

1 Asymmetry in kinematic generalization between visual and passive
2 lead-in movements are consistent with a forward model in the
3 sensorimotor system

4

5 Abbreviated title: Spatiotemporal generalization of lead-in movements

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24 Keywords: motor learning, context, transfer, dynamic learning, motor
25 memories, human

26

27 **Number of pages: 18**

28 **Number of figures: 6**

29 **Number of tables: 1**

30 **Number of words for Abstract: 248**

31 **Number of words for Introduction: 641**

32 **Number of words for Discussion: 1497**

33

34 **Conflict of Interest**

35 The authors declare that they have no financial, personal, or professional interests
36 that could be construed to have influenced the paper.

37

38 **Acknowledgements**

39 Financial support was provided by the Centre for Robotics and Neural Systems at
40 Plymouth University and by the Bavarian State Ministry for Science, Research & the
41 Arts

42

43 **Abstract**

44

45 In our daily life we often make complex actions comprised of linked
46 movements, such as reaching for a cup of coffee and bringing it to our mouth
47 to drink. Recent work has highlighted the role of such linked movements in the
48 formation of independent motor memories, affecting the learning rate and
49 ability to learn opposing force fields. However, while such work has described
50 the angular generalization function representing the neural tuning of motor
51 memory formation in state space, we have no understanding of how different
52 movement kinematics (such as distance, speed or duration) affects the
53 formation of these independent motor memories. Here we investigate such
54 kinematic generalization for both passive and visual lead-in movements to
55 probe their individual characteristics. After participants adapted to opposing
56 force fields using training lead-in movements, the lead-in kinematics were
57 modified on random trials to test generalization. For both visual and passive
58 modalities, predictive compensation was sensitive to lead-in duration and
59 peak speed, falling off away from the training condition. However, little decay
60 was found with increasing lead-in distance. Interestingly, asymmetric transfer
61 between lead-in movement modalities was also observed, with partial transfer
62 from passive to visual, but very little vice versa. Overall these tuning effects
63 were stronger for passive compared to visual lead-ins demonstrating the
64 difference in these sensory inputs in regulating motor memories. Our results
65 suggest these effects are a consequence of state estimation, with differences
66 across modalities reflecting their different levels of sensory uncertainty arising
67 as a consequence of dissimilar feedback delays.

68

69

70 **Significance Statement**

71

72 Using a force field interference paradigm, we show that the generalization of
73 motor memory is strongly tuned to variations in lead-in kinematics, with
74 passive lead-ins exhibiting a stronger influence and sharper tuning than visual
75 lead-ins. This asymmetry is mirrored in the transfer of adaptation between
76 modalities, with stronger transfer from the passive to visual condition. We
77 suggest these differences arise due to state estimation during the lead-in, with
78 larger delays in visual signals increasing their uncertainty. This reduces their
79 feedback weighting compared to proprioceptive signals, producing a smaller
80 estimated state change, and therefore smaller decay in predictive force.
81 Overall these results provide further evidence that the human motor system
82 uses observer-based control, based on a forward model to estimate state.

83

84

85 **Introduction**

86

87 Recent studies have highlighted key aspects for neural rehabilitation using
88 robotic systems (Reinkensmeyer et al., 2016). However, continual progress in
89 this area depends on understanding the mechanisms of human sensorimotor
90 learning in order to determine the optimal presentation of sensory information
91 to improve the rate, retention and generalization of adaptation. Although
92 adaptation is often studied on single movements in the laboratory, we rarely

93 produce movements in isolation in everyday life. Rather, one movement often
94 directly leads into another. For example, to catch a ball, we make use of
95 visual motion information to estimate its state in order to plan and execute an
96 interception movement. Thus, natural movements often follow directly from
97 previous movements or from visual motion.

98
99 Recent work has shown that closely linking multiple movements together in
100 time reduces interference in learning opposing tasks (Howard et al., 2012;
101 2015; Sheahan et al., 2016; Howard et al., 2017). In particular, distinct past
102 movements act like a contextual cue, enabling adaptation to opposing viscous
103 curl fields when these movements are preceded by unique lead-in motions,
104 each associated with one of the dynamics (Howard et al., 2012). This shows
105 that motor learning and recall depends not only on the current state of the arm
106 during a movement, but also on its preceding states. Interestingly, active,
107 passive or visual lead-in movements were all equally effective at reducing
108 interference. This indicates that sensory feedback relating to motion is
109 sufficient to affect adaptation, even when no active movement is involved. The
110 contextual effect of this prior movement disappears as the time between lead-
111 in and adaptation movements exceeds about half a second, indicating that the
112 representation of past state decays quickly over time. This suggests a strong
113 link between the representation of state and the theory of neural population
114 dynamics (Churchland et al., 2012; Pandarinath et al., 2015).

115
116 Dynamic adaptation to a single force field occurs locally; after training in a
117 specific movement, the recall of predictive compensation decays as the
118 movement angle (Thoroughman and Shadmehr, 2000; Donchin et al., 2003;
119 Howard and Franklin, 2015; 2016) or distance (Gandolfo et al., 1996;
120 Goodbody and Wolpert, 1998; Mattar and Ostry, 2007) deviates from the
121 training condition. The Gaussian-like angular generalization observed in these
122 studies has also be found for lead-in movements, with different lead-in
123 modalities exhibiting different characteristics, both in terms of their absolute
124 level of influence, but also in their sharpness of tuning. In particular both
125 active (Sarwary et al., 2015) and passive lead-in movements (Howard and
126 Franklin, 2015) show narrower and deeper tuning than visual lead-in
127 movements (Howard and Franklin, 2016).

128
129 Interference studies have been widely adopted to investigate contextual
130 effects on motor learning, and to examine if contextual cues can assist in the
131 learning of opposing dynamics (Brashers-Krug et al., 1996; Gandolfo et al.,
132 1996; Krakauer et al., 1999; Karniel and Mussa-Ivaldi, 2002; Caithness et al.,
133 2004; Nozaki et al., 2006; Howard et al., 2013). Such interference paradigms
134 are more sensitive to generalization effects of contextual cues than single field
135 paradigms, and have been used effectively to examining the angular
136 generalization characteristics of lead-in movements (Howard and Franklin,
137 2015; 2016). Using these paradigms it has been possible to extract features
138 of the neural basis functions underlying dynamical adaptation, allowing for the
139 development of simple computational models (Howard et al., 2017). However,
140 we still lack basic information on the generalization features of lead-in
141 movements for different kinematics such as duration or distance.

142

143 Here, we first characterize the generalization of passive and visual lead-in
144 movements across different kinematics using an interference paradigm. In two
145 separate experiments, we examine generalization across distance and
146 duration (and the dependent variable of speed) of passive and visual lead-in
147 movements. Second, in order to gain insight into any commonality between
148 the neural resources employed in passive and visual lead-in movements, we
149 also investigate how adaptation transfers between these two different lead-in
150 modalities.

151
152

153 **Methods**

154

155 **Experimental Design**

156

157 *Subjects.* Sixteen human participants were randomly allocated to two
158 experimental groups that each performed one experiment. Eight participants
159 (7 female, aged 24.8 ± 5.0 years, mean \pm sd) performed the passive lead-in
160 experiment. Eight further participants (6 female; aged 27.4 ± 6.7 years)
161 participated in the visual lead-in experiment. All participants were right handed
162 according to the Edinburgh handedness questionnaire (Oldfield, 1971), and
163 naïve to the aims of the study. All participants provided written informed
164 consent to the protocol before participating in the experiment, which had been
165 approved by the University of Cambridge Ethics Committee. The methods
166 were carried out in accordance with the approved guidelines.

167

168 *Apparatus.* Experiments were performed using a vBOT planar robotic
169 manipulandum and its associated virtual reality system (Howard et al., 2009).
170 Handle position is measured using optical encoders sampled at 1000 Hz, and
171 motors operating under torque control allow the application of end-point
172 forces. A force transducer (Nano 25; ATI), mounted under the handle,
173 measures the applied forces, and its output signals were low-pass filtered at
174 500 Hz using analogue 4th pole Bessel filters prior to digitization. To reduce
175 body movement participants were seated in a sturdy chair in front of the
176 apparatus and firmly strapped against the backrest with a four-point seatbelt.
177 During an experiment, participants grasped the robot handle in their right
178 hand while their right forearm was supported by an air sled, constraining arm
179 movement to the horizontal plane. Participants could not view their hand
180 directly. Instead veridical visual feedback was used to overlay images of the
181 starting location, via point, final target, (all 1.25 cm radius disks) and a hand
182 cursor (0.5 cm radius red disk) using the virtual reality system. This ensured
183 that the visual cursor appeared to the participant in the same plane and at the
184 same location as their hand. Data was collected at 1000 Hz and logged to
185 disk for offline analysis using Matlab (Matlab, The MathWorks Inc., Natick,
186 MA, USA).

187

188 *Force Fields.* In the adaptation movement, participants performed reaching
189 movements either in a null field condition, a velocity-dependent curl force field
190 (Gandolfo et al., 1996), or a mechanical channel (Scheidt et al., 2000). The
191 curl force field was implemented as:

192

193

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = k \begin{bmatrix} 0 & -1 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \quad (1)$$

194

195 where the field constant k was set to a value of $\pm 16 \text{ Nm}^{-1}\text{s}$, and the sign
 196 determines the direction (CW or CCW) of the force-field. Each participant
 197 experienced both force field directions. The direction of the force field was
 198 always associated with a specific direction of a prior contextual movement.
 199 The relationship between the contextual movement direction and curl field
 200 direction (CW/CCW) was counterbalanced across participants.

201

Condition	Duration [ms]	Distance [cm]
Passive training	700	10
Visual training	700	10
Passive/Visual test channel	700	10
Passive/Visual probe channel	1400	20
Passive/Visual probe channel	1050	15
Passive/Visual probe channel	420	6
Passive/Visual probe channel	210	3
Passive/Visual probe channel	1400	10
Passive/Visual probe channel	1050	10
Passive/Visual probe channel	420	10
Passive/Visual probe channel	350	10
Passive/Visual probe channel	700	20
Passive/Visual probe channel	700	15
Passive/Visual probe channel	700	6
Passive/Visual probe channel	700	3
Passive/Visual probe channel	1050	20
Passive/Visual probe channel	350	3

202

203

Table 1. Generalization conditions

204

205 Mechanical channel trials were implemented using a spring constant of $6,000$
 206 Nm^{-1} and a damping constant of $30 \text{ Nm}^{-1}\text{s}$ perpendicular to the direction of
 207 motion throughout the movement between the central location and the final
 208 target. Channel trials were only produced on the movements to the 0° target
 209 with corresponding lead-in movements starting at 135° or 225° .

210

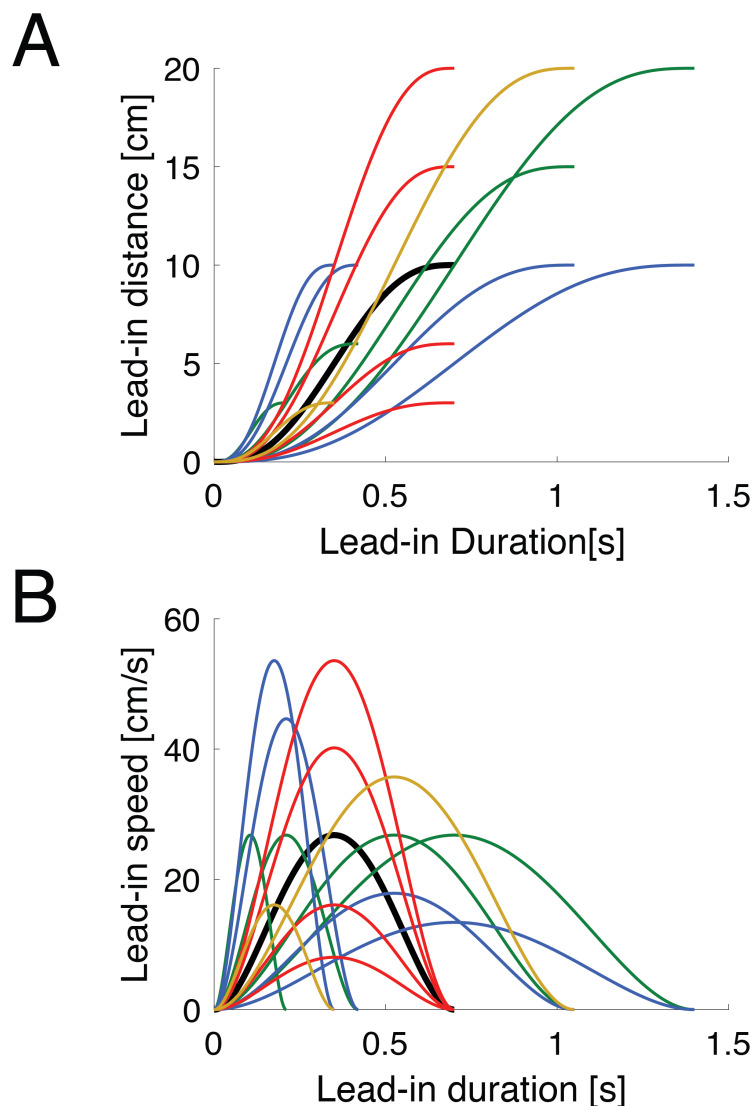
211 **Protocol**

212

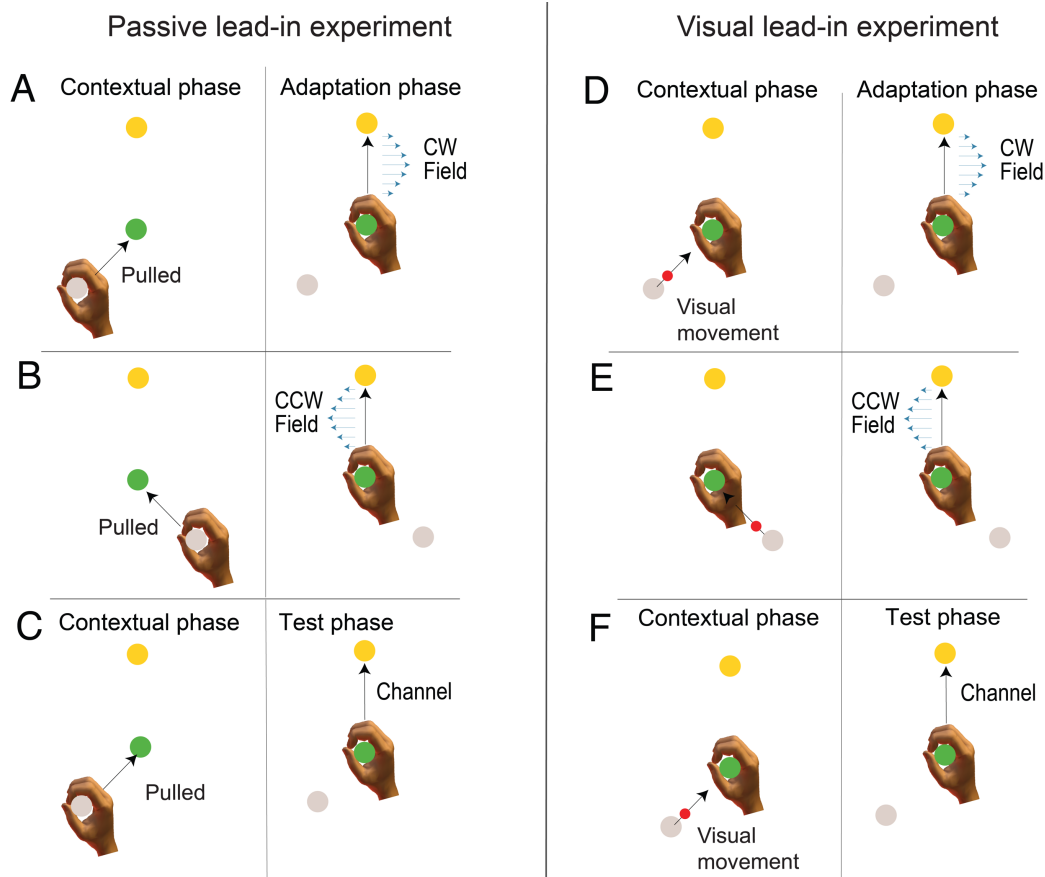
213 Two separate experiments were performed to examine the generalization of
 214 the learning associated with one contextual movement to other contextual
 215 movements with different kinematic profiles (within the same modality), as
 216 well as the transfer of learning between passive and visual lead-in conditions
 217 (across the modalities).

218

219 After an initial pre-learning session in a null field, participants were exposed to
220 the curl force fields (learning phase). Channel trials were used to examine
221 adaptation to the novel dynamics, in which the lead-in movement duration,
222 speed and distance were varied. In addition, the modality of the lead-in
223 movement was occasionally changed to examine transfer. The trial
224 parameters for both experiments are shown in Table 1 and the kinematics of
225 the lead-in movements can be seen in Fig 1. On these trials, the lead-in
226 movement was chosen from one of 15 different movements with distances
227 ranging from 3 cm to 20 cm and durations ranging between 210 ms to 1400
228 ms.
229
230



231
232
233 Figure 1. Kinematics of lead-in movements used for testing generalization. **A**
234 Profiles of movement distance versus duration of lead-in probe conditions
235 across all conditions. Thick black line indicates the training lead-in motion.
236 Colors indicate specific conditions that are matched across duration (red),
237 peak speed (green), or duration (blue). **B** Lead-in movement kinematics of
238 peak speed as a function of duration.
239



240
241

242 **Figure 2. Experimental Design. A-C:** Passive lead-in generalization
243 experiment. **A** Participants first experienced an initial passive lead-in motion
244 from a starting position (grey circle) to the central target (green circle) and
245 then immediately made a second active movement to the target (yellow circle)
246 on which a curl force field (blue arrows) could be applied. **B** An initial
247 movement from a different starting target was associated with the opposite
248 force field on the second movement. The direction of curl force field and lead-
249 in movements were counterbalanced across participants. **C** In order to
250 examine learning rate and generalization, random trials in which the
251 contextual movement was followed by a mechanical channel on the second
252 movement to the target were applied. **D-F:** Visual lead-in generalization
253 experiment. **D** Participants initially observed an initial visual cursor movement
254 (red circle) from the grey starting circle to the central target (green circle).
255 Once the cursor entered the central target, participants immediately
256 performed a second active movement to the target (yellow circle) on which a
257 curl force field (blue arrows) could be applied. **E** An initial cursor movement
258 from a different starting target was associated with the opposite force field on
259 the second movement. **F** On random trials, after the visual lead-in motion, a
260 mechanical channel was applied on the active movement to the target to
261 measure predictive compensation.

262

263 *Experiment 1. Passive lead-in movements.*

264

265 All trials consisted of a two-part movement: an initial lead-in movement
266 followed directly by an adaptation movement (Fig 2A-C). The first part was a

267 contextual lead-in movement from a starting location to a central via point.
268 This contextual lead-in movement was normally 10 cm in length during all null
269 and force field training conditions. The second part was an 18cm adaptation
270 movement to the final target. Only during the adaptation part of the movement
271 could participants experience a force field (or channel trial). The lead-in
272 movement direction (+45° or -45° relative to final target direction) was
273 indicative of the direction of the curl force field on the adaptation movement
274 (clockwise or counterclockwise). The adaptive part of the movement was
275 made to one of two final targets, located at 0° and 270° degrees relative to the
276 via point. The preceding contextual movements started from one of 3
277 locations, namely at 135° or 225° and 45° or 135° degrees respectively, and
278 end at a central via-point. Together this produced four possible two-part
279 movements (combinations of lead-in and adaptation movement).

280
281 In experiment 1, the contextual lead-in movement was comprised of a passive
282 movement of the participant's hand. This passive movement was produced by
283 the robotic manipulandum passively moving the participant's hand while no
284 cursor was presented. Each trial began by displaying the start location for the
285 lead-in movement, the central location and final target. The vBOT then moved
286 the participant's hand to the lead-in start location. Once the handle was
287 stationary within the start location for 300 ms, a beep was generated
288 indicating the start of the trial. At this time, the handle of the robotic system
289 moved to the central via-point following a minimum jerk trajectory. The training
290 contextual movement was a 10cm movement of duration 700 ms. Once the
291 hand reached the central location, participants were required to produce an
292 active adaptation movement from the central location to the final target
293 location. The dwell time of the hand within the central via point was required
294 to between 0-250 ms, otherwise a warning was provided. If dwell time
295 exceeded 500ms then the trial was aborted and repeated. If the second
296 movement (adaptation movement) duration was between 450 ms and 600 ms
297 a "Great" message was displayed; otherwise an appropriate "Too Fast" or
298 "Too Slow" warning was shown. Force fields and channel trials were only ever
299 presented during this second movement.

300 As many trials were required, each experiment was performed in two separate
301 sessions on different days. There were 1546 and 1580 trials on days 1 and 2
302 respectively, providing a total of 3126 trials. Participants were required to take
303 short rest breaks approximately every 200 trials (195-205 trials) but could rest
304 at any time between trials. The trials were organized as follows:

305

306 Day 1

307

308 Pre-exposure: The pre-exposure phase started with 2 blocks of 40 trials. A
309 block consisted of 36 Null trials and 4 channel trials (Total 80 trials: 72 null
310 trials, 8 training condition channel trials). Next, participants were provided with
311 three repetitions of each of the 34 generalization channel trials (Total 102
312 generalization condition channel trials) to ensure they had prior experience of
313 the generalization trial conditions. Finally, 2 blocks of null field trials (36 null
314 trials and 4 channel trial) were performed.

315

316 Exposure Training: During the exposure phase, the participants were exposed
317 to the curl force fields during the adaptation movement. This phase consisted
318 of 12 blocks of 40 trials (Total 480 trials: 432 field trials, 48 training condition
319 channel trials).

320

321 Generalization Testing: This examined generalization of the learned predictive
322 compensation by pseudo-randomly interspersing trials with curl field exposure
323 with trials in which channel trials were preceded by the full range of contextual
324 movements (different durations and distances). This consisted of 6 blocks of
325 134 trials, which meant that there were 6 repetitions of each of the 34
326 generalization channel trials. (Total 804 trials: 600 field trials, 204
327 generalization condition channel trials). Generalization conditions are
328 graphically illustrated in Fig. 1.

329

330 Day 2

331

332 Exposure Training: In the second session, training was briefly resumed. The
333 phase consisted of 6 blocks of 40 trial blocks (Total 240 trials: 216 field trials,
334 24 training condition channel trials).

335

336 Generalization Testing: Similar to the session of Day 1, participants performed
337 10 blocks of 134 trials, providing 10 repetitions of each of the 34
338 generalization channel trials. (Total 1340 trials: 1000 field trials, 340
339 generalization condition channel trials).

340

341 Generalization lead-in conditions, which were always followed by a channel
342 trial on the adaptation movement, were chosen to sample lead-in distances
343 between 3 - 20 cm, peak speeds between 8.04 - 53.57 cms^{-1} and durations
344 between 210 - 1400 ms. In addition, a transfer condition was included in
345 which the lead-in motion was occasionally substituted by a visual moving
346 cursor and a reversed direction visual cursor.

347

348 *Experiment 2. Visual lead-in movements.*

349

350 Experiment 2 was had a similar design to Experiment 1, except that the
351 contextual lead-in movements for both training and testing consisted of a
352 visual movement of the cursor (Fig 2D-F). The training contextual lead-in
353 movement again followed a minimum jerk trajectory of duration 700 ms from
354 the start to the central location. During this time, the participant's hand
355 remained stationary at the central location. Immediately after the cursor
356 reached the central location, the participant made an active reaching
357 adaptation movement from the central location to the final target. The same
358 variations of generalization movement trials were performed (but with visual
359 instead of passive motion). In addition, a transfer condition was used in which
360 a passive movement lead-in was performed. Again, a reversed visual cursor
361 condition was also employed.

362

363

364 **Data Analysis**

365

366 The experimental data was analyzed offline using Matlab R14. Statistics to
367 examine differences between the generalization from visual lead-in and
368 passive lead-in movements were performed in JASP 0.9.2 (JASP Team,
369 2018) using both the ANOVA and Bayesian ANOVA. To examine learning,
370 kinematic error on the adaptation movements and force compensation on the
371 channel trials were used.

372
373 *Kinematic error.* For each null and curl field trial, the kinematic error was
374 calculated on the adaptation portion of the movement. This was quantified as
375 the maximum perpendicular error (MPE), which is the maximum deviation of
376 the hand path to the straight line joining the movement starting location to the
377 target. For each participant, the average MPE over 8 trials was calculated.
378 The sign of the MPE was flipped appropriately so that results from CW and
379 CCW field trials could be appropriately combined together in this calculation.
380 The mean and standard error (SE) of MPE was then computed across all
381 participants.

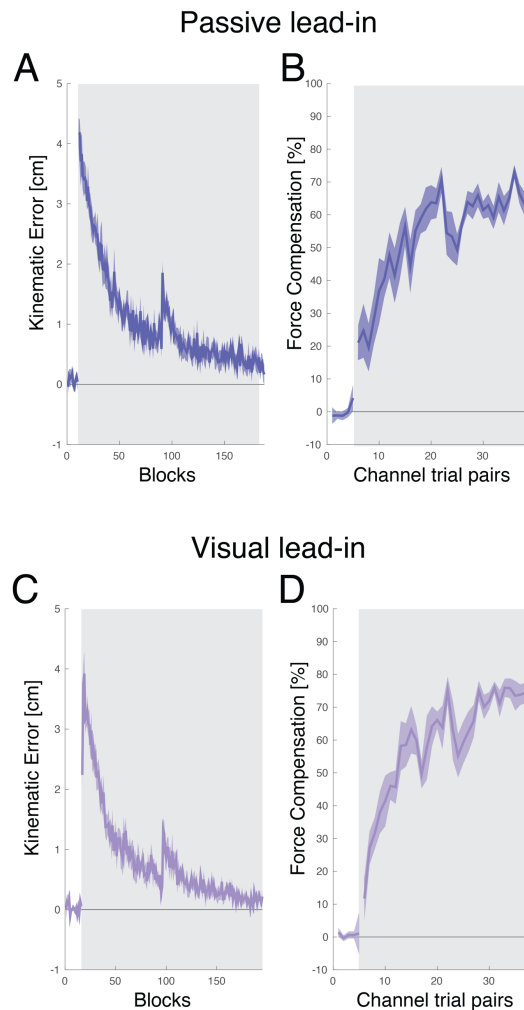
382
383 *Force compensation.* On each channel trial, force exerted by participants
384 perpendicularly into the wall of the simulated channel was measured to
385 estimate predictive feedforward adaptation. This method is preferable to
386 relying on a reduction in kinematic error during force field learning, which can
387 also arise from muscle co-contraction (Burdet et al., 2001; Franklin et al.,
388 2003; Milner and Franklin, 2005). The measured channel force was regressed
389 with the velocity of movement along the channel during the same period and
390 then scaled by the field strength. This yielded an estimate of the level of force
391 compensation present on the given channel trial (Smith et al., 2006). For
392 plotting purposes, the force compensation data was averaged across 2
393 channel trials for each participant. The mean and standard error (SE) of
394 compensation was then computed across all participants to examine the
395 generalization functions.

396
397

398 **Results**

399

400 In the passive lead-in experiment, participants performed active reaching
401 movements to a target after being passively moved from a start position to a
402 central target. After initial movements in a null field, participants were
403 presented with a curl force field during the active movement. The direction of
404 the curl field depended on the angle between the passive movement and
405 active movement (Fig 2A,B). When presented with the curl force field,
406 participants' adaptation movements were disturbed, producing large errors
407 that were gradually reduced over the exposure phase (Fig 3A). Throughout
408 the experiment channel trials were introduced on random trials in order to
409 measure the predictive force compensation throughout adaptation (Fig 2C).
410 Over a similar timescale as the reduction in kinematic error, force
411 compensation increased, reaching just over 63% compensation averaged
412 over both force fields (Fig 3B). A small decay in the force compensation and
413 increase in the kinematic error can be seen between day 1 and the start of
414 day 2.



415
416

417 Figure 3. Adaptation to two opposing force fields. **A** Mean and SE of MPE
418 across over 8 participants for the passive lead-in experiment as a function of
419 blocks of 8 trials. **B** Mean and SE of percentage force compensation for pairs
420 of channel trials (one for each force field direction) throughout the passive
421 lead-in experiment where the lead-in movement was the same as the training
422 trials. **C** Mean and SE of MPE for the visual lead-in experiment. **E** Mean and
423 SE of percentage force compensation for the visual lead-in experiment.

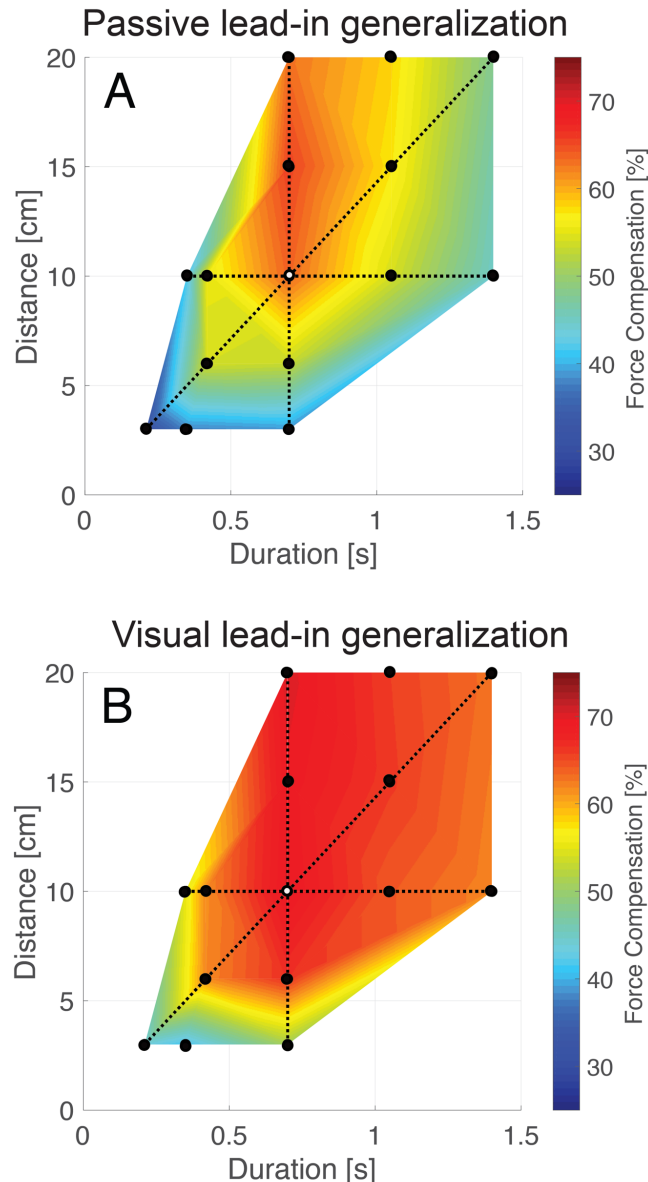
424

425 Participants in the visual lead-in experiment performed a similar protocol but
426 where the lead-in movements were purely visual in nature (Fig 2D-F). Again,
427 when presented with the curl force field, participants' adaptation movements
428 were disturbed, producing large errors that were gradually reduced over the
429 exposure phase (Fig 3C). Over a similar timescale, force compensation
430 increased, reaching approximately 70% compensation averaged over both
431 force fields (Fig 3D).

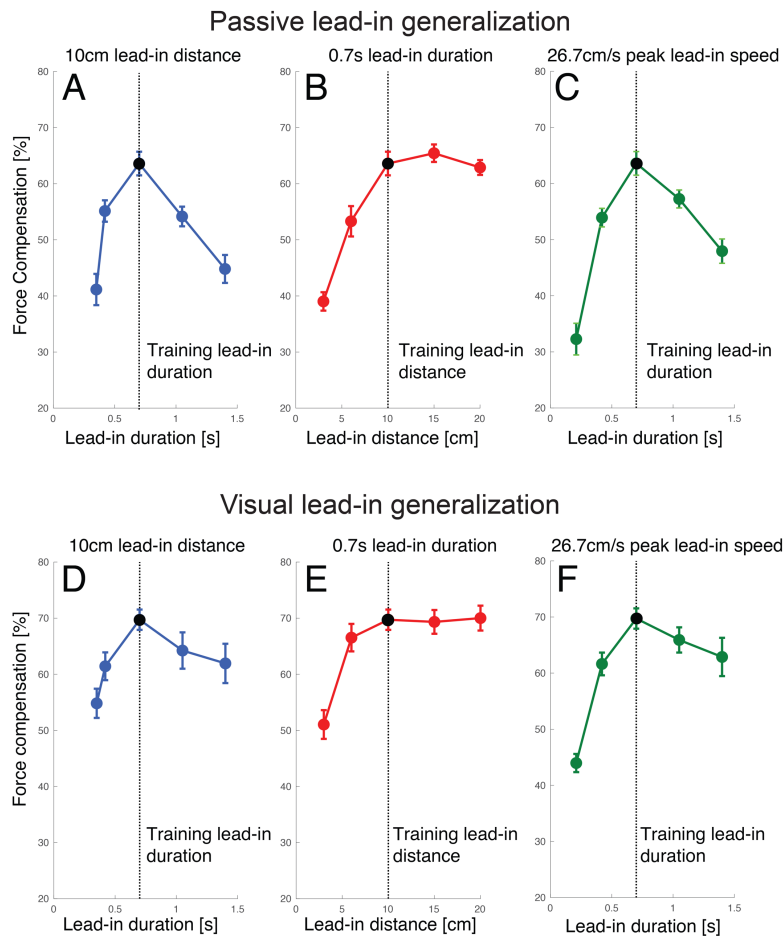
432

433 On random trials late in the adaptation phase, channel trials were applied with
434 a range of different lead-in movement kinematics (Fig 1) in order to examine
435 generalization. After learning the force fields with the passive lead-in
436 movement, variations in the kinematics of this lead-in movement produced a
437 range of generalization levels (Fig 4A). As the testing lead-in movements

438 varied further away from the training kinematics the predictive force level
439 decreased. A similar finding is shown for the generalization after learning a
440 visual lead-in movement (Fig 4B). However, in this condition only small
441 decreases in the predictive force is seen over a wide range of changes in the
442 lead-in kinematics.
443



444
445
446 Figure 4. Generalization surface plots for passive and visual lead-in
447 movements. **A** Surface plot of generalization for passive lead-in movements.
448 The percentage force compensation is represented by color and plotted
449 against lead-in duration and lead-in distance. The black circle with a white
450 center indicates the result at the training condition. The solid black dots
451 indicate points for which measurements were made on probe trials. The black
452 dotted lines correspond to conditions with the same training lead-in distance
453 of 10cm, same training lead-in duration of 0.7s or same training lead-in speed
454 of 26.7cm/s. The legend shows the correspondence between color and
455 percentage perfect force compensation. **B** Surface plot of generalization for
456 the visual lead-in condition.



457
458

459 Figure 5. Generalizations results for both passive and visual lead-in conditions
460 plotted for fixed values of lead-in distance, lead-in duration and lead-in speed.
461 **A-C** Results of passive lead-in experiments. The dotted lines indicate the
462 training values of lead-in distance and lead-in duration. Error bars indicate
463 standard error of the mean. **A** Effect of changing lead-in duration for fixed
464 10cm lead-in distance. In this panel, lead-in distance is held constant and the
465 movement duration (shown on the x-axis) and speed vary. **B** Effect of
466 changing lead-in distance (and peak speed) across conditions with a fixed
467 700ms lead-in duration. **C** Effect of changing lead-in duration (and distance)
468 across conditions with a fixed 26.7cm/s lead-in speed. **D-F** Corresponding
469 results for visual lead-in condition.

470

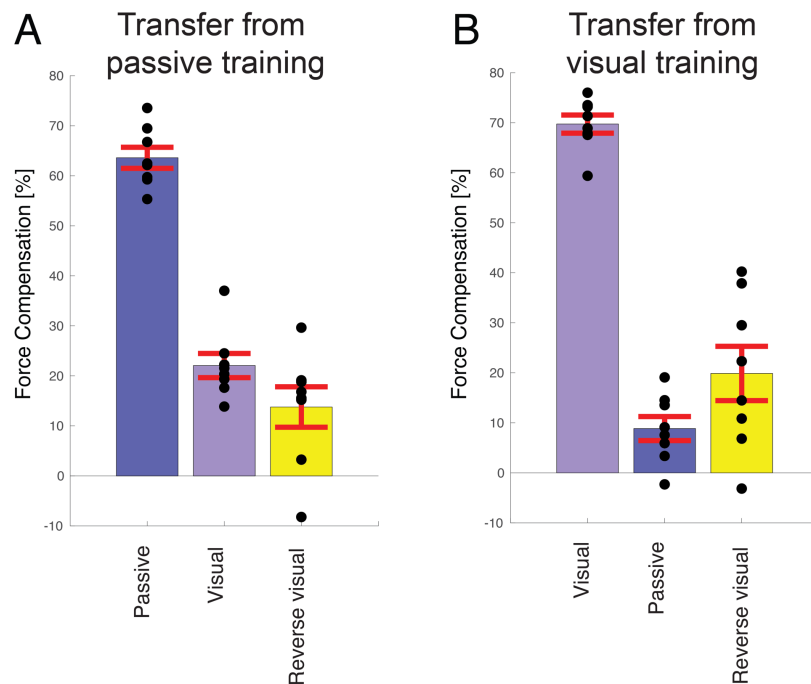
471 Across the different lead-in movement kinematics, several conditions had the
472 same duration, peak velocity or distance as the learned training condition
473 (dotted lines in Fig 4). Here we examine the predictive force compensation
474 values over these conditions in more detail (Fig 5). The results for the passive
475 lead-in condition show strong variations over changes in all three parameters
476 (Fig 5A-C). In panel A, lead-in distance is held constant and the movement
477 duration (shown on the x-axis) and speed vary. In panel B, lead-in duration is
478 held constant and the movement distance (shown on the x-axis) and speed
479 vary. In panel C, lead-in speed is held constant and the movement duration
480 (shown on the x-axis) and the distance vary. The dotted lines indicate the
481 training values of lead-in distance and lead-in duration. It can be seen that the
482 recall of predictive compensation was strongly affected by changes in the

483 duration of the movement (shown for constant distance conditions in Fig 5A
484 and constant speed conditions on Fig 5C). There was a strong tuning effect
485 centered around the movement duration used for training, with compensation
486 falling off as movement duration either increased or decreased from that
487 value. However, changing lead-in distance produced different effects. While
488 reducing lead-in distance again reduced compensation, increasing movement
489 distance from the training value had little effect (Fig 5B).

490

491 In the visual lead-in condition, we found slightly less pronounced decay as the
492 some of the kinematics were varied while others remained constant (Fig 5 D-
493 F). Again, it can be seen that compensation was affected by changes in the
494 duration of the movement. Although there was a tuning effect centered around
495 the movement duration using for training, the fall off as duration deviated from
496 the training value was less than in the passive lead-in condition (Fig 5D). As
497 the training distance varied but duration was fixed, we saw the least decay,
498 especially for longer distances (Fig 5E). Finally, as the peak speed was fixed,
499 we found small decay the other variables were changed. (Fig 5F).

500



501

502

503 Figure 6. Comparison of transfer across sensory modality or to reversed
504 visual cursor. **A** Transfer from passive lead-in to visual lead-in or reversed
505 visual lead-in. For comparison the learned force compensation on passive
506 movements is shown. Black circles indicate the results of individual
507 participants. Error bars indicate standard error of the mean. **B** Transfer from
508 visual lead-in to passive lead-in or reversed visual lead-in.

509

510 If we compare the generalization of the predictive compensation across the
511 two experiments, we can see one major finding; namely that the overall tuning
512 effects were much more pronounced for the passive lead-in condition
513 compared to the visual lead-in condition. Visual lead-in generalization showed
514 much less sensitivity to variations in lead-in kinematics. Indeed, whereas
515 passive lead-ins resulted in a 2D monotonic curved surface in the dimensions

516 of duration and distance (Fig. 4A), the corresponding surface for visual lead-
517 ins (Fig. 4B) exhibits a large region consisting of a flat planar surface. To test
518 if this difference in the generalization across kinematics between passive and
519 visual lead-in movements is statistically significant, we performed ANOVAs on
520 the force compensation results (with main effects of kinematic condition (14
521 levels) and lead-in modality (2 levels: visual or passive)). To do so, the force
522 compensation for each testing condition was normalized with respect to the
523 value at the trained condition for each participant. We found strong
524 differences between the generalization results of the visual and passive lead-
525 in movements (lead-in modality) using both frequentist ($F_{1,196}=32.477$;
526 $p<0.001$) and Bayesian ($BF=13.664$) ANOVAs. This highlights a clear
527 difference between visual inputs and passive inputs as a contextual signal for
528 motor adaptation, extending our previous findings (Howard and Franklin,
529 2015; 2016).

530

531 We also investigated how learning opposing force fields with contextual cues
532 in one sensory modality would transfer to the other sensory modality. To
533 investigate this, occasional channel trials were used with a lead-in in the other
534 modality. It can be seen that there is asymmetric transfer between passive
535 lead-in and visual lead-in movements (Fig 6). Although there was partial
536 transfer from passive to visual lead-in movements (Fig 6A) with values
537 reaching just above 20%, there was much less transfer from visual to passive
538 lead-in movements (Fig 6B) with values just under 10%. To compare the level
539 of transfer between the two modalities, the transferred adaptation was scaled
540 according to the final level of adaptation in each experiment. The transfer from
541 passive to visual was significantly larger than the transfer from visual to
542 passive ($F_{1,14}=15.9$, $p<0.001$; $BF=23.2$). Thus, there is a clear asymmetry
543 between the transfer of adaptation between these two sensory modalities.

544

545 Finally, we examined how learning the visual lead-in movement would transfer
546 to a completely reversed visual cursor (with the same duration and distance).
547 To balance conditions and the number of trials across experiments, this was
548 also tested for the passive lead-in. As expected, there was little transfer from
549 passive lead-in to reverse visual lead-ins, although this value was only about
550 75% of the forward visual lead-in transfer. The transfer from the visual training
551 to the reversed visual lead-in was also low (approximately 20%) showing that
552 the predictive compensation is sensitive to the direction of the visual motion.
553 The recall of compensation in the reversed cursor transfer conditions were
554 quite variable, as indicated by the spread of data points (black dots) shown as
555 the mean of each individual participant.

556

557

558 Discussion

559

560 We investigated the kinematic generalization characteristics of passive and
561 visual lead-in movements using a force field interference paradigm.
562 Participants first experienced a lead-in movement and then immediately made
563 an active movement in a curl force field where the field direction was
564 associated with the lead-in movement. Channel trials within the active
565 movement examined how predictive compensation varied as lead-in

566 kinematics were varied. In the first experiment lead-in movements were
567 passive, whereas in the second experiment they were visual. For both
568 modalities, recall of predictive compensation decreased as the duration of the
569 lead-in movements deviated from the training condition. Reducing lead-in
570 distance also reduced compensation but increasing lead-in distance had little
571 effect on the force generalization. Our results show that although passive and
572 visual lead-in movements influence memory formation and recall in
573 subsequent movement, passive motion exhibits narrower generalization
574 characteristics, whereas visual motion is much less sensitive to kinematic
575 change.

576
577 These generalization results further characterize the neural tuning exhibited
578 by lead-in movements, extending beyond the directional tuning seen
579 previously. The observation that passive lead-ins were more sensitive to
580 changes in kinematics than visual lead-ins is consistent with the prior
581 observations examining angular generalization (Howard and Franklin, 2015;
582 Sarwary et al., 2015; Howard and Franklin, 2016). Namely that active and
583 passive tuning was more pronounced and narrower than the wider tuning
584 seen in the visual condition. More recently it was shown that the tuning
585 characteristics of different lead-in modalities could explain why angular
586 variability of active lead-in movements affects the learning rate in two-part
587 movement tasks, whereas no such effect exists for visual lead-in movements
588 (Howard et al., 2017). Our current results suggest that variations in the speed
589 or duration of lead-in movements could provide similar decrements in learning
590 rate, whereas an increase in movement distance would not have much effect.
591 This might have important implications for rehabilitation, suggesting learning
592 and recovery would be faster for training routines with consistent lead-in
593 kinematics. One caveat is that such routines might also produce less
594 generalization across tasks, as the adaptation is more likely to be learned
595 specifically for the trained lead-in movement.

596
597 In both experiments, to examine transfer of adaptation across modality, a
598 visual lead-in cursor motion occasionally replaced the passive lead-in, and
599 vice versa. Interestingly, there was an asymmetric transfer between passive
600 and visual lead-in movements, with partial transfer from passive lead-in
601 movements to visual lead-in movements, but almost no transfer from visual to
602 passive lead-in movements. Transfer could arise because passive lead-in
603 movement partially engages neural mechanisms shared by the visual
604 observation of movement, but not the converse. This result may be due to
605 asymmetry in the connections between the neural substrates. Alternatively, it
606 could arise because the visual feedback pathway has a lower gain due to the
607 uncertainly introduced by the longer time delay associated with visual
608 information (Crevecoeur et al., 2016). The current observation that passive
609 lead-in are more strongly tuned in duration than visual lead-ins, as well as the
610 former results that the absolute level of influence of passive lead-ins (Howard
611 and Franklin, 2015) is higher than for visual lead-in (Howard and Franklin,
612 2016) supports the latter hypothesis.

613
614 The wide ranging results from studies examining contextual cues for learning
615 opposing dynamics have demonstrated that not all sensory signals are able to

616 influence motor learning (Hwang et al., 2003a; 2003b; Wainscott, 2004;
617 Cothros et al., 2009; Addou et al., 2011; Yokoi et al., 2011; Hirashima and
618 Nozaki, 2012; Howard et al., 2013; Sarwary et al., 2015; Nozaki et al., 2016).
619 For example, color has essentially no effect (Howard et al., 2013). In addition
620 to the strong effects of prior movements, it has been shown that particularly
621 effective contextual cues relate to state; for example limb state and physical
622 locations (Hwang and Shadmehr, 2005; Yeo et al., 2015), or different visual
623 locations of the cursor and targets (Hirashima and Nozaki, 2012). Indeed, a
624 location cue could constitute a complete physical shift of the movement task,
625 or just a shift of one of its two essential components; namely a change in the
626 location of the visual feedback, or a change in the physical location of the task
627 with identical visual feedback. Further experiments have shown that future
628 state also effects motor learning in an analogous way (Howard et al., 2015),
629 with this effect depending on movement planning rather than execution
630 (Sheahan et al., 2016).

631
632 On the face of it, it appears that there are multiple types of contextual cues
633 that strongly influence motor memory formation. Here we propose that a
634 factor they all have in common is that they are related to either past, current,
635 or future state of the limb; or are signals used in the estimation of such limb
636 states. That is, setting up the sensorimotor system in a different state before
637 (or at the end of) a movement allows the formation and recall of different
638 motor memories. This suggests that some contextual cues (such as visual
639 lead-in movement or location in the visual workspace) are simply effective
640 because the motor system makes use of these signals within a state
641 estimation mechanism to determine the state of the arm. Such state
642 estimation can only be made on the basis of sensory feedback and efference
643 copy. This hypothesis would be consistent with the observation that visual or
644 proprioceptive movements are as effective an active movement. It would also
645 explain why a visual change of state can be as effective as a complete
646 change in the physical state of the limb. Moreover, it can explain why
647 vestibular inputs could also be used to learn opposing dynamics (Sarwary et
648 al., 2015) but why color cues have much less effect on the adaptation system
649 (Howard et al., 2013).

650
651 In order to reach with our arm to a specific location, our sensorimotor control
652 system needs to know the initial limb state, and then activate the appropriate
653 muscles in a specific pattern to generate forces that bring the arm into the
654 final state to meet the task requirements. To make this movement robust in
655 the face of noise and disturbances, this process does not simply rely on
656 feedforward control, but makes use of sensory feedback of our arm's state,
657 enabling online correction in any task-relevant deviation from the goal of our
658 movement. Arm state can be estimated through the combination of
659 appropriate sensory feedback signals such as proprioception from the skin
660 muscles and joints, visual information, and vestibular inputs. However due to
661 neural signal transmission and processing delays, motor responses to
662 proprioceptive and visual feedback only start producing force after delays of
663 50 ms and 140 ms respectively. Such delays represent a challenge in the
664 design of a feedback control systems, since using direct feedback from
665 delayed signals can lead to instability.

666

667 To deal with delay, Smith proposed an architecture which involves using
668 immediate feedback from the output of a forward model of the plant, (known
669 as an observer), rather than from the plant output directly (Smith, 1959). Miall
670 and Wolpert suggested that the Smith predictor architecture could account for
671 delays in the human motor system (Miall et al., 1993; Miall and Wolpert,
672 1996). This approach is also often use engineering applications, where an
673 observer is used to estimate the state of the plant, which can then be used in
674 feedback control. To make an observer robust to inaccuracies of the forward
675 model and to deal with disturbances, there is normally a state correction
676 pathway term based on actual output error calculated as the difference
677 between the actual output and a delayed prediction of plant output. This
678 results in the state prediction based on the efference copy of the motor
679 command being combined with a correction term based on the delayed
680 sensory feedback, something which has been shown to occur during the
681 control of human movement (Wolpert et al., 1995).

682

683 Within such an observer-based controller framework, the observer performs
684 state estimation for an active movement using efference copy, while
685 improving the estimate using the delayed feedback signals. In the case of a
686 purely visual observation or passive movement of the arm, the observer can
687 still make a state estimate, but only based on the state corrections from
688 feedback. From the premise that state is the key issue in formation of
689 separate motor memory, such a framework would account for the observation
690 that either active, passive or visual lead-in movements would influence state
691 estimation.

692

693 To conclude, we have shown the current and previous observations of lead-in
694 phenomena are consistent with the hypothesis that the human motor system
695 operates as an observer-based controller mechanism, that makes use of a
696 forward model to estimate state. In particular, our results support the proposal
697 (Crevecoeur et al., 2016) that even though the variances of visual positional
698 information is known to be lower than that obtained from proprioception, its
699 longer temporal delay reduces its weighting in state estimation. As a
700 consequence of this, visual information has less effect on the motor system
701 than proprioceptive information, an effect that we have extended to the
702 learning and generalization of opposing dynamics.

703

704 **Author contributions**

705

706 ISH and DWF designed and implemented the study. SF performed data
707 collection. ISH performed data analysis. ISH, SF and DWF wrote the
708 manuscript.

709

710 **Competing interest statement**

711

712 The authors declare that they have no financial, personal, or professional
713 interests that could be construed to have influenced the paper.

714

715 **Acknowledgements**

716

717 Financial support was provided by the Centre for Robotics and Neural
718 Systems at Plymouth University and by the Bavarian State Ministry for
719 Science, Research & the Arts.

720

721

722 **References**

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