the absence of any commercial or financial*
535 *relationships that could be construed as a potential conflict of interest.*

536

537 **Author contributions**

538 GM and PA designed the study, GM collected and analysed the data and wrote the paper. PA,
539 HN, JD assisted in writing the paper. HN assisted in amending the paper. We thank Sophie
540 Chesney for providing illustrations for Figure 1.

541

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544

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546 **Bibliography**

547 Adank, P., Kennedy-Higgins, D., Maegherman, G., Hannah, R., & Nuttall, H. E. (2018).

548 Effects of Coil Orientation on Motor Evoked Potentials From Orbicularis Oris.

549 *Frontiers in Neuroscience*, 12(November), 1–8.

550 <https://doi.org/10.3389/fnins.2018.00683>

551 Alderson-day, B., & Fernyhough, C. (2015). Inner Speech : Development , Cognitive

552 Functions , Phenomenology , and Neurobiology, *141*(5), 931–965.

553 British Society of Audiology. (2011). Recommended procedure: Pure-tone air-conduction

554 and bone-conduction threshold audiometry with and without masking.

555 Cattaneo, L., & Pavesi, G. (2014). The facial motor system. *Neuroscience and Biobehavioral*

556 *Reviews*, 38, 135. <https://doi.org/10.1016/j.neubiorev.2013.11.002>

557 Chipchase, L., Schabrun, S., Cohen, L., Hodges, P., Ridding, M., Rothwell, J., ... Ziemann,

558 U. (2012). A checklist for assessing the methodological quality of studies using

559 transcranial magnetic stimulation to study the motor system: An international consensus

560 study. *Clinical Neurophysiology*, 123(9), 1698–1704.

561 <https://doi.org/10.1016/j.clinph.2012.05.003>

562 Deiber, M. P., Ibañez, V., Honda, M., Sadato, N., Raman, R., & Hallett, M. (1998). Cerebral

563 processes related to visuomotor imagery and generation of simple finger movements

564 studied with positron emission tomography. *NeuroImage*, 7(2), 73–85.

565 <https://doi.org/10.1006/nimg.1997.0314>

566 Fadiga, L., Buccino, G., Craighero, L., Fogassi, L., Gallese, V., & Pavesi, G. (1998).

567 Corticospinal excitability is specifically modulated by motor imagery: A magnetic

568 stimulation study. *Neuropsychologia*, 37(2), 147–158. [https://doi.org/10.1016/S0028-](https://doi.org/10.1016/S0028-3932(98)00089-X)

569 [3932\(98\)00089-X](https://doi.org/10.1016/S0028-3932(98)00089-X)

570 Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). SHORT

571 COMMUNICATION Speech listening specifically modulates the excitability of

572 tongue muscles : a TMS study, *15*(September 2001), 399–402.

573 Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic

574 stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex*, 10(2),

575 175–180. <https://doi.org/10.1093/cercor/10.2.175>

576 Groppa, S., Oliviero, A., Eisen, A., Quartarone, A., Cohen, L. G., Mall, V., ... Siebner, H. R.

577 (2012). Clinical Neurophysiology A practical guide to diagnostic transcranial magnetic

578 stimulation : Report of an IFCN committee. *Clinical Neurophysiology*, 123(5), 858–882.

579 <https://doi.org/10.1016/j.clinph.2012.01.010>

580 Hashimoto, R., & Rothwell, J. C. (1999). Dynamic changes in corticospinal excitability

581 during motor imagery. *Experimental Brain Research*, 125(1), 75–81.

582 <https://doi.org/10.1007/s002210050660>

583 Huang, J., Carr, T., & Cao, Y. (2001). Comparing Cortical Activations for Silent and Overt
584 Speech Using Event-Related fMRI. *Human Brain Mapping, 15*(26), 26–38.
585 <https://doi.org/10.1002/hbm.XXXX>

586 Hyde, C., Fuelscher, I., Lum, J. A. G., Williams, J., He, J., & Enticott, P. G. (2017). Primary
587 Motor Cortex Excitability Is Modulated During the Mental Simulation of Hand
588 Movement. *Journal of the International Neuropsychological Society, 23*(02), 185–193.
589 <https://doi.org/10.1017/S1355617717000029>

590 Izumi, S., Findley, T., Ikai, T., Andrews, J., Daum, M., & Chino, N. (1995). Izumi et al
591 1995.pdf. *American Journal of Physical Medicine & Rehabilitation, 75*(3), 207–213.

592 Jeannerod, M. (2001). Neural Simulation of Action: A Unifying Mechanism for Motor
593 Cognition. *NeuroImage, 14*(1), S103–S109. <https://doi.org/10.1006/nimg.2001.0832>

594 Kasess, C. H., Windischberger, C., Cunnington, R., Lanzenberger, R., Pezawas, L., & Moser,
595 E. (2008). The suppressive influence of SMA on M1 in motor imagery revealed by
596 fMRI and dynamic causal modeling. *NeuroImage, 40*(2), 828–837.
597 <https://doi.org/10.1016/j.neuroimage.2007.11.040>

598 Kosslyn, S. M., Digirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation
599 of objects versus hands: Neural mechanisms revealed by positron emission tomography.
600 *Psychophysiology, 35*(2), S0048577298001516.
601 <https://doi.org/10.1017/S0048577298001516>

602 Kosslyn, S. M., Thompson, W. L., Wraga, M., & Alpert, N. M. (2001). Comparing Cortical
603 Activations for Silent and Overt Speech Using Event-Related fMRI: Distinct neural
604 mechanisms. *NeuroReport, 12*(11), 2519–2525. [https://doi.org/10.1097/00001756-](https://doi.org/10.1097/00001756-200108080-00046)
605 [200108080-00046](https://doi.org/10.1097/00001756-200108080-00046)

606 McCarthy-Jones, S., & Fernyhough, C. (2011). The varieties of inner speech: Links between
607 quality of inner speech and psychopathological variables in a sample of young adults.
608 *Consciousness and Cognition, 20*(4), 1586–1593.
609 <https://doi.org/10.1016/j.concog.2011.08.005>

610 McGuire, P. K., Silbersweig, D. A., Wright, I., Murray, R. M., Frackowiak, R. S., & Frith, C.
611 D. (1996). The neural correlates of inner speech and auditory verbal imagery in
612 schizophrenia: relationship to auditory verbal hallucinations. *Br J Psychiatry, 169*(2),
613 148–159. Retrieved from
614 [http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Cita-](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=8871790)
615 [tion&list_uids=8871790](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=8871790)

616 Munzert, J., Lorey, B., & Zentgraf, K. (2009). Cognitive motor processes: The role of motor
617 imagery in the study of motor representations. *Brain Research Reviews, 60*(2), 306–326.
618 <https://doi.org/10.1016/j.brainresrev.2008.12.024>

619 Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I.,
620 ... Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: a brief screening
621 tool for mild cognitive impairment. *J Am Geriatr Soc, 53*(4), 695–699.
622 <https://doi.org/10.1111/j.1532-5415.2005.53221.x>

623 Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory.
624 *Neuropsychologia, 9*(1), 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)

625 Oppenheim, G. M., & Dell, G. S. (2008). Inner speech slips exhibit lexical bias, but not the
626 phonemic similarity effect. *Cognition, 106*(1), 528–537.
627 <https://doi.org/10.1016/j.cognition.2007.02.006>

628 Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in
629 mentally simulated action. *Journal of Experimental Psychology. Human Perception and*
630 *Performance, 20*(4), 709–730. <https://doi.org/10.1037/0096-1523.20.4.709>

631 Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., ... di

632 Prampero, P. E. (1996). Primary motor and sensory cortex activation during motor
633 performance and motor imagery: a functional magnetic resonance imaging study. *The*
634 *Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *16*(23),
635 7688–7698. <https://doi.org/8922425>

636 Richter, W., Somorjai, R., Summers, R., Jamarsz, M., Menon, R. S., Gati, J. S., ... Kim, S.-
637 G. (2000). Motor Area Activity During Mental Rotation\rStudied by Time-Resolved
638 Single-Trial fMRI. *Journal of Cognitive Neuroscience*, *12*(2), 310–320.
639 <https://doi.org/10.1162/089892900562129>

640 Roosink, M., & Zijdwind, I. (2010). Corticospinal excitability during observation and
641 imagery of simple and complex hand tasks: Implications for motor rehabilitation.
642 *Behavioural Brain Research*, *213*(1), 35–41. <https://doi.org/10.1016/j.bbr.2010.04.027>

643 Rossini, P., Barker, A., Berardelli, A., Caramia, M., Caruso, G., Cracco, R., ... Tomberg, C.
644 (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and
645 roots: basic principles and procedures for routine clinical application. Report of an
646 IFCN. *And Clinical*, *91*, 79–92.

647 Rossini, P. M., Burke, D., Chen, R., Cohen, L. G., Daskalakis, Z., Di Iorio, R., ... Ziemann,
648 U. (2015). Non-invasive electrical and magnetic stimulation of the brain, spinal cord,
649 roots and peripheral nerves: Basic principles and procedures for routine clinical and
650 research application: An updated report from an I.F.C.N. Committee. *Clinical*
651 *Neurophysiology*, *126*(6), 1071–1107. <https://doi.org/10.1016/j.clinph.2015.02.001>

652 Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., Segebarth, C., ...
653 Jeannerod, M. (1996). Roth et al., 1996. *Neuroreport*, *7*(7), 1280–1284.

654 Shepard, R. N., & Metzler, J. (1971). Mental Rotation of Three-Dimensional Objects
655 Abstract . The time required to recognize that two perspective drawings portray. *Science*
656 *(New York, N.Y.)*, *171*(FEBRUARY), 701–703.
657 <https://doi.org/10.1126/science.171.3972.701>

658 Shuster, L. I., & Lemieux, S. K. (2005). An fMRI investigation of covertly and overtly
659 produced mono- and multisyllabic words. *Brain and Language*, *93*(1), 20–31.
660 <https://doi.org/10.1016/j.bandl.2004.07.007>

661 Sokolov, A. (1972). *Inner speech and thought*. New York: Plenum/Rosetta Press.

662 Solodkin, A., Hlustik, P., Chen, E. E., & Small, S. N. (2004). Phylogeography of a nematode
663 (*Heligmosomoides polygyrus*) in the western Palearctic region: Persistence of northern
664 cryptic populations during ice ages? *Cerebral Cortex*, *14*(11), 1246–1255.
665 <https://doi.org/10.1093/cercor/bhh086>

666 Stippich, C., Ochmann, H., & Sartor, K. (2002). Stippich02, 331, 1–5. Retrieved from
667 papers3://publication/uuid/0432B5E0-D0FF-4033-8BF7-D82E0AA4ECD4

668 Szenkovits, G., Peelle, J. E., Norris, D., & Davis, M. H. (2012). Individual differences in
669 premotor and motor recruitment during speech perception. *Neuropsychologia*, *50*(7),
670 1380–1392. <https://doi.org/10.1016/j.neuropsychologia.2012.02.023>

671 Tian, X., & Poeppel, D. (2010). Mental imagery of speech and movement implicates the
672 dynamics of internal forward models. *Frontiers in Psychology*, *1*(OCT), 1–23.
673 <https://doi.org/10.3389/fpsyg.2010.00166>

674 Tian, X., & Poeppel, D. (2012). Mental imagery of speech: linking motor and perceptual
675 systems through internal simulation and estimation. *Mental Imagery*, 152.

676 Tian, X., Zarate, J. M., & Poeppel, D. (2016). Mental imagery of speech implicates two
677 mechanisms of perceptual reactivation. *Cortex*, *77*, 1–12.
678 <https://doi.org/10.1016/j.cortex.2016.01.002>

679 Tomasino, B., Borroni, P., Isaja, A., & Rumiati, R. I. (2005). The role of the primary motor
680 cortex in mental rotation: A TMS study. *Cognitive Neuropsychology*, *22*(3–4), 348–363.
681 <https://doi.org/10.1080/02643290442000185>

682 Tremblay, F., Tremblay, L. E., & Colcer, D. E. (2001). Modulation of corticospinal
683 excitability during imagined knee movements. *Journal of Rehabilitation Medicine*,
684 33(5), 230–234. <https://doi.org/10.1080/165019701750419635>
685 Vogt, S., Di Rienzo, F., Collet, C., Collins, A., & Guillot, A. (2013). Multiple roles of motor
686 imagery during action observation. *Frontiers in Human Neuroscience*, 7(November),
687 807. <https://doi.org/10.3389/fnhum.2013.00807>
688 Watkins, K. E., Strafella, A. P., & Paus, T. (2003). Seeing and hearing speech excites the
689 motor system involved in speech production. *Neuropsychologia*, 41(8), 989–994.
690 [https://doi.org/10.1016/S0028-3932\(02\)00316-0](https://doi.org/10.1016/S0028-3932(02)00316-0)
691 Yahagi, S., Shimura, K., & Kasai, T. (1996). An increase in cortical excitability with no
692 change in spinal excitability during motor imagery. *Perceptual and Motor Skills*, 83(1),
693 288–290. <https://doi.org/10.2466/pms.1996.83.1.288>

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696 **Figure legends**

697 Figure 1: Examples of the tweezers as used in the hand (left panel) and lip (right panel)
698 conditions. Participants were instructed to maintain a baseline level of activity as trained
699 on in a pre-thresholding session. New tools were provided for each participant, with a
700 white cotton filling acting as a spring to provide tension for muscle activation.

701

702 Figure 2: (A) Chronometric design of the study showing the six time points in relation to the
703 stimulus; (B) the grid surface for the MNI brain used in thresholding.

704

705 Figure 3: (A) Box plot showing z-scores for all data. Lip results appear as smaller due to their
706 naturally smaller size. ME= Motor execution, MI = Motor imagery, Base = Baseline. (B) Line
707 plot showing mean MEP AUC (raw) by timepoint. Error bars represent $\pm 1SE$, $\alpha = .001$.

708

709 Figure 4: Line graphs showing change in mean MEP AUC per time point and effects of
710 condition. ME= Motor execution, MI = Motor imagery, Base = Baseline.

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