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4 Rapid learning of associations between sound and action through observed movement. A

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TMS study.

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Jacques Launay¹, Roger T. Dean² & Freya Bailes³

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MARCS Insitute, University of Western Sydney

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¹Corresponding Author: Department of Experimental Psychology, University of

19

Oxford, Oxford, OX1 3UD, jacques.launay@psy.ox.ac.uk, (+44) 1865271367.

20

²MARCS Institute, University of Western Sydney, Locked Bag 1797, Penrith,

21

NSW, 2751, Australia, roger.dean@uws.edu.au, (+61) 297 726902.

22

³School of Drama, Music and Screen, University of Hull, Hull, UK, HU6 7RX

23

f.bailes@hull.ac.uk, (+44) 1482 466398.

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28

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29

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30
31

Abstract

32 Research has established that there is a cognitive link between perception and production
33 of the same movement. However, there has been relatively little research into the
34 relevance of this for non-expert perceivers, such as music listeners who do not play
35 instruments themselves. In two experiments we tested whether participants can quickly
36 learn new associations between sounds and observed movement without performing
37 those movements themselves. We measured motor evoked potentials (MEPs) in the first
38 dorsal interosseous muscle of participants' right hands while test tones were heard and
39 single transcranial magnetic stimulation (TMS) pulses were used to trigger motor
40 activity. In Experiment 1 participants in a 'human' condition (n=4) learnt to associate the
41 test tone with finger movement of the experimenter, while participants in a 'computer'
42 condition (n=4) learnt that the test tone was triggered by a computer. Participants in the
43 human condition showed a larger increase in MEPs compared with those in the computer
44 condition. In a second experiment pairing between sounds and movement occurred
45 without participants repeatedly observing the movement and we found no such difference
46 between the human (n=4) and computer (n=4) conditions. These results suggest that
47 observers can quickly learn to associate sound with movement, so it should not be
48 necessary to have played an instrument to experience some motor resonance when
49 hearing that instrument.

50

51 Keywords: TMS; perception; action; timing; sound

52

53

54 Rapid learning of associations between sound and action through observed movement. A
55 TMS study

56

57 Within psychology there has been a longstanding interest in the relationship
58 between perception and performance of movement and the possibility that these share
59 common cognitive roots (e.g. James, 1890). More recently, research with non-human
60 primates demonstrated that ‘mirror neurons’ are active both during perception and
61 performance of the same actions, providing supporting evidence for this theory (Gallese
62 & Goldman, 1998; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Related evidence from
63 humans has shown that the perception of actions leads to some increase in activity in
64 regions of the brain involved in making those movements oneself, which can be
65 described as ‘motor resonance’ (see Rizzolatti, 2005). However, there is a relative
66 paucity of evidence relating to auditory aspects of the perception-action link (i.e. when
67 we hear the sounds of human movement rather than seeing movement), likely due to a
68 bias towards research in the visual domain.

69 Auditory research has often focussed on well-established associations between
70 sound and movement, showing for example that the perception of words that relate to
71 limbs can lead to activity in regions of the brain involved in movement of those limbs
72 (Galati et al., 2008; Hauk, Johnsrude, & Pulvermüller, 2004; Tettamanti et al., 2005) and
73 that the sounds of relevant actions alone can evoke this motor resonance (Aziz-Zadeh,
74 Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Gazzola, Aziz-Zadeh, & Keysers, 2006).
75 Motor responses to sound are more pronounced if the sound has an established
76 association with movement, as occurs with musical training (Münte, Altenmüller, &

77 Jäncke, 2002), and are absent in people with apraxias specific to the actions they are
78 hearing (Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008), suggesting that when we have the
79 capacity to perform an action this becomes a part of perception (Maes, Leman, Palmer, &
80 Wanderley, 2014).

81 There has been some contention about the acquisition of action-perception
82 associations however (Heyes, 2009). Hebbian learning, which suggests that any neurons
83 that fire together can wire together, regardless of specific predictive value, has the
84 potential to explain how movements could become associated with visual perception of
85 those movements ((Keysers & Perrett, 2004). However, empirical research using novel
86 associations between produced and perceived movement suggests that contingency
87 learning leads to better action-perception links (Catmur, Walsh, & Heyes, 2007; Cook,
88 Press, Dickinson, & Heyes, 2010). With regards to music it is clear that with any form of
89 learning musicians will repeatedly associate their own movement with the perceived
90 sound of instruments, while this is not the case for non-musicians, and is also likely to be
91 subject to gradual learning processes (Novembre & Keller, 2014). As such, musicians
92 have been shown to exhibit more motor resonance for their instruments than non-
93 musicians (e.g. Bangert et al., 2006; Buccino et al., 2004; Haueisen & Knösche, 2001),
94 but importantly motor resonance can be acquired by non-musicians through learning an
95 instrument (Lahav, Saltzman, & Schlaug, 2007), and associations can take as little as 20
96 minutes to acquire (Bangert & Altenmüller, 2003; D’Ausilio, Altenmüller, Olivetti
97 Belardinelli, & Lotze, 2006)

98 The relationship between action and perception has been used as a potential
99 explanation for empathy that is experienced when engaging with music (e.g. Molnar-

100 Szakacs & Overy, 2006; Overy & Molnar-Szakacs, 2009). When we listen to music
101 which has been created by another person we might mirror their motions and to some
102 extent therefore empathise with their experience, leading to the both pleasurable and
103 emotional experiences that people have. This is supported by evidence showing that
104 people with higher trait empathy do have greater motor resonance in musical situations
105 (Novembre, Ticini, Schütz-Bosbach, & Keller, 2014, 2012). However, action-perception
106 research to date does not directly relate to the experience of non-musicians, who can
107 generally enjoy music without necessarily having knowledge of how it is performed. An
108 important gap in our knowledge concerns whether novices (here defined as people who
109 do not have experience of playing the instrument they are listening to) are likely to
110 experience motor resonance for musical sounds, given that they have not directly learnt
111 associations with the movements that make those sounds.

112 Another underexplored area of the relationship between action and perception
113 relates to the temporal specificity for motor resonance. If motor resonance acts as a part
114 of the perception process then we would expect it to be tightly locked to the time at
115 which stimuli are presented, yet motor regions of the brain appear to be active throughout
116 perception of musical sound, in response to rhythm in general rather than locked to
117 specific tones (Zatorre, Chen, & Penhune, 2007). Experiments have often presented
118 stimuli for some considerable period of time, meaning temporal specificity was not
119 investigated (e.g. Aziz-Zadeh et al., 2004; Ticini, Schüz-Bosbach, Weiss, Casile, &
120 Waszak, 2012), but recent investigations into the relationship between more musical
121 sounds, involving predictable rhythmic beats, have demonstrated that motor resonance is
122 more pronounced at the time of beats rather than in between them (Cameron, Stewart,

123 Pearce, Grube, & Muggleton, 2012; Fujioka, Trainor, Large, & Ross, 2012; Stupacher,
124 Hove, Novembre, Schütz-Bosbach, & Keller, 2013). If people learn to anticipate the time
125 of predictable sounds we would expect motor resonance to occur selectively shortly
126 anticipating the time of those sounds.

127 Over the current set of experiments we test two main hypotheses:

128

129 1. Participants can quickly learn associations between observed movement and
130 sound, resulting in greater motor resonance when subsequently hearing those sounds.

131 2. Motor resonance for sound is temporally specific (i.e. occurs only at the time
132 that the sound is perceived).

133

134 In Experiment 2 we additionally test whether people need to observe pairings
135 between sound and movement, or whether believing that a sound is being created by
136 movement is sufficient to lead to motor resonance.

137

138 **General Methods**

139

140 **Equipment and stimuli**

141

142 A Magstim Rapid² with a figure-of-8 coil was used for transcranial magnetic
143 stimulation. Pulses were triggered by a Dell PC running DMDX software version
144 4.0.4.4., which also played auditory tones to participants via an Edirol UA-25X
145 soundcard, and Philips SHS4700 ear clip headphones during the TMS/MEP testing

146 phase. A Northern Digital Incorporated Polaris Spectra Neuronavigation system was used
147 to track head and coil movements so that the experimenter could hold the coil in place
148 throughout the experiment, with Advanced Source Analysis software version 4.7.41.
149 (visor) running on a separate Dell Optiplex Gx745.

150 Muscle twitches were recorded using surface electromyography with adhesive
151 Ag/AgCl ECG conductive electrodes and a dry earth strap connected to an
152 ADInstruments Dual BioAmp, and ADInstruments Powerlab 16/30 recording system, via
153 ADInstruments Chart software version 5.5.6., and Scope software version 3.9.2.

154 During the learning phase of the experiment, auditory tones were played to
155 participants using a MacBook Pro running MAX/MSP v. 5.0.8. using an Edirol UA-25
156 Soundcard and Philips SHS4700 ear clip headphones. The tones used were a MIDI
157 woodblock sound, and cowbell sound, corresponding to midi-note 31 and 67 with
158 MAX/MSPs default MIDI channel 10. The experimenter tapped on a Roland Handsonic
159 HPD-10 drum pad to trigger sounds during the learning phase of the experiment.

160

161 **Procedure**

162

163 Participants were invited to the lab a day before any TMS testing occurred. On
164 this first meeting they were given an information sheet about the study, and two safety-
165 screening questionnaires, which they were asked to read, fill in and return before the full
166 study. A 15-minute interview session then followed, during which the experimenter gave
167 each participant full information about what is involved in TMS, including the associated
168 risks and potential side effects. Participants were then invited to attend a second 1 hour

169 15 minute session during which the experiment would occur. The procedure was
170 approved by the University of Western Sydney Ethics Committee

171 During the testing session the ‘hot-spot’ for triggering first finger movement was
172 identified by varying coil scalp position. Motor thresholds were then defined as the
173 minimum machine power required to evoke MEPs greater than $50\mu\text{V}$ from trough to
174 peak, 50 % of the time (5 out of 10 pulses). The experimental procedure then began,
175 which included three phases: a TMS/MEP testing phase, a learning phase, then a repeat
176 of the TMS/MEP testing phase (see Figure 1).

177

178 **TMS/MEP testing phase.** Participants heard a series of isochronous tones (test
179 timbre) played over headphones, each 600 ms apart, while TMS pulses were delivered at
180 120 % of each individual participant’s motor threshold. Every seven tones, either a TMS
181 pulse occurred (two thirds of the time) or no TMS pulse occurred. Half of these TMS
182 pulses occurred ‘with’ the tone (110 ms before the tone 10 times, 120 ms before the tone
183 10 times and 130 ms before the tone 10 times), and the other half occurred ‘between’ two
184 tones (at 360 ms after the tone 10 times, 370 ms after the tone 10 times, and 380 ms after
185 the tone 10 times) – although note that these times could also be characterised as
186 anticipating the tones by 240 ms, 230 ms and 220 ms respectively. TMS pulses preceded
187 the sound because we expected participants to anticipate the predictable test tone, and
188 pilot testing (described below) confirmed that 120 ms was a sufficient anticipatory
189 period, and we used three different periods in order to introduce some jitter into the
190 sequence. The order of timing of the pulses was determined by DMDX software. Within
191 every set of 21 tones, the three different TMS pulse conditions (with tone, between tone,

192 or no pulse) would occur, in a randomly determined order (see Figure 2). This part of the
193 experiment lasted approximately 6.3 minutes. Participants were asked to keep their hand
194 relaxed during this phase but we did not monitor muscle activity continuously between
195 TMS pulses.

196

197 **Learning phase.** Next, participants heard isochronous tones played over
198 headphones while watching the experimenter generate half of them by tapping on an
199 electronic drum pad. Two different timbres occurred in a predetermined
200 pseudorandomised order - one was the test timbre (as heard in the preceding phase) and
201 the other was a control timbre. Six different trials occurred, each with 50 tones. In every
202 trial the participant was instructed to either count the tones generated by the
203 experimenter's tapping (three rounds), or count the tones generated by the computer
204 (three rounds). The instruction changed in each trial, and the instruction for the first trial
205 was counterbalanced across participants. At the end of each trial, participants reported the
206 number they had counted back to the experimenter, and were given feedback about their
207 performance. The experimenter made 26 taps in the first trial, then 23, 24, 27, 25 and 25
208 in the following trials respectively. This procedure was designed to emulate a recent
209 single pulse TMS study showing that abstract visual stimuli could be associated with
210 hand movement (Fecteau, Tormos, Gangitano, Thèoret, & Pascual-Leone, 2010).

211 In the human condition, the test timbre corresponded to sounds associated with
212 the tapping of the experimenter (i.e. the experimenter visibly tapped on an electronic
213 drumpad to generate the sound), while in the computer condition, the test timbre was not
214 associated with any visible signal, and was described as being generated by the computer.

215 Apart from this there were no differences between the ‘human’ and ‘computer’
216 conditions. Throughout the learning phase of the experiment, participants should learn
217 associations between the test timbre and first finger movement of the experimenter in the
218 human condition, or associations between the test timbre and the computer in the
219 computer condition. This part lasted approximately 5 minutes in total, and occurred
220 between two instances of the TMS/MEP testing phase.

221 Participants experienced the TMS/MEP testing phase, followed by the learning
222 phase, followed by another round of the TMS/MEP testing phase. At the end of this,
223 participants were fully debriefed about the experiment. The only difference between
224 Experiment 1 and Experiment 2 was whether participants observed the experimenter
225 making finger movements during the learning phase of the experiment.

226

227 **Design**

228

229 Experiment 1 and Experiment 2 both used a 2 (association condition:
230 human/computer, between-subjects) x 2 (pulse timing condition: with tone/ between tone,
231 within-subjects) design. The dependent variable was change in MEP amplitude, as
232 measured using EMG (electromyography) signals recorded from the first dorsal
233 interosseous muscle of the right hand.

234

235 **Analysis**

236

237 MEPs were recorded by Scope with a sample rate of 2048 Hz, a bandpass filter of
238 10 Hz – 1 kHz, and with an amplitude range of 10 mV. No 50 Hz noise was observed so
239 a notch filter at 50 Hz was not used. Recordings were taken from when the pulse was
240 triggered for a total period of 60 ms. Each trace that was recorded was initially visually
241 inspected to determine whether it contained an MEP (i.e. whether the TMS pulse had
242 triggered a motor response, 56 % of data were included on this basis in Experiment 1, and
243 55 % in Experiment 2¹). Following this exclusion, the minimum value measured during
244 the 60ms period was subtracted from the maximum value, to give a size of MEP from
245 peak to trough. Values were then log-transformed to approximate normality.

246 Following this transformation, each of the values collected after the learning
247 phase was subtracted from the average for that participant before the learning phase. This
248 was done separately for MEPs collected at each time relative to sounds (i.e. TMS pulse
249 with sound, compared with TMS pulse between sounds). Multilevel linear modelling was
250 used to compare the different conditions (condition: human/computer, between-subjects;
251 timing: pulse with tone/pulse between tone, within-subjects), with a random intercept for
252 each individual. For all models, the statistical package R (version 2) was used with the
253 package lme4 (Bates & Sarkar, 2008) to create models, and lmerTest to test the
254 significance of models.

255

256

Pliot Study

257

¹ Further details of excluded data are given in supplementary material, including analyses with all data included.

258 In a pilot study one participant (aged 28, F) was exposed to the learning phase of
259 the experiment, and subsequently experienced a version of the testing phase in which
260 TMS pulses were triggered at different timepoints in relation to the tones (90 ms before
261 tones, 120 ms before tones or 370 ms after tones). MEPs were then averaged over the 30
262 repeats of each of these timepoints, and values compared to see which timepoints might
263 best elicit large MEPs relating to the tones. TMS pulses occurring 120 ms before the
264 tones were found to have the greatest response. Given likely individual differences in
265 when anticipation of tones might occur, some jitter was introduced into the temporal
266 sequence during subsequent experiments.

267

268

Experiment 1

269

270 Experiment 1 was designed to test the basic hypothesis that people can learn to
271 associate sound with their own movement after repeated pairing between the sound and
272 observed movement.

273

Participants

275

276 Eight undergraduate psychology students from the University of Western Sydney
277 were tested: 4 in the human condition (2 male, age $M = 19$ years, $SD = 1$) and 4 in the
278 computer condition (1 male, age $M = 23$ years, $SD = 7$). All participants reported being
279 right-handed, and reported having normal hearing.

280

281 Results

282

283 Participants' mean motor threshold was 66 % of the maximum stimulator output,
284 SD = 9 (human condition: M = 61 %, SD = 9.0; computer condition: M = 72 %, SD = 5.6;
285 these are not significantly different from one another, $t(5) = 2.0$, $p = 0.1$). Accuracy when
286 asked to count the number of taps made by the experimenter or computer during the
287 learning phase was assessed using the average (over 6 trials) absolute difference between
288 the correct number and the participant's answer. The group mean of this accuracy score
289 was 1.58 (SD = 0.51). Multilevel linear modelling to compare change in MEP size in the
290 human and computer condition and for the time of pulse (either between or just before
291 the tone) revealed a fixed effect of condition, $b = 0.28$, $se = 0.061$, $t(4) = 4.6$, $p = .011$, but
292 no main effect of pulse timing ($b = 0.01$, $se = 0.038$, $t(300) = 0.30$, $p = 0.76$) and no
293 significant interaction between the two ($b = -0.07$, $se = 0.038$, $t(300) = 1.86$, $p = 0.06$).
294 The main effect of condition is indicative of a significantly larger increase in MEP size in
295 the human condition (see Table 1 and Figure 3) following the learning phase.

296

297 Summary

298

299 In Experiment 1, results demonstrated the hypothesised increase in MEP size
300 while listening to sounds associated with movement in the human condition. No
301 significant differences were observed between the different TMS pulse timepoints (i.e.
302 pulse occurring with the tone, or occurring between tones).

303

304

Experiment 2

305

306 Experiment 2 was designed to test whether participants could learn associations between
307 sound and movement without watching repeated pairing of the two. This should assess
308 whether knowing that a sound is caused by a certain movement is sufficient to make
309 people associate sound with that movement (without repeated visual confirmation of that
310 association). Here, participants were exposed to just one visual pairing between
311 movement and sounds, but were similarly asked to count the number of sounds made by
312 the experimenter or the computer in subsequent rounds of the learning phase. If their
313 belief that sounds are human generated is sufficient to induce motor resonance then this
314 learning phase should have similar effects to that in Experiment 1.

315

Participants

317

318 Eight undergraduate psychology students from the University of Western Sydney
319 were tested: 4 in the human condition (1 male, age $M = 24$ years, $SD = 11$) and 4 in the
320 computer condition (0 male, age $M = 23$ years, $SD = 9$). All participants reported being
321 right-handed, and having normal hearing, and none of the participants had been tested
322 during Experiment 1.

323

Procedure

325

326 The procedure was similar to Experiment 1, but during the learning phase
327 participants were told to face away from the experimenter and close their eyes. In this
328 way, they would not be able to visually associate sounds with the movement of the
329 experimenter. Before the learning phase, the experimenter tapped the drumpad once,
330 triggering the test tone, indicating that this would be the general mechanism by which the
331 sound would be triggered, so participants would be aware of this association. They were
332 then required to count the tones based solely on this timbre, and might therefore imagine
333 the movement associated with it.

334

335 **Results**

336

337 Participants' mean motor threshold was 62 % of the maximum stimulator output,
338 SD = 5 (human condition: M = 64 %, SD = 2.2; computer condition: M = 59 %, SD = 6.2;
339 these are not significantly different from one another, $t(4) = 1.6$, $p = 0.19$). Accuracy
340 scores in the learning phase of the experiment are given in Table 1. Multilevel linear
341 modelling demonstrated no main effects of condition ($b = -0.087$, $se = 0.097$, $t(6) = 0.90$,
342 $p = 0.40$) or timepoint ($b = -0.024$, $se = 0.034$, $t(258) = 0.70$, $p = 0.49$), and no interaction
343 between the two ($b = 0.044$, $se = 0.034$, $t(258) = 1.28$, $p = 0.20$, see Table 2 and Figure
344 3).

345

346 **Summary**

347

348 In Experiment 2, results did not demonstrate any pairing of sound with
349 movement: the change in MEP size was similar in both the condition in which
350 participants were taught to associate sound with human movement, and the condition in
351 which participants were taught to associate sound with a computer. The result suggest
352 that visual pairing might be required to learn associations between sound and movement
353 in this paradigm. We also found no support for the hypothesis that motor resonance could
354 be temporally locked to the time of sound, but this is unsurprising given that motor
355 associations were not learnt.

356

357

General Discussion

358

359 The results of Experiment 1 suggest that there is an increase in motor resonance
360 after learning associate observed movement with sound. Finding that sounds with newly
361 learnt associations with observed movement can lead to increased motor resonance is a
362 significant and original finding, and can be compared to a recent study (Ticini et al.,
363 2012) which had a similar result when participants learnt to associate their own hand
364 movement with sound. The major difference in the current study is that the result occurs
365 when participants learn to make associations with observed movement, as might occur
366 when observing a musician play. Learning associations with one's own motor system
367 after observing that movement can be explained by the theory that the perceived
368 movements of other people are processed using motor regions of the brain (Rizzolatti &
369 Craighero, 2004). When participants see the experimenter move at the same time as
370 hearing sounds generated by that movement, they process information about the

371 movement using motor regions of the brain, and this processing becomes paired with the
372 sounds that are occurring at the same time. This means that after watching other people
373 create sounds (e.g. during musical performance) we can experience motor engagement
374 when listening to those sounds.

375 With regards to musical sounds, our findings suggest that people with no
376 experience of playing an instrument can develop motor resonance associated with the
377 sounds of that instrument. While the current result suggests that some visual pairing
378 between action and sound is required to lead to changes in motor resonance, a short
379 period of such pairing appeared to have substantial effects. It is therefore possible that
380 with limited experience of observing a performer on a musical instrument, people may
381 develop some motor resonance for that instrument, and potentially experience some
382 empathy and emotional investment in that sound (Overy & Molnar-Szakacs, 2009). Here
383 we do not measure from multiple effectors so we cannot determine the level of specificity
384 of this motor resonance, and further research would be required to confirm whether this
385 effect is related to the particular movements that were observed.

386 Experiment 2 was designed to test whether associations could develop even in the
387 absence of repeated visual pairing of movement with sound (an ‘imagined sound’
388 version of Experiment 1). Effectively this should demonstrate whether people’s belief
389 that a sound is triggered by a human movement, rather than repeated observation of the
390 movement and sound co-occurring, is sufficient to lead to motor resonance for that
391 sound, and we did not find this to be the case. In this experiment, participants did not
392 observe movements being paired with sound, but they had been informed that the
393 specified sound was triggered by movements during the learning phase. This suggests

394 that without having visual pairing of sound and movement people do not learn
395 associations between the two. However, an alternative explanation for the null result is
396 that the amount of pairing between sound and movement required for learning is different
397 without visual observation. The current number of pairings was taken from a comparable
398 visual association study (Fecteau et al., 2010). It is possible that when associations are
399 imagined they require a greater number of pairings in order to be learnt, or even just that
400 a greater number of initial demonstrations of the finger movement might be required in
401 order for participants to start imagining the movement in time with sound. A further
402 experiment could also involve asking participants to actively imagine finger movement
403 whilst counting tones in the learning phase, as this might be sufficient to encourage
404 associations to be learnt.

405 Taking the results of Experiment 1 and Experiment 2 together we provide support
406 for the hypothesis that associations between sound and movement must be visible for it to
407 be learnt and lead to motor resonance. Thus in Experiment 2, without direct pairing
408 between movements and sound we did not find any increase in motor resonance for
409 sounds for participants who had seen those sounds paired with human movement.
410 Associative learning has been put forward as an explanation for all effects that could be
411 attributed to mirror neurons in humans, and generally there is good experimental
412 evidence to support this theory (Heyes, 2009; Petroni, Baguear, & Della-Maggiore,
413 2010), with which the current experiment concurs.

414 A limitation of the current experiment is that we did not take into account musical
415 experience of participants, which might lead to some individual differences in
416 performance on the tasks. None of the participants reported having extensive musical

417 training, but it is likely that experience of listening to music and attending live music
418 events might affect the current results, as has been shown with observers of dance (Jola,
419 Abedian-Amiri, Kuppaswamy, Pollick, & Grosbras, 2012). The current movement-sound
420 associations were almost certainly novel for participants though, and this should
421 minimise this effect. The very small number of participants should also be taken into
422 account when interpreting the current results, although Figure 3 demonstrates that the
423 changes were identified similarly in most participants, and although we have not used
424 ANOVAs or compared the two experiments due to low statistical power and the
425 probability of this causing Type I and Type II errors there is a clear pattern of increase
426 MEPs in the human condition of Experiment 1 only. In addition, one participant in
427 Experiment 2 demonstrated a significantly later MEP response to other participants
428 (occurring approximately 10 ms later than other participants) suggesting some problem
429 with recording equipment in this case.

430 We did not find evidence for the temporal specificity for motor resonance in the
431 current experiments. TMS pulses that were coordinated with sounds demonstrated the
432 same increase in motor resonance as those pulses which occurred at a time unrelated to
433 the sounds. Although the timings of TMS pulses in the current experiment were based on
434 pilot testing, it is possible that they were not optimal for testing temporal specificity of
435 motor resonance. The pulses occurring ‘between’ and ‘with’ sounds in the current studies
436 were actually very close to one another (the smallest difference between these being just
437 90 ms), so it is feasible that this led to the null result regarding temporal specificity.
438 Further investigation into the temporal specificity of motor resonance could use a variety
439 of different TMS pulse timings (e.g. every 50 ms between two sounds) in order to

440 determine whether there is some fine-grained temporal specificity that was not identified
441 in the current study. It would also be possible to use isochronous stimuli that occurred
442 with a larger interval (e.g. 1000 ms), allowing greater space between sounds for the TMS
443 pulses.

444 We did, however, find a near significant interaction between condition and timing
445 of TMS pulse in Experiment 1. This was suggestive of a smaller increase in MEP size in
446 the human condition when the TMS pulse occurred with the tones compared with when
447 they occurred between the tones (see Table 2). Given that we had no specific predictions
448 about this kind of interaction and the effect was not quite significant it is quite hard to
449 interpret. However, as the values indicate change in motor resonance it is possible that
450 the interaction is primarily because motor resonance was higher at the time of the tone
451 before the learning phase, and increased relatively less compared with when the pulse
452 occurred between tones.

453 In the current set of experiments we demonstrate that it is possible to learn
454 associations between sound and movement when observing movement, without making
455 movement oneself. Experiment 2 suggests that these associations were not made in the
456 same way when there was not repeated visual pairing of sound with movement. These
457 findings have implications both for the way that we understand how associations between
458 perception and action develop, and also for our understanding of how people perceive
459 sound with agency, such as musical sound.

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References

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463 Aziz-Zadeh, L., Iacoboni, M., Zaidel, E., Wilson, S., & Mazziotta, J. (2004). Left
464 hemisphere motor facilitation in response to manual action sounds. *European*
465 *Journal of Neuroscience*, 19(9), 2609–12. doi:10.1111/j.0953-816X.2004.03348.x

466 Bangert, M., & Altenmüller, E. O. (2003). Mapping perception to action in piano
467 practice: a longitudinal DC-EEG study. *BMC Neuroscience*, 4(1), 26.
468 doi:10.1186/1471-2202-4-26

469 Bangert, M., Peschel, T., Schlaug, G., Rotte, M., Drescher, D., Hinrichs, H., ...
470 Altenmüller, E. (2006). Shared networks for auditory and motor processing in
471 professional pianists: evidence from fMRI conjunction. *Neuroimage*, 30(3), 917–
472 926. doi:10.1016/J.Neuroimage.2005.10.044

473 Bates, D., & Sarkar, D. (2008). lme4: Linear mixed-effects models using S4 classes,
474 Retrieved from <http://CRAN.r-project.org/package=lme4>.

475 Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G.
476 (2004). Neural circuits underlying imitation learning of hand actions: an event-
477 related fMRI study. *Neuron*, 42(2), 323–34. doi:10.1016/S0896-6273(04)00181-3

478 Cameron, D. J., Stewart, L., Pearce, M. T., Grube, M., & Muggleton, N. G. (2012).
479 Modulation of motor excitability by metricality of tone sequences.
480 *Psychomusicology: Music, Mind, and Brain*, 22(2), 122–8. doi:10.1037/a0031229

481 Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor learning configures the human
482 mirror system. *Current Biology*, 17(17), 1527–31. doi:10.1016/j.cub.2007.08.006

483 Cook, R., Press, C., Dickinson, A., & Heyes, C. (2010). Acquisition of automatic
484 imitation is sensitive to sensorimotor contingency. *Journal of Experimental*
485 *Psychology: Human Perception and Performance*, 36(4), 840–52.
486 doi:10.1037/a0019256

487 D'Ausilio, A., Altenmüller, E. O., Olivetti Belardinelli, M., & Lotze, M. (2006). Cross-
488 modal plasticity of the motor cortex while listening to a rehearsed musical piece.
489 *European Journal of Neuroscience*, 24(3), 955–8. doi:10.1111/j.1460-
490 9568.2006.04960.x

491 Fecteau, S., Tormos, J. M., Gangitano, M., Théoret, H., & Pascual-Leone, A. (2010).
492 Modulation of cortical motor outputs by the symbolic meaning of visual stimuli.
493 *European Journal of Neuroscience*, 32(1), 172–7. doi:10.1111/j.1460-
494 9568.2010.07285.x

- 495 Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of
496 isochronous sounds is represented in neuromagnetic beta oscillations. *Journal of*
497 *Neuroscience*, 32(5), 1791–802. doi:10.1523/JNEUROSCI.4107-11.2012
- 498 Galati, G., Committeri, G., Spitoni, G., Aprile, T., Di Russo, F., Pitzalis, S., &
499 Pizzamiglio, L. (2008). A selective representation of the meaning of actions in the
500 auditory mirror system. *Neuroimage*, 40(3), 1274–86.
501 doi:10.1016/j.neuroimage.2007.12.044
- 502 Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-
503 reading. *Trends in Cognitive Sciences*, 2(12), 493–501. doi:10.1016/S1364-
504 6613(98)01262-5
- 505 Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic
506 auditory mirror system in humans. *Current Biology*, 16(18), 1824–9.
507 doi:10.1016/j.cub.2006.07.072
- 508 Haueisen, J., & Knösche, T. R. (2001). Involuntary motor activity in pianists evoked by
509 music perception. *Journal of Cognitive Neuroscience*, 13(6), 786–92.
510 doi:10.1162/08989290152541449
- 511 Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action
512 words in human motor and premotor cortex. *Neuron*, 41(2), 301–7.
513 doi:10.1016/S0896-6273(03)00838-9
- 514 Heyes, C. (2009). Where do mirror neurons come from? *Neuroscience & Biobehavioral*
515 *Reviews*, 34(4), 575–83. doi:10.1016/j.neubiorev.2009.11.007
- 516 James, W. (1890). *The Principles of Psychology*. New York: Dover Publications.
- 517 Jola, C., Abedian-Amiri, A., Kuppaswamy, A., Pollick, F. E., & Grosbras, M. H. (2012).
518 Motor simulation without motor expertise: Enhanced corticospinal excitability in
519 visually experienced dance spectators. *PLoS ONE*, 7(3).
520 doi:10.1371/journal.pone.0033343
- 521 Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: a Hebbian
522 perspective. *Trends in Cognitive Sciences*, 8(11), 501–7.
523 doi:10.1016/j.tics.2004.09.005
- 524 Lahav, A., Saltzman, E., & Schlaug, G. (2007). Action representation of sound:
525 audiomotor recognition network while listening to newly acquired actions. *Journal*
526 *of Neuroscience*, 27(2), 308–14. doi:10.1523/JNEUROSCI.4822-06.2007
- 527 Maes, P.-J., Leman, M., Palmer, C., & Wanderley, M. M. (2014). Action-based effects on
528 music perception. *Frontiers in Psychology*, 4. doi:10.3389/fpsyg.2013.01008

- 529 Molnar-Szakacs, I., & Overy, K. (2006). Music and mirror neurons: from motion to
530 “e”motion. *Social Cognitive and Affective Neuroscience*, 1(3), 235–41.
531 doi:10.1093/scan/nsl029
- 532 Münte, T. F., Altenmüller, E. O., & Jäncke, L. (2002). The musician’s brain as a model
533 of neuroplasticity. *Nature Reviews Neuroscience*, 3(6), 473–8. doi:10.1038/nrn843
- 534 Novembre, G., & Keller, P. E. (2014). A conceptual review on action-perception
535 coupling in the musicians’ brain: what is it good for? *Frontiers in Human*
536 *Neuroscience*, 8, 1–11. doi:10.3389/fnhum.2014.00603
- 537 Novembre, G., Ticini, L. F., Schütz-Bosbach, S., & Keller, P. (2014). Motor simulation
538 and the coordination of self and other in real-time joint action. *Social Cognitive and*
539 *Affective Neuroscience*, 9(8), 1062–8. doi:10.1093/scan/nst086
- 540 Novembre, G., Ticini, L. F., Schütz-Bosbach, S., & Keller, P. E. (2012). Distinguishing
541 self and other in joint action. Evidence from a musical paradigm. *Cerebral Cortex*,
542 22(12), 2894–903. doi:10.1093/cercor/bhr364
- 543 Overy, K., & Molnar-Szakacs, I. (2009). Being together in time: musical experience and
544 the mirror neuron system. *Music Perception*, 26(5), 489–504.
545 doi:10.1525/Mp.2009.26.5.489
- 546 Pazzaglia, M., Pizzamiglio, L., Pes, E., & Aglioti, S. M. (2008). The sound of actions in
547 apraxia. *Current Biology*, 18(22), 1766–72. doi:10.1016/j.cub.2008.09.061
- 548 Petroni, A., Baguear, F., & Della-Maggiore, V. (2010). Motor resonance may originate
549 from sensorimotor experience. *Journal of Neurophysiology*, 104(4), 1867–71.
550 doi:10.1152/jn.00386.2010
- 551 Rizzolatti, G. (2005). The mirror neuron system and its function in humans. *Anatomy and*
552 *Embryology*, 210(5), 419–21. doi:10.1007/s00429-005-0039-z
- 553 Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of*
554 *Neuroscience*, 27, 169–92. doi:10.1146/Annurev.Neuro.27.070203.144230
- 555 Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the
556 recognition of motor actions. *Cognitive Brain Research*, 3(2), 131–41.
557 doi:10.1016/0926-6410(95)00038-0
- 558 Stupacher, J., Hove, M. J., Novembre, G., Schütz-Bosbach, S., & Keller, P. E. (2013).
559 Musical groove modulates motor cortex excitability: A TMS investigation. *Brain*
560 *and Cognition*, 82(2), 127–36. doi:10.1016/j.bandc.2013.03.003
- 561 Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., ...
562 Perani, D. (2005). Listening to action-related sentences activates fronto-parietal

- 563 motor circuits. *Journal of Cognitive Neuroscience*, 17(2), 273–81.
564 doi:10.1162/0898929053124965
- 565 Ticini, L. F., Schüz-Bosbach, S., Weiss, C., Casile, A., & Waszak, F. (2012). When
566 sounds become actions: higher-order representation of newly learnt action sounds in
567 the human motor system. *Journal of Cognitive Neuroscience*, 24(2), 464–74.
568 doi:10.1162/jocn_a_00134
- 569 Zatorre, R. J., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music:
570 auditory-motor interactions in music perception and production. *Nature Reviews*.
571 *Neuroscience*, 8(7), 547–58. doi:10.1038/nrn2152
- 572
- 573

574 Table 1. Accuracy scores in each condition
575

	Human Condition	Computer Condition
	M (SD)	M (SD)
Experiment 1	1.71 (0.70)	1.46 (0.28)
Experiment 2	1.83 (1.11)	1.83 (0.56)

576

577 Table 2. Summary statistics for change in log-transformed MEP size in each of the four
 578 conditions in both experiments.
 579

	Human Condition		Computer Condition	
	With tones	Between tones	With tones	Between tones
	M (SD)	M (SD)	M (SD)	M (SD)
Experiment 1	0.60 (0.77)	0.72 (0.78)	0.14 (0.50)	-0.02 (0.55)
Experiment 2	0.14 (0.42)	0.10 (0.38)	0.35 (0.67)	0.50 (0.74)

580

581 Figure 1. Summary of procedure.

582

583 Figure 2. Example of 21 tones in the testing phase. Each diamond indicates a test tone,
584 arrows indicate a TMS pulse, and X's indicate a target tone (not known to participant).

585

586 Figure 3. Mean MEP trough to peak amplitudes for each participant before and after
587 learning phase in Experiment 1 and Experiment 2.

588