Statistics of Natural Movements Are Reflected in Motor Errors

Ian S. Howard,1 James N. Ingram,1 Konrad P. Körding,2 and Daniel M. Wolpert1
1Department of Engineering, University of Cambridge, Cambridge, United Kingdom; and 2Physiology and Physical Medicine and Rehabilitation, Rehabilitation Institute of Chicago, Northwestern University, Chicago, Illinois

Submitted 6 January 2009; accepted in final form 9 July 2009

Howard IS, Ingram JN, Körding KP, Wolpert DM. Statistics of natural movements are reflected in motor errors. J Neurophysiol 102: 1902–1910, 2009. First published July 15, 2009; doi:10.1152/jn.00013.2009. Humans use their arms to engage in a wide variety of motor tasks during everyday life. However, little is known about the statistics of these natural arm movements. Studies of the sensory system have shown that the statistics of sensory inputs are key to determining sensory processing. We hypothesized that the statistics of natural everyday movements may, in a similar way, influence motor performance as measured in laboratory-based tasks. We developed a portable motion-tracking system that could be worn by subjects as they went about their daily routine outside of a laboratory setting. We found that the well-documented symmetry bias is reflected in the relative incidence of movements made during everyday tasks. Specifically, symmetric and antisymmetric movements are predominant at low frequencies, whereas only symmetric movements are predominant at high frequencies. Moreover, the statistics of natural movements, that is, their relative incidence, correlated with subjects’ performance on a laboratory-based phase-tracking task. These results provide a link between natural movement statistics and motor performance and confirm that the symmetry bias documented in laboratory studies is a natural feature of human movement.

INTRODUCTION

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

One feature of movement performance, which has been extensively studied in the laboratory, is the phase relation between left and right body parts during rhythmic movements (Kelso 1984, 1995; Li et al. 2005; Mechsner et al. 2001; Schmidt et al. 1993; Swinnen et al. 1998, 2002). In this context, bimanual movements can be described in terms of the phase relation between the left and right arms (see Fig. 1, A and B). In common with previous studies, we use the convention that a $0^\circ$ phase difference between the two arms corresponds to their moving in a mirror-symmetric way in extrinsic space with respect to the mid sagittal plane. In muscle-based definitions of symmetry, such $0^\circ$ phase differences correspond to the use of homologous muscles (Kelso 1984).

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

To examine whether performance is related to the statistics of natural movements, we developed a wearable motion-tracking system to record the arm movements of human subjects as they went about their daily life. The system allowed our subjects to engage spontaneously in normal everyday tasks while we recorded the kinematics of their right and left arms. Our results suggest that the symmetry bias reported from laboratory-based tasks is present in natural everyday movements. Moreover, when the same subjects performed a laboratory-based tracking task that measured error as a function of different phase relationships between the arms, we found that the incidence of natural movements correlated with subjects performance in the task. Both the form of the phase-related errors on the task and the incidence of particular phase relations in the natural data set replicated the “seagull effect” (Kelso 1995; Tuller and Kelso 1989). Moreover, the relation-
ship between the errors and incidence was well fit using a logarithmic relation, consistent with previous studies (Heathcote et al. 2000). These results represent a novel contribution to the field by, first, documenting the relative phase relations that occur in natural arm movements and, second, demonstrating that the incidence of these phase relations is correlated with performance.

METHODS

Data acquisition

After providing written informed consent, six subjects took part in the experiment. A local ethics committee approved the experimental protocol. Two of the participants were authors (ISH and JN) and four participants were naïve to the purpose of the experiment. No qualitative differences were observed between the subjects. Liberty sensors (Polhemus, Colchester, VT) were attached to the left and right upper arms, just above the elbow, and also to the wrists (Fig. 1C). Subjects carried a backpack containing the modified Liberty hardware, battery power supply, and a computer logging the data at 120 Hz. The Polhemus transmitter was firmly attached to the participant’s chest (Fig. 1C). The initial version of the backpack weighed about 11 kg and allowed subjects to carry out most everyday tasks and move around freely both indoors and outdoors. The design was later improved, reducing its weight to 5.5 kg. In total, >31 h of recording was obtained from the subjects. The first three subjects wore the original backpack design (8.8, 9.1, and 3.9 h recorded in blocks of ~1 h) and the final three subjects wore the improved design (3.1, 3.1, and 3.0 h also recorded in blocks of ~1 h). Several of the subjects wore backpacks regularly, rather than using a briefcase, so were accustomed to performing daily tasks in the presence of a backpack. Results were qualitatively the same with both types of backpack and across the subjects, independent of whether they regularly wore a backpack. Subjects were told to avoid close proximity to large metallic objects, which could distort the measurements, and were informed that signal quality could be monitored using a visible status indicator. Subjects were requested to perform typical activities they would do normally; questioning revealed that recording sessions included a wide range of activities such as walking, going shopping, reading, doing jigsaw puzzles, constructing model airplanes, food preparation, and having lunch.

Joint angle analysis

Each sensor provided position and orientation, which was used to calculate the elbow angles and the angular speed of the elbow and shoulder joints of each arm. The Polhemus system records the three-dimensional (3D) position (3 × 1 vectors $\mathbf{T}_i$) and 3D orientation (3 × 3 matrices $\mathbf{R}_i$) of each sensor with respect to the transmitter (the subscript $k = 1, 2$ refers to the upper and lower sensors for a particular arm and the superscript $i$ is the time sample). The center of rotation for the elbow joint can be estimated from the sensors proximal and distal to the joint (Fig. 1D). Each sensor can be considered to represent a coordinate system that translates and rotates with the sensor. $\mathbf{D}_k$ is a vector that defines the center of rotation of the elbow joint relative to sensor $S_k$ (Fig. 1D)—that is, using the coordinate system defined by the position and orientation of sensor $S_k$, vector $\mathbf{D}_k$ corresponds to the location of the elbow joint within that coordinate system. $\mathbf{D}_k$ is constant because the relative locations of the sensors and elbow joint do not change as the arms move. We used the measurements from each sensor to estimate the location of the center of the elbow joint in the coordinate system of the transmitter: that is, $\mathbf{R}'_k \mathbf{D}_k + \mathbf{T}_k$ and $\mathbf{R}'_k \mathbf{D}_k + \mathbf{T}_k$. Because both of these represent the same location—that is, the center of the elbow joint in the coordinate system of the transmitter—they should coincide (subject to noise in the sensor readings and the fact that the elbow joint does not have a single point of rotation). Therefore we can
estimate $D_1$ and $D_2$ by finding their values that minimize the error between the two estimates across time samples. Specifically, we seek to minimize the squared error given by

$$E = \langle (R_1 \Delta t + T_1) - (R_2 \Delta t + T_2) \rangle^\top (R_1 \Delta t + T_1) - (R_2 \Delta t + T_2) \rangle$$

where $\langle \cdot \rangle$ denotes the average across time samples. For simplicity, we define concatenated matrices and vectors

$$R' = [R_1 | R_2], \quad D = [D_1 | D_2]$$

and $T' = T_1' - T_2'$.

That is

$$R' = \begin{bmatrix} R_{1,1}' & R_{1,2}' & R_{1,3}' & -R_{2,1}' & -R_{2,2}' & -R_{2,3}' \\ R_{1,1}' & R_{1,2}' & R_{1,3}' & -R_{2,1}' & -R_{2,2}' & -R_{2,3}' \\ R_{1,1}' & R_{1,2}' & R_{1,3}' & -R_{2,1}' & -R_{2,2}' & -R_{2,3}' \end{bmatrix}$$

which is a $3 \times 6$ matrix, where the first subscript on each element identifies the original rotation matrix and the second subscript defines its corresponding element. As stated earlier, the superscript $t$ defines time. Similarly

$$D = \begin{bmatrix} D_{1,1} \\ D_{1,2} \\ D_{1,3} \\ D_{2,1} \\ D_{2,2} \\ D_{2,3} \end{bmatrix}$$

which is a $6 \times 1$ vector where the first subscript on each element identifies the original displacement vector and the second subscript defines its corresponding element.

Thus we can rewrite the expression for error as

$$E = \langle (R'D + T')^\top (R'D + T') \rangle$$

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

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

which gives

$$\langle (R')^\top R'D + (R')^\top T' \rangle = 0$$

and thus

$$D = -\langle (R')^\top R' \rangle^{-1} \langle (R')^\top T' \rangle$$

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

$$E' = (R_1 \Delta t + T_1 + R_2 \Delta t + T_2)/2$$

where $E'$ is the location of the elbow joint, in the coordinate frame of the transmitter, at time $t$. The elbow angle was then calculated using the cosine rule as the angle between the vectors linking the proximal sensor to the elbow joint ($T'_1 - E'$) and the distal sensor to the elbow joint ($T'_2 - E'$). The elbow speed was obtained by computing the difference between elbow angles over consecutive time points and dividing by the sampling interval $\Delta t$.

To calculate the angular speed of the shoulder joint we use the fact that rotation of a rigid object, such as the upper arm, can be represented by a single scalar rotation angle about a given axis. This is the basis of the quaternion representation that specifies both the axis of rotation (three parameters defining the vector for the axis of rotation) and the (scalar) angle of rotation. To calculate the shoulder speed we computed the change in rotation angle for the upper arm between consecutive time samples. To do this we first calculated the change in the rotation matrix between time samples $\Delta R' = (R')^{-1}R'$. This rotation matrix was used to determine the angular change ($\Delta \theta$) using standard conversion to quaternion form

$$\Delta \theta = 2 \cos^{-1}\left(\frac{1}{2} \sqrt{1 + \Delta R_{kk} + \Delta R_{22} + \Delta R_{33}}\right)$$

where $\Delta R_{kk}$ is the $(k, k)$ element of the matrix. The shoulder rotation speed is then given by $\Delta \theta/\Delta t$. We performed these analyses for the left and right arms.

Wavelet phase analysis

Short-term frequency-dependent phase analysis was performed on the two elbow angle time series. Because the elbow angle depends on the relative angle between the two sensors on each arm, it is less sensitive than the raw data to any movements of the transmitter. Moreover, in distinction to the convention needed to define symmetry in terms of movement of the limbs in extrinsic space, there is no ambiguity when defining symmetry in terms of the angular motion of the elbow joints (see Fig. 1, A and B). Position trajectories of point-to-point reaching movements are similar in form to a half cosine and thus have an associated fundamental frequency and phase. An analysis was required that was able to extract the phase of such signals as a function of frequency. Of course, there will also be movements involving oscillations of the arms, especially during activities such as walking, with the arms swinging. Although short-term fast Fourier transform (FFT) analysis can be used to estimate phase, it is not as effective as dealing with localized events such as discrete movements. One way to improve this is to match window length as a function of frequency. In this way, the window length will better fit a discrete event in the signal. This is effectively what wavelet analysis does—

the time window of the wavelet is a function of its bandwidth (Mallat 1999). The Hilbert transform is often used to decompose a signal into instantaneous phase and amplitude. However, it is not appropriate here because it does not provide the necessary frequency-dependent phase analysis. Moreover, wavelet analysis is being increasingly applied to biological signals such as electroencephalograms (Selesnick et al. 2005).

We performed a dual-tree complex wavelet transform (DT-CWT) (Kingsbury 2001) on the left and right elbow angles, using eight levels of wavelet decomposition. The complex nature of the subband outputs from this transform produces analytic waveforms that have both amplitude and phase in subbands that are each approximately one octave wide. The DT-CWT has the important property of shift invariance, which ensures that all input signals are analyzed in equivalent ways.

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

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

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

Validation of wavelet phase analysis

We validated the wavelet phase analysis on two different data sets. For the first data set, we generated synthetic left and right elbow angle data by simulating two independent random walks. For the second data set, we inserted a set of relative time shifts between the left and right elbow angles from the natural movement data set. In all cases the data were analyzed at low- (0.45–0.9) and high-frequency bands (3.2–6.4 Hz). Analysis of the random walk data set resulted in uniform phase incidences at both low- and high-frequency bands, as expected. For the time-shifted data sets, analysis resulted in the expected shifts in the relative phase incidences. Full details of these two validations are available in the Supplemental Material.1

Conditioning for similar versus different joints

We also performed a phase analysis of the positions of the distal sensors at the wrists in extrinsic space, for subsets of the data based on whether the arms were moved predominantly by rotations around the same or different joints (see Fig. 5, A and C). If the phase distributions are similar between the two subsets of the data, this would suggest that the symmetry bias (defined in external space) does not occur because we use homologous muscle groups, as previously suggested (Kelso 1984). Elbow and shoulder angular speeds were used to divide the data into either a “similar-joint” subset or “dissimilar-joint” subset. The similar-joint subset included all the data in which, for both arms, either the angular speeds of the shoulders were greater than those of the elbows or the angular speeds of the elbows were greater than those of the shoulders (Fig. 5A). In this case, movement of the distal sensors on both arms was dominated by either both shoulders or by both elbows. In contrast, the dissimilar-joint subset included the complement of the similar-joint subset. Specifically, it included data in which the angular speed of the shoulder in one arm was greater than that of the elbow and in the other arm the converse was true (Fig. 5C). In this case, movement of the distal sensors on both arms was dominated by different joints on each arm.

For both subsets of the data set we calculated the phase relations for each of the three Cartesian axes for movement of the distal sensor using the same methods as described earlier. The phase relations for the three Cartesian axes were then averaged to calculate the relative incidence. We used the convention that a 0° phase difference between the two arms corresponds to their moving in a mirror-symmetric way with respect to the midsagittal plane.

Tracking paradigm

To obtain a quantitative measure of performance at different phase relations for the same subjects who participated in the natural movement data collection, subjects were also required to perform a phase-tracking task. The tracking task was designed to compare phase-tracking performance with the incidence of relative phases between the distal sensors at the wrists in the natural movement data set. The task was similar to

RESULTS

We attached sensors to the elbows and wrists of six volunteers who wore a backpack containing motion-tracking equipment. The sensors recorded the position and orientation of both wrists and elbows over extended periods of time (3.0–9.1 h/subject). The boundary enclosing the 0.9 percentile of the distributions of wrist and elbow positions for one subject is shown in Fig. 2. This shows that the majority of wrist and elbow positions fall within a region close to the body.

From this natural data set we calculated the phase relations between flexion–extension movements of the right and left elbows for a range of movement frequencies (Fig. 3). For each frequency band we examined how often each phase relation was observed during natural movement, which allowed us to determine the relative incidence of each phase relation. Figure 3A illustrates how this measure of relative incidence changes with increasing frequency, showing a progression from a bimodal to unimodal distribution as the frequency increases.

At low movement frequencies (0.45–0.90 Hz, Fig. 3B) each subject’s distribution was bimodal with symmetric (phases at 0/360°) movements occurring significantly more often than asymmetric (phase of 180°) movements (P < 0.01, average ratio of incidence of 2.0 across subjects). Moreover, asymmetric movements at 180° occurred significantly more often than did the intermediate phase relations of 90° (P < 0.05) and 270° (P < 0.05). At higher movement frequencies (3.2–6.4 Hz, Fig. 3C) the distribution became unimodal, with symmetric

1 The online version of this article contains supplemental data.
movements still occurring significantly more often than antisymmetric movements ($P < 0.01$, average ratio of incidence of 2.0 across subjects). However, at these higher frequencies the second peak for antisymmetric movements was no longer present and their incidence was significantly less than those of $90^\circ$ ($P < 0.001$) and $270^\circ$ ($P < 0.01$). Taken together, these results parallel laboratory observations showing that movements with a phase relation other than symmetric and antisymmetric are especially difficult and that antisymmetric movements become unstable as the frequency of movement increases (Kelso 1984).

Another fundamental issue that has been addressed in laboratory experiments (Mechsner et al. 2001; Swinnen et al. 1998) relates to the coordinate system for the symmetry bias. Elbow joint angles were used for the preceding phase analysis because these were most precisely measured with our apparatus (see METHODS). Consequently, such an analysis quantified symmetry bias in joint (intrinsic) space. An important question is whether the symmetry bias is similarly present in extrinsic space. This would be expected if the demands on natural motor tasks are defined in extrinsic space. To examine this, we compared the relative incidence of phase relations for the distal sensors on the wrist moving in extrinsic space (Fig. 4, A and B) with that of the elbow angles in joint space (Fig. 4, C and D). Interestingly, the incidence of $180^\circ$ phase is significantly higher for the movements defined in extrinsic space than those defined in intrinsic space ($P < 0.05$ for each subject; averaged incidence ratio = 1.6). Similarly, the incidence of $0^\circ$ phase was significantly lower ($P < 0.01$ for each subject; averaged incidence ratio = 0.9). This suggests a stronger component of antisymmetric movement for task-based (extrinsic) coordinates.

Another important question is whether the bias favoring symmetric movements arises because they are executed in the same direction in extrinsic space or because they involve movements around the same joints. To address this issue in the natural movement data set, we split the distal sensor data recorded at the wrists into two parts. The first part contained samples in which movement of the left and right arms predominantly resulted from rotations around similar joints (Fig. 5A). The second part contained samples in which movement of the arms predominantly resulted from rotations around the dissimilar joints (Fig. 5C) (see METHODS for details). For these two data sets, we analyzed phase relations between the two distal sensors in a midfrequency band (0.9−1.8 Hz). We chose this range so we could examine whether the bimodal peaks in incidence for symmetric and antisymmetric movements were different between the two subsets of the data.

For both the similar- and dissimilar-joint subsets of the natural movement data the distributions were bimodal, preserving the peaks in incidence for symmetric and antisymmetric movements (Fig. 5, B and D, respectively). Moreover, there were no significant differences in the relative incidences between the two data sets at either 0 or $180^\circ$ phase. Thus the
effect of selecting movements on the basis of different joint usage preserves the basic form of the distributions. This finding is in close correspondence with experimental data that show that the symmetry bias is present in extrinsic coordinates, regardless of the joints used (Mechsner et al. 2001; Swinnen et al. 2002).

Previous studies have shown a relationship between the amount of training on perceptual tasks and performance (Heathcote et al. 2000). To investigate the relationship between performance and the relative incidence of movement phases in our natural movement data set, subjects performed a bimanual tracking task in a virtual reality environment (Fig. 1E; see METHODS). This required subjects to track two targets that moved sinusoidally at various phase relations at a low frequency (0.5 Hz) and a high frequency (5.0 Hz). The phase error at 0.5 Hz on the tracking task (Fig. 6A) is small for symmetric (0°/360°) and antisymmetric (180°) movements, mirroring the relative incidence of these phases in the natural movement data set (Fig. 6B). Similarly, the phase error at 5 Hz on the tracking task (Fig. 6C) mirrors the relative incidence of these phases in the natural movement data set (Fig. 6D). However, in this case there was a stronger tendency to move symmetrically on the tracking task, as indicated by the almost linear relationship between error and phase between 0 and 90° and 270 and 360° (Fig. 6C). To further quantify the relationship between phase incidence in our natural movement data set and performance on the tracking task, we used linear regression to fit the performance errors to the log incidence of the phases. We found a good fit at both low ($r^2 = 0.86, P < 0.001$, Fig. 6E) and high ($r^2 = 0.88, P < 0.001$, Fig. 6F) frequencies. This demonstrates that the logarithmic
law for training is also present between the natural incidence of a movement and motor performance on a laboratory task.

**Discussion**

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

The aim of the current study was to acquire data for movements that corresponded to what subjects do during everyday activities. Because there are many laboratory studies that look at only specific movements or tasks, our study was specifically designed to avoid such constraints. To achieve this we let subjects go about their daily routine with only a few instructions, such as avoiding large metallic objects or water. We examined the statistics of the movements and did not try to categorize the specific tasks that subjects were performing. However, it was important that the samples we acquired were representative of normal activities and we therefore collected >30 h of kinematic data. Although subjects may have engaged in different tasks during the recording period, the statistics across subjects were very similar, as demonstrated by the low SEs (Figs. 3–6). This suggests that we have captured representative statistics in all our subjects.

An interesting question arising from the current study is whether the symmetry bias exists because successful interaction with the environment requires both symmetrical movements (such as bimanual grasping of objects) and antisymmetric movements (such as laterally moving a handheld object). Alternatively, the symmetry bias may be an immutable property of the musculoskeletal and nervous systems. As such, it would fundamentally constrain the way we can interact with the world. Previous studies have assumed that fundamental constraints on performance arising from the perceptual (Mechsnner et al. 2001) or motor systems (Swinnen et al. 2002) explain the symmetry bias. Indeed Mechsnner et al. (2001) reported that symmetry in external space, or visual symmetry, can override this bias. However, as shown here and in laboratory-based experiments, the symmetry bias is present in intrinsic task space. This may be understood in terms of the requirement to interact with the external world. In contrast, constraints on the musculoskeletal and nervous systems would be expected to be manifest in intrinsic (joint space) coordinates. For example, it is intuitively obvious why symmetric and antisymmetric movements may be common in bimanual object manipulation.

![Image](https://example.com/image.png)
tasks (Fig. 7). If we seek to simultaneously bring both hands together from different positions to pick up an object this requires phases of 0 or 180°, depending on the axis. For example, bringing the hands laterally together to grasp an object from the left and right or moving them apart to release it requires movement phases of 0° (Fig. 7A). In contrast, bringing the hands vertically together to grasp an object from above and below or moving them apart to release it requires movement phases of 180° (Fig. 7B). Once the object is grasped, transporting it then requires movement with phases of either 0 or 180°, depending on the direction of transport. For example, moving a bimanually grasped object left or right requires movement phases of 180° (Fig. 7C). In contrast, moving a bimanually grasped object up or down requires movement phases of 0° (Fig. 7D). Consequently, interaction with objects typically requires movements with phases at 0 and 180° in extrinsic space.

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

As previously discussed, the symmetry bias does not appear to be an immutable property of the musculoskeletal and nervous systems. For example, extensive training on the novel phase relation of 90° over the course of several days improves performance at this phase, but leads to a decrement in performance at other phases (Schoner and Kelso 1988; Zanone and Kelso 1992). Such training significantly changes the distribution of phases experienced by subjects and the observed results reflect these novel statistics. Similarly, if subjects are trained at new polyrhythms (Summers et al. 1993), significant improvement is observed (Klaiman and Karniel 2006). Interestingly, improving at one class of movement can come at the expense of a decrease in performance at others (Van Damme et al. 2002). One hypothesis consistent with these results is that there are limited neural resources available and that improvement at one phase necessarily involves a decrement in performance at others. This hypothesis is further supported by the finding that training on a particular task increases the size of its neural representation (Classen et al. 1998; Elbert et al. 1995; Kaas 1991; Karni et al. 1995). Interference between two similar motor tasks that are performed sequentially also suggests

**FIG. 7.** Bimanual phase relations during object manipulation. Arrowheads on the left and right indicate the direction of symmetric and antisymmetric movements, as in Fig. 1. A: bringing the hands laterally together to grasp an object (G) from the left and right or moving them apart to release it (R) requires symmetric movements. B: bringing the hands vertically together to grasp an object (G) from above and below or moving them apart to release it (R) requires antisymmetric movements. C: moving a bimanually grasped object left (L) or right (R) requires antisymmetric movements. D: moving a bimanually grasped object up (U) or down (D) requires symmetric movements.
competition for finite neural resources (Brashers-Krug et al. 1996; Caithness et al. 2004; Miall et al. 2004; Tong et al. 2002). Taken in the context of the current study, this suggests that neural resources are indeed finite and that the statistics of natural movements will influence their allocation. This view provides a potential link between the occurrence of particular movements and performance.

ACKNOWLEDGMENTS

We thank N. Kingsbury for advice and assistance with the wavelet analysis and R. Symonds and O. Krömer for technical assistance.

GRANTS

This research was supported by the Wellcome Trust and European Project Grant SENSPAC IST-2005-028056. K. Körding was supported by a Deutsche Forschungsgemeinschaft Heisenberg Fellowship.

REFERENCES


Supplementary material

The statistics of natural movements are reflected in motor errors

Ian S. Howard\textsuperscript{1}, James N. Ingram\textsuperscript{1}, Konrad P. Körding\textsuperscript{2} and Daniel M. Wolpert\textsuperscript{1}

\textsuperscript{1} Department of Engineering, University of Cambridge, Trumpington Street, Cambridge CB2 1PZ, UK

\textsuperscript{2} Physiology and PM and R, Rehabilitation Institute of Chicago, Northwestern University, 345 E Superior Street, 60611 Chicago, IL, USA

Wavelet phase analysis

To determine the phase relations between movements of the left and right arms as a function of frequency, we performed a Dual-Tree Complex Wavelet Transform (DT-CWT), as described in the Methods of the main text. We generated phase incidence histograms by binning the relative phases into 18 bins each 20° wide. The total incidences across all bins in a given frequency band were then normalized to sum to 1. We validated this analysis on two different datasets. For the first dataset, we generated synthetic left and right elbow angle data by simulating two independent random walks. For the second dataset, we inserted a set of relative time shifts between the left and right elbow angles from the natural movement dataset. In all cases the data was analyzed at low and high frequency bands, as described in the main text. That is, 0.45-0.9 Hz for the low frequency band and 3.2-6.4 Hz for the high frequency band.

Validation using a random walk dataset

The first validation dataset simulated the angular trajectories of the left and right elbows using two independent random walks. Approximately 18 hours of synthetic data was generated by cumulatively summing $8 \times 10^6$ samples (assuming a 120 Hz sampling rate) which were drawn from a zero mean Gaussian distribution with unit variance. The initial 1 second of data is shown in Figure S1.

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{figureS1.png}
\caption{Synthetic random walk elbow angle data for the left (A) are right (B) elbows.}
\end{figure}
The wavelet relative phase analysis was run on this dataset and the resulting relative incidence of phase occurrences are shown in Figure S2. It can be seen that the relative incidence of phase is essentially uniformly distributed at both high (Figure S2 A) and low frequencies (Figure S2 B), as expected from two independent random signals.

**Figure S2** Relative phase analysis for the synthetic random walk dataset. **A** Normalized phase incidences at 3.2-6.4 Hz (high frequency band). **B** Normalized phase incidences at 0.45-0.9 Hz (low frequency band).

**Validation using time shifted natural movement dataset**

The second validation dataset was generated by introducing a set of time shifts between the left and right elbow angle time series from the natural movement dataset. The effect of such a time shift is to change the phase relations between the left and right datasets in a frequency dependent fashion. We note that only time shifts that lead to small phase shifts (for example, less than 180°) lead to meaningful interpretations. This is because for larger phase shifts, we should expect the phase relationships to tend towards a uniform distribution since the movements of the left and right elbow will no longer correspond to the same action in time.

We selected 6 time shifts which include the two extremes cases of zero (the normal non-shifted case used in the main analysis) and a large time shift of 5 s which, as discussed above, should remove the correspondence between movements of the right and left elbow and result in a uniform distribution of phase relations. The additional time shifts were selected to give rise to specific phase shifts for the high and low frequency bands. Since our phase bins increase in steps of 20°, we then select time delays that would lead to phase shifts that correspond to this bin width.

Two time shifts were selected to correspond to 40° and 80° phase shifts at the low frequency band, as follows. The frequency at the centre of this band is 0.67 Hz, which corresponds to a period of 1.5 s. Therefore, a phase shift of 40° corresponds to a time shift of 0.17 s and a phase shift of 80° corresponds to a time shift of 0.33 s. The two time shifts for the high frequency band were similarly selected to correspond to 40° and 80° phase shifts. The frequency at the centre of this band is 4.78 Hz, which corresponds to a period of 0.21 s. Therefore, a phase shift of 40° corresponds to a time shift of 0.023 s and a phase shift of 80° corresponds to a time shift of 0.047 s.
The wavelet relative phase analysis was run on the time-shifted datasets for the 6 time-shift values and across the 6 subjects. The results are shown if Figure S3. At the large time shift of 5 s, the phase relation at both low and high frequencies was uniform (Figure S3 A and F).

This is to be expected because at such a large time shift, movements of left and right elbows will be unrelated. For time shifts corresponding to an 80° phase shift, it can be seen that the peak in incidence that occurs at 0° in the non-shifted data, has been shifted towards 80°, for both the low (Figure S3 B) and high frequency bands (Figure S3 G). A similar effect occurs for time shifts corresponding to a 40° phase shift (Figure S3 C and H). For comparison the zero time shift incidences are shown (Figure S3 D and I). Finally, results for the 40° and 80° phase shifts for the low and high frequency bands were aligned by shifting each curve by its expected phase shift and overlaying on the original non-shifted analysis (Figures S3 E and J).

It can be seen that there is a good agreement between these curves, indicating that the relative time shifts have resulted in the expected phase shifts.

**Figure S3** Validation of wavelet phase analysis with a dataset generated by inserting a relative time shift between the left and right elbow angle data from the natural movement dataset, averaged over all six subjects. 

- **A & E** Relative phase incident at 0.45–0.9 Hz (low frequency band) 
- **F & J** Relative phase incident at 3.2–6.4 Hz (high frequency band) 

For a large time shift (5 s), relative phase incidence is uniform. 

- **B & G** A time shift corresponding to 80° results in the expected phase shift (see text for details). 
- **C & H** A time shift corresponding to 40° results in the expected phase shift (see text for details). 

- **D & I** The relative phase incidences for zero time shift. 
- **E & J** Good agreement of curves is
obtained when the relative phase incidences for different time shifts are aligned and overlaid with the zero time shift data.

Conclusions

To summarize, analysis of a random walk dataset yielded a uniform phase incidence and inserting various relative time shifts in the natural movement dataset resulted in the expected shifts relative phase incidence. These two experiments thus demonstrate the validity of the wavelet phase analysis that was used in the analysis of the natural movement dataset described in the main text.