

1 Title: The Statistics of Natural Movements are Reflected in Motor Errors

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3 Running head: Statistics of Natural Movements

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41 **The statistics of natural movements are reflected in motor errors**

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47

48 **Abstract**

49

50 Humans use their arms to engage in a wide variety of motor tasks during everyday life.

51 However, little is known about the statistics of these natural arm movements. Studies of

52 the sensory system have shown that the statistics of sensory inputs are key to

53 determining sensory processing. We hypothesized that the statistics of natural everyday

54 movements may, in a similar way, impact on motor performance as measured in

55 laboratory-based tasks. We developed a portable motion tracking system that could be

56 worn by subjects as they went about their daily routine outside of a laboratory setting.

57 We found that the well-documented symmetry bias is reflected in the relative incidence

58 of movements made during everyday tasks. Specially, symmetric and anti-symmetric

59 movements dominate at low frequencies whereas only symmetric movements dominate

60 at high frequencies. Moreover, the statistics of natural movements, that is their relative

61 incidence, correlated with subjects' performance on a laboratory-based phase tracking

62 task. These results provide a link between natural movement statistics and motor

63 performance and confirm that the symmetry bias documented in laboratory studies is a

64 natural feature of human movement.

65

66 Keywords: motor control, arm movement statistics, motor learning, symmetry bias

67

68 **Introduction**

69

70 Studies of sensory systems have shown that their representations are adapted to the
71 statistical structure of natural sensory stimuli (Barlow 1961). For example, the
72 receptive fields of cells in the visual cortex appear to be optimized for the statistical
73 properties of natural scenes (Körding et al. 2004; Olshausen and Field 1996). Although
74 the statistics of natural sensory inputs has received a great deal of attention and detailed
75 characterization (Klein et al. 2003; Ruderman and Bialek 1994; Schwartz et al. 2003),
76 the statistics of natural movements has received little attention (Ingram et al. 2008;
77 Kilbreath and Heard 2005; Slijper et al. 2009). Rather, human movement has been
78 predominantly studied in a laboratory setting using predefined tasks. Just as the study
79 of the sensory system has benefited from analysis of the statistics of natural sensory
80 stimuli, we suggest that the study of the motor system can similarly benefit from an
81 analysis of the statistics of natural movements.

82

83 One feature of movement performance, which has been extensively studied in the
84 laboratory, is the phase relation between left and right body parts during rhythmic
85 movements (Kelso 1995; Kelso 1984; Li et al. 2005; Mechsner et al. 2001; Schmidt et
86 al. 1993; Swinnen et al. 2002; Swinnen et al. 1998). In this context, bimanual
87 movements can be described in terms of the phase relation between the left and right
88 arms (see Figure 1A & B). In common with previous studies, we use the convention
89 that a 0° phase difference between the two arms corresponds to them moving in a
90 mirror symmetric way in extrinsic space with respect to the mid-sagittal plane. In

91 muscle based definitions of symmetry, such 0° phase differences correspond to the use
92 of homologous muscles (Kelso 1984).

93

94

95 Studies of symmetry bias clearly demonstrate that not all movements are equally easy
96 to perform and highlight two cardinal features. First, at low frequencies both symmetric
97 and anti-symmetric movements (phase difference between the two arms of 0° and 180° ,
98 respectively) can be performed easily and stably, whereas movements with
99 intermediate phase relations are more difficult to perform. Second, as the frequency of
100 movement increases, only symmetric movements can be performed stably and all other
101 phase relations tend to transition to a symmetric mode (Tuller and Kelso 1989;
102 Wimmers et al. 1992). The properties of this symmetry bias have been extensively
103 documented and modeled using oscillator and nonlinear dynamical systems models.
104 These models can explain the two modes of observed stable behaviors as well as the
105 discontinuous phase transitions between them (Haken et al. 1985). Here we
106 hypothesize that the symmetry bias will also be present in everyday movements.
107 Moreover, we suggest that the incidence of particular movement phases, that is how
108 often they occur, will be related to performance. For example, previous laboratory
109 studies have found that measures of performance depend on the logarithm of the
110 number of training trials (Heathcote et al. 2000) and this suggests that the logarithm of
111 the incidence of different phase relations in everyday movements (corresponding to
112 training) may also relate to measures of laboratory performance. This hypothesis
113 would not preclude a dynamical systems model accounting for the empirical data.

114

115 To examine whether performance is related to the statistics of natural movements we
116 developed a wearable motion tracking system to record the arm movements of human

117 subjects as they went about their daily life. The system allowed our subjects to engage
118 spontaneously in normal everyday tasks while we recorded the kinematics of their right
119 and left arms. Our results suggest that the symmetry bias reported from laboratory-
120 based tasks is present in natural everyday movements. Moreover, when the same
121 subjects performed a laboratory-based tracking task that measured error as a function of
122 different phase relationships between the arms, we found that the incidence of natural
123 movements correlated with subject performance in the task. The form of the phase-
124 related errors on the task, as well as the incidence of particular phase relations in the
125 natural dataset replicated the “seagull effect” (Kelso 1995; Tuller and Kelso 1989).
126 Moreover, the relationship between the errors and incidence was well fit using a
127 logarithmic relation, consistent with previous studies (Heathcote et al. 2000). These
128 results represent a novel contribution to the field by firstly documenting the relative
129 phase relations that occur in natural arm movements and secondly demonstrating that
130 the incidence of these phase relations is correlated with performance.

131

132

133 **Materials and Methods**

134

135 *Data acquisition*

136

137 After providing written informed consent, 6 subjects took part in the experiment. A
138 local ethics committee approved the experimental protocol. Two of the participants
139 were authors (ISH & JNI) and 4 participants were naïve to the purpose of the
140 experiment. No qualitative differences were observed between the subjects. Liberty
141 Polhemus sensors were attached to the left and right upper arms, just above the elbow,
142 and also to the wrists (Figure 1C). Subjects carried a backpack containing the modified

143 Liberty hardware, battery power supply and a computer logging the data at 120 Hz. The
144 Polhemus transmitter was firmly attached to the participant's chest (Figure 1C). The
145 initial version of the backpack weighed about 11 kg and allowed subjects to carry out
146 most everyday tasks and move around freely both indoors and outdoors. The design
147 was later improved, reducing its weight to 5.5 kg. In total over 31 hours of recording
148 was obtained from the subjects. The first 3 subjects wore the original backpack design
149 (8.8, 9.1 and 3.9 hours recorded in blocks of about 1 hour) and the final 3 subjects wore
150 the improved design (3.1, 3.1 and 3.0 hours also recorded in blocks of about 1 hour).
151 Several of the subjects wore backpacks regularly rather than using a briefcase so were
152 accustomed to performing daily tasks in the presence of a backpack. Results were
153 qualitatively the same with both types of backpack and across the subjects, independent
154 of whether they regularly wore a backpack. Subjects were told to avoid close proximity
155 to large metallic objects which could distort the measurements and informed that signal
156 quality could be monitored using a visible status indicator. Subjects were requested to
157 perform typical activities they would do normally, and questioning revealed that
158 recording sessions included a wide range of activities such as walking, going shopping,
159 reading, doing jigsaw puzzles, constructing model airplanes, food preparation, and
160 having lunch.

161

162 *Joint angle analysis*

163

164 Each sensor provided position and orientation which was used to calculate the elbow
165 angles and the angular speed of the elbow and shoulder joints of each arm. The
166 Polhemus system records the 3D position (3x1 vectors T_k^t) and 3D orientation (3x3
167 matrices R_k^t) of each sensor with respect to the transmitter (the subscript $k = 1, 2$ refers

168 to the upper and lower sensors for a particular arm and the superscript t is the time
169 sample). The centre of rotation for the elbow joint can be estimated from the sensors
170 proximal and distal to the joint (Figure 1D). Each sensor can be considered to represent
171 a coordinate system that translates and rotates with the sensor. D_k is a vector which
172 defines the centre of rotation of the elbow joint relative to sensor S_k (Figure 1D) , That
173 is, using the coordinate system defined by the position and orientation of sensor S_k ,
174 vector D_k corresponds to the location of the elbow joint within that coordinate system.
175 D_k is constant because the relative locations of the sensors and elbow joint do not
176 change as the arms move. We use the measurements from each sensor to estimate the
177 location of the center of the elbow joint in the coordinate system of the transmitter: that
178 is $R_1^t D_1 + T_1^t$ and $R_2^t D_2 + T_2^t$. As both of these represent the same location, that is, the
179 centre of the elbow joint in the coordinate system of the transmitter, they should
180 coincide (subject to noise in the sensor readings and the fact that the elbow joint does
181 not have a single point of rotation). Therefore, we can estimate D_1 and D_2 by finding
182 their values that minimize the error between the two estimates across time samples.
183 Specifically, we wish to minimize the squared error given by

184

$$185 \quad E = \left\langle \left[(R_1^t D_1 + T_1^t) - (R_2^t D_2 + T_2^t) \right]^T \left[(R_1^t D_1 + T_1^t) - (R_2^t D_2 + T_2^t) \right] \right\rangle$$

186

187 where $\langle \rangle$ denotes the average across time samples. For simplicity, we define

188 concatenated matrices and vectors

189

$$190 \quad R^t = [R_1^t \mid -R_2^t], \quad D = \begin{bmatrix} D_1 \\ - \\ D_2 \end{bmatrix}$$

191

192 and $T^t = T_1^t - T_2^t$

193

194

195 That is

196 $R^t = \begin{bmatrix} R_{1,1}^t & R_{1,2}^t & R_{1,3}^t & -R_{2,1}^t & -R_{2,2}^t & -R_{2,3}^t \\ R_{1,2,1}^t & R_{1,2,2}^t & R_{1,2,3}^t & -R_{2,2,1}^t & -R_{2,2,2}^t & -R_{2,2,3}^t \\ R_{1,3,1}^t & R_{1,3,2}^t & R_{1,3,3}^t & -R_{2,3,1}^t & -R_{2,3,2}^t & -R_{2,3,3}^t \end{bmatrix}$ which is a 3x6 matrix, where the

197 first subscript on each element identifies the original rotation matrix and the second

198 subscript defines its corresponding element. As stated above, the superscript t defines

199 time. Similarly,

200 $D = \begin{bmatrix} D_{1_1} \\ D_{1_2} \\ D_{1_3} \\ D_{2_1} \\ D_{2_2} \\ D_{2_3} \end{bmatrix}$ which is a 6x1 vector where the first subscript on each element identifies

201 the original displacement vector and the second subscript defines its corresponding

202 element.

203

204 Thus, we can re-write the expression for error as

205

206 $E = \langle (R^t D + T^t)^T (R^t D + T^t) \rangle$

207 To find the minimum we differentiate with respect to D and equate it to zero, that is

208 $\frac{dE}{dD} = 0$

209 which gives

$$210 \quad \langle ((R^t)^T R^t D + (R^t)^T T^t) \rangle = 0$$

211 thus

$$212 \quad D = - \langle (R^t)^T R^t \rangle^{-1} \langle (R^t)^T T^t \rangle$$

213

214 To calculate the centre of the elbow joint for each time point, we take the average of
215 the estimates derived from the proximal and distal sensors

$$216 \quad E^t = (R_1^t D_1 + T_1^t + R_2^t D_2 + T_2^t) / 2$$

217 where E^t is the location of the elbow joint, in the coordinate frame of the transmitter,
218 at time t . The elbow angle was then calculated using the cosine rule as the angle
219 between the vectors linking the proximal sensor to the elbow joint ($T_1^t - E^t$) and the
220 distal sensor to the elbow joint ($T_2^t - E^t$). The elbow speed was obtained by computing
221 the difference between elbow angles over consecutive time points and dividing by the
222 sampling interval Δt .

223

224 To calculate the angular speed of the shoulder joint we use the fact that rotation of a
225 rigid object, such as the upper arm, can be represented by a single scalar rotation angle
226 about a given axis. This is the basis of the quaternion representation that specifies both
227 the axis of rotation (3 parameters defining the vector for the axis of rotation) and the
228 (scalar) angle of rotation. To calculate the shoulder speed we computed the change in
229 rotation angle for the upper arm between consecutive time samples. To do this we first
230 calculated the change in the rotation matrix between time samples $\Delta R^t = (R_1^t)^{-1} R_1^{t+1}$.

231 This rotation matrix was used to determine the angular change ($\Delta\theta'$) using standard
232 conversion to quaternion form

$$233 \quad \Delta\theta' = 2\cos^{-1}\left(\frac{1}{2}\sqrt{1 + \Delta R'_{11} + \Delta R'_{22} + \Delta R'_{33}}\right)$$

234 where $\Delta R'_{kk}$ is the (k, k) the element of the matrix. The shoulder rotation speed is then
235 given by $\Delta\theta' / \Delta t$. We performed these analyses for the left and right arms.

236

237 *Wavelet phase analysis*

238

239 Short-term frequency-dependent phase analysis was performed on the two elbow angle
240 time series. Because the elbow angle depends on the relative angle between the two
241 sensors on each arm, it is less sensitive than the raw data to any movements of the
242 transmitter. Moreover, in distinction to the convention needed to define symmetry in
243 terms of movement of the limbs in extrinsic space, there is no ambiguity when defining
244 symmetry in terms of the angular motion of the elbow joints (see Figure 1A & B).

245 Position trajectories of point-to-point reaching movements are similar in form to a half
246 cosine and thus have an associated fundamental frequency and phase. An analysis was
247 required that was able to extract the phase of such signals as a function of frequency.

248 Of course, there will also be movements involving oscillations of the arms, especially
249 during activities such as walking, with the arms swinging. Although short-term Fourier
250 analysis (FFT) can be used to estimate phase, it is not as effective in dealing with
251 localized events such as discrete moments. One way to improve this is to match
252 window length as a function of frequency. In this way, the window length will better
253 fit a discrete event in the signal. This is effectively what wavelet analysis does – the
254 time window of the wavelet is a function of its bandwidth (Mallet 1999). The Hilbert

255 transform is often used to decompose a signal into instantaneous phase and amplitude.
256 However it is not appropriate here since it does not provide the necessary frequency-
257 dependent phase analysis. Moreover, wavelet analysis is being increasingly applied to
258 biological signals such as EEG (Selesnick et al. 2005).

259

260 We performed a Dual-Tree Complex Wavelet Transform (DT-CWT) (Kingsbury 2001)
261 on the left and right elbow angles, using 8 levels of wavelet decomposition. The
262 complex nature of the sub-band outputs from this transform produces analytic
263 waveforms that have both amplitude and phase in sub-bands that are each
264 approximately one octave wide. The DT-CWT has the important property of shift
265 invariance, which ensures that all input signals are analyzed in equivalent ways.

266

267 The analysis was repeated several times on re-sampled input data so as to shift the
268 centre frequencies of the wavelet analysis, resulting in 30 overlapping bands ranging
269 from a 0.45-0.9 Hz band to a 3.2-6.4 Hz band. For each band we obtained the time
270 series of phase relations and amplitude in the left and right elbow angle signals. To
271 obtain a relative incidence for each phase relation for a band, we first calculated a
272 weighted incidence using the cross power (i.e. the product of the left and right
273 amplitudes). As phase is always defined, even when the cross power is close to zero,
274 this ensured the statistics only reflected the phase relations that occurred during
275 significant movements of both arms, thereby excluding periods in which one or both of
276 the arms were stationary. As such, the contributions of unimanual movements to the
277 relative phase distributions are suppressed.

278

279 *Computation of relative phase incidence*

280

281 Within a frequency band the relative phase incidences were first allocated to one of 18
282 bins each 20° wide. The total incidences across all bins in a given frequency band were
283 then normalized to sum to 1. Statistical tests were performed for each subject using t-
284 tests of the relative incidence of phase relations at $0/360^\circ$ (symmetric) versus 180°
285 (anti-symmetric), and at 180° versus the average incidence at 90° and 270° .

286

287 Similar phase analyses were performed for movements of the distal sensors for the
288 three Cartesian axes, except that in this case only the low frequency band of 0.9 – 1.8
289 Hz was examined.

290

291 *Validation of wavelet phase analysis*

292

293 We validated the wavelet phase analysis on two different datasets. For the first dataset,
294 we generated synthetic left and right elbow angle data by simulating two independent
295 random walks. For the second dataset, we inserted a set of relative time shifts between
296 the left and right elbow angles from the natural movement dataset. In all cases the data
297 was analyzed at low (0.45-0.9 Hz) and high frequency bands (3.2-6.4 Hz). Analysis of
298 the random walk dataset resulted in uniform phase incidences at both low and high
299 frequency bands, as expected. For the time shifted datasets, analysis resulted in the
300 expected shifts in the relative phase incidences. Full details of these two validations are
301 available in the Supplementary Material section.

302

303 *Conditioning for similar versus different joints*

304

305 We also performed a phase analysis of the positions of the distal sensors at the wrists in
306 extrinsic space, for subsets of the data based on whether the arms were moved

307 predominantly by rotations around the same or different joints (see Figure 5A & C). If
308 the phase distributions are similar between the two subsets of the data, this would
309 suggest that the symmetry bias (defined in external space) does not occur because we
310 use homologous muscle groups, as has been previously suggested (Kelso 1984). Elbow
311 and shoulder angular speeds were used to divide the data into either a “similar-joint”
312 subset or “dissimilar-joint” subset. The similar-joint subset included all the data where,
313 for both arms, either the angular speeds of the shoulders were greater than that of the
314 elbows or the angular speeds of the elbows were greater than that of the shoulders
315 (Figure 5A). In this case, movement of the distal sensors on both arms was dominated
316 by either both shoulders or by both elbows. In contrast, the dissimilar-joint subset
317 included the compliment of the similar-joint subset. Specifically, it included data where
318 the angular speed of the shoulder in one arm was greater than that of the elbow and in
319 the other arm or the converse was true (Figure 5C). In this case, movement of the distal
320 sensors on both arms was dominated by different joints on each arm.

321

322 For both subsets of dataset we calculated the phase relations for each of the three
323 Cartesian axes for movement of the distal sensor using the same methods as above. The
324 phase relations for the three Cartesian axes were then averaged to calculate the relative
325 incidence. We use the convention that a 0° phase difference between the two arms
326 corresponds to them moving in a mirror symmetric way with respect to the mid-sagittal
327 plane.

328

329 *Tracking paradigm*

330

331 To obtain a quantitative measure of performance at different phase relations for the
332 same subjects who participated in the natural movement data collection, subjects were

333 also required to perform a phase tracking task. The tracking task was designed to
334 compare phase tracking performance with the incidence of relative phases between the
335 distal sensors at the wrists in the natural movement dataset. The task was similar to that
336 used by previous studies of symmetry bias (Tuller and Kelso 1989). Specifically,
337 subjects were required to track two targets in a virtual reality system, as shown in
338 Figure 1E (Howard et al. 2009). Each target moved sinusoidally towards and away
339 from the body in the horizontal plane over a range of 16 cm at 0.5 Hz (all subjects) or
340 1.6 cm at 5.0 Hz (4 subjects). Movement amplitude was scaled down for the higher
341 frequency to maintain the same peak movement velocities. We chose the frequencies of
342 0.5 Hz and 5 Hz as we wanted to use two values that were quite far apart in terms of
343 the distribution of phases from our natural dataset to test the logarithmic law
344 hypothesis.

345

346 Subjects held the handles of two robotic manipulanda which were separated by 13 cm
347 and were used to record hand movements at 1000 Hz (Howard et al. 2009). The
348 handles were constrained to move in channels limiting movements to a single degree-
349 of-freedom (DOF). The position of each handle was represented by its own virtual
350 cursor that was used to track each of the two targets. Although the movement of each
351 hand was constrained to a single DOF in extrinsic space, the arm itself was
352 unconstrained with regards to joint recruitment.

353

354 Subjects each performed 20 trials of 15 s duration at each of the 18 relative phases in a
355 pseudorandom order. On each trial the two targets moved with a relative phase that was
356 chosen out of the set (0, 20, ... 340°). The last 13 s of each trial was analyzed using
357 wavelets as described above for the distal sensor positions. This allowed us to

358 determine the relative phase between the two hands and thus compute the RMS phase
359 error for the tracking task.

360

361 We fit the incidence of relative phases for the distal sensors from the natural movement
362 dataset to the performance data from the tracking task. Specifically, we analyzed wrist
363 translation in the y-axis (Figure 1E), which is the direction used for the tracking task.
364 To estimate incidence at low frequencies, we averaged over several low-frequency
365 bands to achieve a wider bandwidth (0.27-1.2 Hz) than could be achieved from a single
366 wavelet band. This ensured the results included components that covered the low
367 frequencies appropriate for the 0.5 Hz tracking task. For the 5.0 Hz tracking task, a
368 single wavelet band was sufficient (3.4-6.8 Hz).

369

370 **Results**

371

372 We attached sensors to the elbows and wrists of six volunteers who wore a backpack
373 containing motion tracking equipment. The sensors recorded the position and
374 orientation of both wrists and elbows over extended periods of time (3.0-9.1 hours per
375 subject). The boundary enclosing the 0.9 percentile of the distributions of wrist and
376 elbow positions for one subject are shown in Figure 2. This shows that the majority of
377 wrist and elbow positions fall within a region close to the body.

378

379 From this natural dataset we calculated the phase relations between flexion-extension
380 movements of the right and left elbow for a range of movement frequencies (Figure 3).
381 For each frequency band we examined how often each phase relation was observed
382 during natural movement which allowed us to determine the relative incidence of each
383 phase relation. Figure 3A illustrates how this measure of relative incidence changes

384 with increasing frequency, showing a progression from a bimodal to unimodal
385 distribution as the frequency increases.

386

387 At low movement frequencies (0.45-0.90 Hz, Figure 3B) each subject's distribution
388 was bimodal with symmetric (phases at $0^\circ/360^\circ$) movements occurring significantly
389 more often than anti-symmetric (phase of 180°) movements ($p < 0.01$, average ratio of
390 incidence of 2.0 across subjects). Moreover, anti-symmetric movements at 180°
391 occurred significantly more often than the intermediate phase relations of 90° ($p < 0.05$)
392 and 270° ($p < 0.05$). At higher movement frequencies (3.2-6.4 Hz, Figure 3C) the
393 distribution became unimodal with symmetric movements still occurring significantly
394 more often than anti-symmetric movements ($p < 0.01$, average ratio of incidence of 2.0
395 across subjects). However, at these higher frequencies the second peak for anti-
396 symmetric movements was no longer present and their incidence was significantly less
397 than those of 90° ($p < 0.001$) and 270° ($p < 0.01$). Taken together, these results parallel
398 laboratory observations showing that movements with a phase relation other than
399 symmetric and anti-symmetric are especially difficult and that anti-symmetric
400 movements become unstable as the frequency of movement increases (Kelso 1984).

401

402 Another fundamental issue that has been addressed in laboratory experiments
403 (Mechsner et al. 2001; Swinnen et al. 1998) relates to the coordinate system for the
404 symmetry bias. Elbow joint angles were used for the phase analysis above because
405 these were most precisely measured with our apparatus (see Methods). Consequently
406 such an analysis quantified symmetry bias in joint (intrinsic) space. An important
407 question is whether the symmetry bias is similarly present in extrinsic space. This
408 would be expected if the demands on natural motor tasks are defined in extrinsic space.
409 To examine this, we compared the relative incidence of phase relations for the distal

410 sensors on the wrist moving in extrinsic space (Figure 4A and B) with that of the elbow
411 angles in joint space (Figure 4C and D). Interestingly, the incidence of 180° phase is
412 significantly higher for the movements defined in extrinsic space than those defined in
413 intrinsic space ($p < 0.05$ for each subject; averaged incidence ratio = 1.6). Similarly, the
414 incidence of 0° phase was significantly lower ($p < 0.01$ for each subject; averaged
415 incidence ratio = 0.9). This suggests a stronger component of anti-symmetric
416 movement for task-based (extrinsic) coordinates.

417

418 Another important question is whether the bias favoring symmetric movements arises
419 because they are executed in the same direction in extrinsic space or because they
420 involve movements around the same joints. To address this issue in the natural
421 movement dataset, we split the distal sensor data recorded at the wrists into two parts.
422 The first part contained samples in which movement of the left and right arms
423 predominately resulted from rotations around similar joints (Figure 5A). The second
424 part contained samples in which movement of the arms predominately resulted from
425 rotations around the dissimilar joints (Figure 5C); (see Methods for details). For these
426 two datasets, we analyzed phase relations between the two distal sensors in a mid
427 frequency band (0.9 – 1.8 Hz). We chose this range so we could examine whether the
428 bimodal peaks in incidence for symmetric and anti-symmetric movements were
429 different between the two subsets of the data.

430

431 For both the similar- and dissimilar-joint subsets of the natural movement data the
432 distributions were bimodal, preserving the peaks in incidence for symmetric and anti-
433 symmetric movements (Figure 5B and 5D, respectively). Moreover, there were no
434 significant differences in the relative incidences between the two datasets at either 0° or
435 180° phase. Thus the effect of selecting movements on the basis of different joint usage

436 preserves the basic form of the distributions. This finding is in close correspondence
437 with experimental data that shows that the symmetry bias is present in extrinsic
438 coordinates, regardless of the joints used (Mechsner et al. 2001; Swinnen et al. 2002).

439

440 Previous studies have shown a relationship between the amount of training on
441 perceptual tasks and performance (Heathcote et al. 2000). To investigate the
442 relationship between performance and the relative incidence of movement phases in our
443 natural movement dataset, subjects performed a bimanual tracking task in a virtual
444 reality environment (Figure 1E, see Methods). This required subjects to track two
445 targets which moved sinusoidally at various phase relations at a low (0.5 Hz) and high
446 frequency (5.0 Hz). The phase error at 0.5 Hz on the tracking task (Figure 6A) is small
447 for symmetric ($0/360^\circ$) and anti-symmetric (180°) movements, mirroring the relative
448 incidence of these phases in the natural movement dataset (Figure 6B). Similarly, the
449 phase error at 5Hz on the tracking task (Figure 6C) mirrors the relative incidence of
450 these phases in the natural movement dataset (Figure 6D). However, in this case there
451 was a stronger tendency to move symmetrically on the tracking task as indicated by the
452 almost linear relationship between error and phase between $0-90^\circ$ and $270-360^\circ$ (Figure
453 6C). To quantify further the relationship between phase incidence in our natural
454 movement dataset and performance on the tracking task, we used linear regression to fit
455 the performance errors to the log incidence of the phases. We found a good fit at both
456 low ($r^2=0.86$ $p<0.001$, Figure 6E) and high ($r^2=0.88$, $p<0.001$, Figure 6F) frequencies.
457 This demonstrates that the logarithmic law for training is also present between the
458 natural incidence of a movement and motor performance on a laboratory task.

459

460 **Discussion**

461

462 We recorded over 30 hours of natural arm movements from 6 subjects who were free to
463 engage spontaneously in everyday tasks. Despite the large range of possible
464 movements, we found that during most normal everyday tasks the arms are confined to
465 a small volume of space around the body. We also analyzed the phase relations
466 between the movements of the left and right arms and found that the relative
467 occurrence of particular phases supports results from previous studies of symmetry bias
468 in humans. Specifically, we found that at low frequencies both symmetric and anti-
469 symmetric movements were prevalent whereas at higher frequencies symmetric
470 movements became increasingly dominant. At low frequencies, the form of the phase
471 incidence curve reflected the “seagull effect” previously described for finger tapping
472 experiments (Tuller and Kelso 1989).

473

474 The aim of the current study was to acquire data for movements that corresponded to
475 what subjects do during everyday activities. As there are many laboratory studies that
476 only look at specific movements or tasks, our study was specifically designed to avoid
477 such constraints. To achieve this we let subjects go about their daily routine with only
478 a few constraints, such as avoiding large metallic objects or water. We examined the
479 statistics of the movements and did not try to categorize the specific tasks that subjects
480 were performing. However, it is important that the samples we acquired were
481 representative of normal activities and we therefore collected over 30 hours of
482 kinematic data. Although subjects may have engaged in different tasks during the
483 recoding period, the statistics across subjects were very similar as demonstrated by the
484 low standard errors (Figures 3 - 6). This suggests that we have captured representative
485 statistics in all our subjects.

486

487 An interesting question arising from the current study is whether the symmetry bias
488 exists because successful interaction with the environment requires both symmetrical
489 movements (such as bimanual grasping of objects) and anti-symmetric movements
490 (such as moving a hand held object laterally). Alternatively, the symmetry bias may be
491 an immutable property of the musculoskeletal and nervous systems. As such, it would
492 fundamentally constrain the way we can interact with the world. Previous studies have
493 assumed that fundamental constraints on performance arising from the perceptual
494 (Mechsner et al. 2001) or motor systems (Swinnen et al. 2002) explain the symmetry
495 bias. Indeed Mechsner et al reported that symmetry in external space, or visual
496 symmetry, can override this bias. However, as shown here and in laboratory-based
497 experiments, the symmetry bias is present in extrinsic task space. This may be
498 understood in terms of the requirement to interact with the external world. In contrast,
499 constraints on the musculoskeletal and nervous systems would be expected to be
500 manifest in intrinsic (joint space) coordinates. For example, it is intuitively obvious
501 why symmetric and anti-symmetric movements may be common in bimanual object
502 manipulation tasks (Figure 7). If we wish to simultaneously bring both hands together
503 from different positions to pick up an object this requires phases of 0° or 180° ,
504 depending on the axis. For example, bringing the hands laterally together to grasp an
505 object from the left and right or moving them apart to release it require movement
506 phases of 0° (Figure 7A). In contrast, bringing the hands vertically together to grasp an
507 object from above and below or moving them apart to release it require movement
508 phases of 180° (Figure 7B). Once the object is grasped, transporting it then requires
509 movement with phases of either 0° or 180° , depending on the direction of transport. For
510 example, moving a bimanually grasped object left or right requires movement phases
511 of 180° (Figure 7C). In contrast, moving a bimanually grasped object up or down

512 requires movement phases of 0° (Figure 7D). Consequently, interaction with objects
513 typically requires movements with phases at 0° and 180° in extrinsic space.

514

515 Another interesting question concerns the relationship between the incidence of
516 particular movements and performance. It is well known that training on a task
517 improves performance, but with diminishing returns as training increases (Newell and
518 Rosenbloom 1981). Specifically, relative performance is often related to the log of the
519 number of training trials. This logarithmic dependence of performance on training
520 appears to be a universal law of learning that applies to a wide range of cognitive
521 problems such as multiplication, visual search, movement sequence learning, rule
522 learning and mental rotation (Heathcote et al. 2000). In the current study, we found
523 evidence for the existence of the logarithmic relationship between natural movement
524 statistics and performance. This suggests that the log incidence of a movement may be
525 a general predictor of motor performance and may provide a parsimonious explanation
526 for the existence of the symmetry bias.

527

528 As previously discussed, the symmetry bias does not appear to be an immutable
529 property of the musculoskeletal and nervous systems. For example, extensive training
530 on the novel phase relation of 90° over the course of several days improves
531 performance at this phase, but leads to a decrement in performance at other phases
532 (Schoner and Kelso 1988; Zanone and Kelso 1992). Such training significantly changes
533 the distribution of phases experienced by subjects and the observed results reflect these
534 novel statistics. Similarly, if subjects are trained at new polyrhythms (Summers et al.
535 1993), significant improvement is observed (Klaiman and Karniel 2006). Interestingly,
536 improving at one class of movement can come at the expense of a decrease in
537 performance at others (Van Damme et al. 2002). One hypothesis consistent with these

538 results is that there are limited neural resources available and that improvement at one
539 phase necessarily involves a decrement in performance at others. This hypothesis is
540 further supported by the finding that training on a particular task increases the size of
541 its neural representation (Classen et al. 1998; Elbert et al. 1995; Kaas 1991; Karni et
542 al. 1995). Interference between two similar motor tasks which are performed
543 sequentially also suggests competition for finite neural resources (Brashers-Krug et al.
544 1996; Caithness et al. 2004; Miall et al. 2004; Tong et al. 2002). Taken in the context
545 of the current study, this suggests that neural resources are indeed finite and that the
546 statistics of natural movements will influence their allocation. This view provides a
547 potential link between the occurrence of particular movements and performance.

548

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550

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650

651 **Figure legends**

652

653 Figure 1: **A** Front view of subject showing movements at the elbow in joint space and
654 at the hands in extrinsic space for the x-axis and z-axis. Dotted line shows the mid-
655 sagittal plane. The directions of symmetric movements are shown by corresponding
656 pairs of either open arrowheads on both sides or filled arrowheads on both sides. The
657 directions of anti-symmetric movements are shown by corresponding pairs of open
658 arrowheads on one side with filled arrowheads on the other. **B** Top view of subject, as
659 in A, showing movements at the elbow in joint space and at the hands in extrinsic space
660 for the x-axis and y-axis. **C** The transmitter and sensor locations shown for the right
661 arm with S_1 located on the upper arm and S_2 on the lower arm near the wrist. The
662 transmitter is mounted on the chest over the sternum and defines the coordinate system
663 for position and orientation of the sensors. Sensors S_3 and S_4 (not shown) are similarly
664 located on the left arm. **D** Details of the joint centre analysis showing sensors proximal
665 and distal to the elbow joint with rotations (R_1 and R_2 for sensors 1 and 2 respectively)
666 and translations (T_1 and T_2) relative to transmitter. The vectors D_1 and D_2 describe the
667 location of the joint centre relative to the upper and lower sensors, respectively. **E**
668 Experimental setup for the phase tracking task. The coordinate system is marked on the
669 figure and the tracking movements were made along the y-axis.

670

671 Figure 2: Distribution of hand and elbow positions. Front (**A**) and size (**B**) view
672 showing the outer boundaries of regions which represent 90% of all locations visited by
673 a typical subject's wrists (green and red) and elbows (only left visible, cyan) during 8.8
674 hours of movement. Small isolated regions have been removed for clarity.

675

676 Figure 3: Distributions of the phase differences in the natural movement dataset
677 between the elbows averaged over 6 subjects. Phase of 0-180° corresponds to the left
678 elbow leading the right. **A** Average incidence against frequency. **B** Average (line) and
679 standard error (shading) for the 0.45-0.9 Hz frequency band. **C** Average (line) and
680 standard error (shading) for the 3.2-6.4 Hz frequency band.

681

682 Figure 4: Comparison of the relative incidence of phase relations in the 0.9-1.8 Hz
683 frequency band for movements of the distal wrist sensors in extrinsic space versus
684 elbow angles in intrinsic space. **A** Front view of subject showing movements in
685 extrinsic space. Arrowheads indicate the direction of symmetric and anti-symmetric
686 movements, as in Figure 1. **B** Relative incidence of phase relations for movements of
687 the distal wrist sensors in extrinsic space. Average over subjects (line) and standard
688 error (shading). **C** Front view of subject showing elbow movements in intrinsic space.
689 Arrowheads indicate the direction of symmetric and anti-symmetric movements, as in
690 Figure 1. **D** Relative incidence on phase relations for movements of the elbows in
691 intrinsic space, plotted as in B.

692

693 Figure 5: Comparison of the relative incidence of phase relations in the 0.9-1.8 Hz
694 frequency band for movements of the distal wrist sensors in extrinsic space conditioned
695 on the use of similar or dissimilar joints. **A** Front view of subject showing movements
696 arising from rotations around similar joints in each arm. **B** Relative incidence of phase
697 relations for movements of the distal wrist sensors in extrinsic space generated by
698 rotations around similar joints. Average over subjects (line) and standard error
699 (shading). **C** Front view of subject showing movements arising from rotations around
700 dissimilar joints in each arm. **D** Relative incidence of phase relations for movements of

701 the distal wrist sensors in extrinsic space generated by rotations around dissimilar
702 joints, plotted as in B.

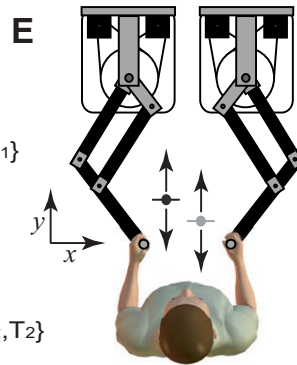
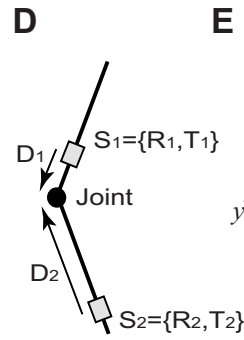
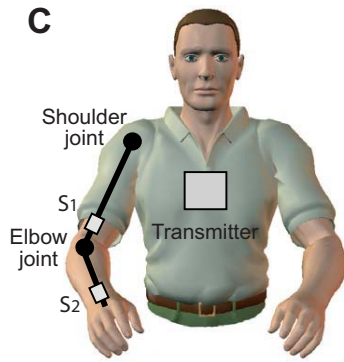
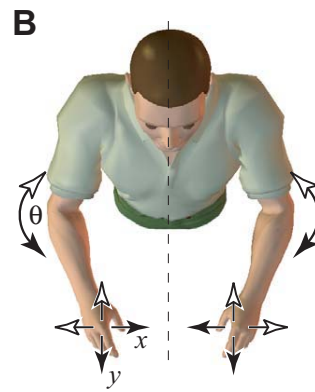
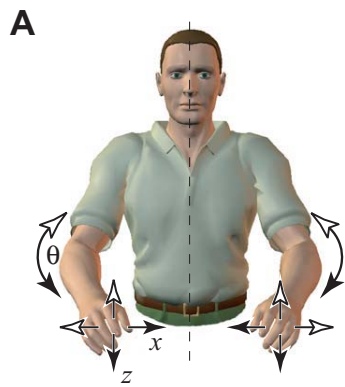
703

704 Figure 6: Performance on the laboratory-based phase tracking task compared with
705 incidences of relative phase in the natural movement dataset at low frequencies (0.5 Hz,
706 A, B & E) and high frequencies (5 Hz, C, D & F). **A, C** The root mean squared error
707 (RMSE) of phase in the tracking task is plotted as a function of the phase angle. **B, D**
708 The incidence of relative phase along the y-axis in the natural movement dataset is
709 plotted as a function of the phase angle. **E, F** Error in the tracking task plotted as a
710 function of the log incidence of relative phase in the natural movement dataset.

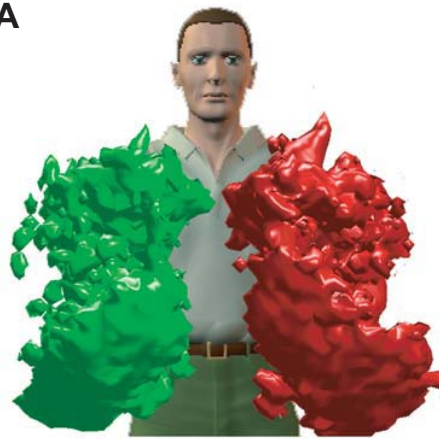
711

712 Figure 7: Bimanual phase relations during object manipulation. Arrowheads on the left
713 and right indicate the direction of symmetric and anti-symmetric movements, as in
714 Figure 1. **A** Bringing the hands laterally together to grasp an object (G) from the left
715 and right or moving them apart to release it (R) require symmetric movements. **B**
716 Bringing the hands vertically together to grasp an object (G) from above and below or
717 moving them apart to release it (R) require anti-symmetric movements. **C** Moving a
718 bimanually grasped object left (L) or right (R) requires anti-symmetric movements. **D**
719 Moving a bimanually grasped object up (U) or down (D) requires symmetric
720 movements.

721



A



B

