Complex Unconstrained Three-Dimensional Hand Movement and Constant Equi-Affine Speed

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1Interdisciplinary Center for Neural Computation, The Hebrew University of Jerusalem, Jerusalem; 2Department of Computer Science and Applied Mathematics, Weizmann Institute of Science, Rehovot, Israel; and 3Laboratoire de Physiologie de la Perception et de l’Action, Centre National de la Recherche Scientifique, College de France, Paris, France

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Maoz U, Berthoz A, Flash T. Complex unconstrained three-dimensional hand movement and constant equi-affine speed. J Neurophysiol 101: 1002–1015, 2009. First published December 10, 2008; doi:10.1152/jn.90702.2008. One long-established simplifying principle behind the large repertoire and high versatility of human hand movements is the two-thirds power law—an empirical law stating a relationship between local geometry and kinematics of human hand trajectories during planar curved movements. It was further generalized not only to various types of human movements, but also to motion perception and prediction, although it was unsuccessful in explaining unconstrained three-dimensional (3D) movements. Recently, movement obeying the power law was proved to be equivalent to moving with constant planar equi-affine speed. Generalizing such motion to 3D space—i.e., to movement at constant spatial equi-affine speed—predicts the emergence of a new power law, whose utility for describing spatial scribbling movements we have previously demonstrated. In this empirical investigation of the new power law, subjects repetitively traced six different 3D geometrical shapes with their hand. We show that the 3D power law explains the data consistently better than both the two-thirds power law and an additional power law that was previously suggested for spatial hand movements. We also found small yet systematic modifications of the power-law’s exponents across the various shapes, which further scrutiny suggested to be correlated with global geometric factors of the traced shape. Nevertheless, averaging over all subjects and shapes, the power-law exponents are generally in accordance with constant spatial equi-affine speed. Taken together, our findings provide evidence for the potential role of non-Euclidean geometry in motion planning and control. Moreover, these results seem to imply a relationship between geometry and kinematics that is more complex than the simple local one stipulated by the two-thirds power law and similar models.

INTRODUCTION

One fundamental problem in the study of motor control is that of trajectory formation—i.e., the selection of the geometrical shape of the path as well as the velocity profile (or speed profile) over that path to accomplish a certain goal. This selection process is highly redundant in many levels (Bernstein 1967), as can be demonstrated by examining the simple act of reaching for a cup of tea. The CNS must choose a specific solution among an infinite number of possible paths leading from the hand’s initial position to that of the cup. It must also choose one of an infinite number of speed profiles along that path, specify joint rotations that would realize the chosen hand trajectory, and then choose from all muscle activation patterns that achieve those joint configurations.

Two important classes of models of trajectory formation that have been suggested to solve the redundancy problem for hand movements are those that rely on optimization principles versus those that are based on motion invariants. Because the motor system is a product of evolution, development, learning, and adaptation—all of which are in a sense processes aimed at reaching the most advantageous performance—optimization-based models stress that attempts to understand this system should emphasize the role of optimization. These models thus suggest that planning and control of movement are optimal in some sense—i.e., they minimize some undesired cost or maximize some sought-after benefit.

One successful optimization criterion has been based on the idea that the brain favors smooth movements and thus strives for movements that are maximally smooth (Flash and Hogan 1985). This implies a cost that penalizes the time derivative of either hand acceleration (i.e., jerk) (Flash and Hogan 1985; Todorov and Jordan 1998), joint torques (Nakano et al. 1999; Uno et al. 1989), or muscle forces (Pandy et al. 1995). Another idea is that because the magnitude of motor noise seems proportional to the amount of muscle activation, the sequence of muscle activations is planned so as to minimize the resulting variance of the final hand positions (Harris and Wolpert 1998). Yet another model, based on stochastic optimal feedback control, stresses the role of closed-loop sensorimotor integration, while allowing trial-by-trial variability in task-irrelevant dimensions of the movement (Braun and Wolpert 2007; Guigon et al. 2007; Todorov 2004; Todorov and Jordan 2002).

The second class of models attempts to identify simplifying principles behind the large repertoire and high versatility of human hand movements. Discovery of these laws of motion goes some way to reduce the apparent redundancies of trajectory formation in the motor system. One of many examples is the long-known isochrony principle (Binet and Courtier 1893; Viviani 1986; Viviani and Flash 1995), which suggests that average movement speed scales with the extent of movement, making movement duration only weakly dependent on movement extent. Other invariants are the bell-shaped speed profiles and almost-straight paths typical of planar reaching movements.

Of special importance for us here is another long-established invariant: the inverse relation between instantaneous tangential

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speed and curvature during planar curvilinear hand trajectories (Binet and Courtier 1893; Jack 1895). More recently it was formally defined as

\[ v = \alpha \kappa^{-1/3} \]  

(1)

and termed the two-thirds power law, which is often denoted 2/3-PL in the following text. The name “two-thirds power law” stems from the originally used equivalent formulation of this kinematic constraint in terms of angular speed \( \omega \), where \( A = \alpha \kappa^{2/3} \) (Lacquaniti et al. 1983). In Eq. 1, the hand’s movement speed is

\[ v = \sqrt{\dot{x}^2 + \dot{y}^2} \]  

(2)

and the curvature of the movement path of the hand is (O’Neill 1997; Oprea 1997)

\[ \kappa = \frac{|\ddot{x} \dot{y} - \ddot{y} \dot{x}|}{(\dot{x}^2 + \dot{y}^2)^{3/2}} \]  

(3)

where for any function of time \( \rho(t) \), the first and second time derivatives are \( \dot{\rho} \) and \( \ddot{\rho} \), respectively (i.e., \( \dot{\rho} = d\rho/dt \) and \( \ddot{\rho} = d^2\rho/dt^2 \)). For the power law of Eq. 1, the velocity (or speed) gain factor \( \alpha \) is roughly constant for simple elliptical shapes, but is piecewise constant for more complex shapes (Viviani 1986; Viviani and Cenzato 1985). The power law is therefore a model of trajectory formation, allowing the derivation of local trajectory kinematics from local path geometry\(^1\) (up to the constant \( \alpha \)).

The power law was shown to describe various types of movement that invoke different effectors and use different muscle groups across the body. Thus, besides drawing movements, it was also established to apply to the hand under isometric force conditions (Massey et al. 1992). Smooth-pursuit eye movements were further demonstrated to obey the power law (deSperati and Viviani 1997), as were tongue movements during speech kinematics (Perrier and Fuchs 2008; Tasko and Westbury 2004). Moreover, locomotive trajectories were found to be congruent with the power law (Hicheur et al. 2005, 2007; Pham et al. 2007; Vieilledent et al. 2001). It was also discovered in the perception of motion (Dayan et al. 2007; Levit-Binnun et al. 2006; Viviani and Stucchi 1992), where motion according to the power law was demonstrated to appear more uniform than constant-speed movement. Moreover, prediction of human movement is facilitated by trajectories conforming to the power law (Kandel et al. 2000). It was discovered that this power law is also represented in proprioceptive information from the hand (Viviani et al. 1997) and leg (Albert et al. 2005). The power law was further observed to develop with age in children (Scialy et al. 1987; Viviani and Schneider 1991), whereas adults find it extremely difficult to produce trajectories that significantly violate this law (Viviani 2002).

Some effort has been invested in associating between different invariants. Thus the isochrony principle was at least partially explained by the two-thirds power law (Viviani and Cenzato 1985; Viviani and Flash 1995; Viviani and Schneider 1991). The ubiquity of many of the invariants motivated attempts at discovering some underlying optimization principles to account for their presence in human movements. Bell-shaped speed profiles and straight paths in planar reaching movements were shown to be an immediate result of the minimum-jerk model (Flash and Hogan 1985). The 2/3-PL was proposed to result from motor-planning strategies of the CNS that favor smoothness maximization (Richardson and Flash 2002; Todorov and Jordan 1998; Viviani and Flash 1995; Wann et al. 1988). The power law was further shown to be a possible consequence of the minimum-variance principle (Harris and Wolpert 1998). It was recently hypothesized that the power law might also stem from correlated noise in the motor system (Maoz et al. 2006).

Others suggested that the power law may stem from more peripheral smoothness effects due to muscle mechanics (Gribble and Ostry 1996) or to the nonlinearities involved in the mapping from joint to hand coordinates and to the smooth oscillatory nature of joint rotations (Dounskaia 2007; Schaal and Sternad 2001). However, single-cell monkey recordings demonstrate that population vector coding in both the motor and the premotor cortical areas obeys the two-thirds power law during motion execution (Polyakov et al. 2001; Schwartz 1994; Schwartz and Moran 1999, 2000). Moreover, a recent functional magnetic resonance imaging (fMRI) study in humans has shown that motion perception seems to reflect this constraint and that the brain’s response to this law of motion is much stronger and more widespread than that to other types of movement (Dayan et al. 2007). These studies provide evidence in favor of the origin of the power law in central motion planning and control.

Importantly, it was proved that planar movement that obeys the 2/3-PL is equivalent to moving at constant equi-affine speed (Flash and Handzel 1996, 2007; Handzel and Flash 1999; Pollick and Sapiro 1997). (For a more intuitive explanation of the notion of equi-affine geometry and equi-affine speed, see Supplemental Material.\(^2\) Formally, for a planar trajectory \( r(t) = [x(t), y(t)] \), equi-affine speed is defined as

\[ v_{ea} := \sqrt{\dot{x}^2 + \dot{y}^2} \]  

which is the cube root of the signed area of the parallelogram created by the instantaneous first and second time-derivative vectors of the position along the trajectory (see Supplemental Fig. S3). Algebraic manipulations of Eqs. 2, 3, and 4 then yield

\[ v = v_{ea} \kappa^{-1/3} \]

and when comparing with the power law (Eq. 1) we see that motion with constant equi-affine speed (i.e., with \( v_{ea} = \text{const} \)) is equivalent to motion that obeys the two-thirds power law.

Within the equi-affine framework, moving at constant equi-affine speed (which is equivalent to moving according to the 2/3-PL) is the simplest kind of motion. Thus if the brain tends to generate movement within this framework, the simplest kind of motion would be that which obeys the 2/3-PL. Indeed, analysis of monkey brain recordings during planar scribbling movements suggest’s that equi-affine speed might be represented in motor-control neurons (Polyakov 2006, Polyakov et al. 2009). This means that the various types of phenomena

\(^1\) Curvature is the inverse of the radius of curvature and is a purely geometric property of the path, irrespective of speed along the path. Moreover, curvature at every point along a planar path completely determines it up to Euclidean transformations (which include translations, rotations, and reflections) (Oprea 1997).

\(^2\) The online version of this article contains supplemental data.
that the power law describes may all result from the CNS planning and controlling movement using constant equi-affine speed. This interpretation suggests that the power law may be more than some empirical, and possibly accidental, invariant of motion.

It was recently shown that three-dimensional (3D) movement at constant equi-affine speed entails a novel power law different from the 2/3-PL (Pollick et al. 1997). This is an empirically testable prediction stemming from the equi-affine framework. If movement at constant equi-affine speed is indeed the guiding principle and the 2/3-PL is just a special case, we would expect general 3D movement to conform to 3D constant equi-affine speed instead of to the 2/3-PL. This was in fact demonstrated when it was shown that the 2/3-PL does not sufficiently explain general 3D drawing movements—the less planar the path is, the less the power law is obeyed (Pollick and Ishimura 1996; Schaal and Sternad 2001; Sternad and Schaal 1999). Yet does the novel 3D power law describe 3D movements better than the 2/3-PL?

Following a similar rationale to that used to prove the equivalence of the two-thirds power law with planar movement at constant equi-affine speed, we derive the formula for motion at constant spatial equi-affine speed (for full details see Pollick et al. 2008). Spatial equi-affine transformations preserve the volume (rather than area) enclosed by the shape. We thus define spatial equi-affine speed at any point on a curve in terms of the volume of the parallelepiped defined by the first-, second-, and third-derivative vectors at that point. More formally, we define

\[ v_{\text{oa}} = \left| \frac{d}{dr} \mathbf{r} \times \frac{d^2}{dr^2} \mathbf{r} \right|^{1/6} \]

where \( \mathbf{r}(t) = [x(t), y(t), z(t)] \) and \( |u, v, w| \) denotes the scalar triple product of any vectors \( u, v, w \in \mathbb{R}^3 \); \( |u, v, w| = u' \times (v \times w) \). Here the “\( \times \)” operator denotes the dot-product between two vectors and “\( \times \)” denotes the cross-product.

We must now introduce torsion, which intuitively speaking is the local deviation from planarity:

\[ \tau = \frac{\left| \frac{d}{dr} \mathbf{r} \times \frac{d^2}{dr^2} \mathbf{r} \right|^{1/3}}{\left| \frac{d}{dr} \mathbf{r} \times \frac{d}{dr} \mathbf{r} \right|} \]

Here for any vector \( u, \| u \| \) is its vector-norm or magnitude. Algebraic manipulations of Eqs. 2, 3, 5, and 6 yield

\[ v = v_{\text{oa}}(\kappa^{1/3} \tau)^{-1/6} \]

Therefore motion at constant equi-affine speed entails a new power law (Pollick et al. 2008)

\[ v = \alpha(\kappa^{1/3} \tau)^{-1/6} = \alpha \kappa^{-1/3} \tau^{-1/6} \]

which we name the one-sixth power law, designated 1/6-PL in the following text. This law suggests that spatial movement speed \( v \) is inversely related to curvature \( \kappa \) and, to a lesser extent, to torsion \( \tau \). It was demonstrated that for the limited case of 3D scribbling movements, the one-sixth power law explains the data rather well and certainly better than the two-thirds power law (Pollick et al. 2008).

Here we test this new power law on repetitive self-paced manual tracings of six different spatial shapes, to investigate how successful the equi-affine framework is at explaining unconstrained 3D drawing movements. We evaluate it against another 3D hand-movement power law suggested in the literature as well as against the two-thirds power law. As detailed in the following text, the one-sixth power law fits our movement data best among the tested power laws, providing evidence in favor of the CNS planning and executing movement according to the constant equi-affine speed framework. Indeed, when averaged over all subjects and shapes the movement is in general agreement with the 1/6-PL. However, we find small, though systematic, deviations of the power-law exponents from the values predicted from the 1/6-PL across the various shapes. These deviations are found to be in correlation with global geometric characteristics of the shape being traced.

M ETHOD S

P articipants

Eight subjects volunteered to participate in the experiment (seven male, ages 28–37 yr; five were right-handed), which was approved by the Ethical Committee of the Weizmann Institute of Science. All gave their full informed consent to participate and none reported any previous arm injuries. They are designated by their initials: A.B., D.L., E.D., F.P., I.Z., J.F., M.O., and S.L.

E xperimental setup

Subjects were seated on a rigid chair with their trunks strapped to its high back from the shoulder of the dominant arm to the contralateral side of the waist by a restraining strap. Sensors were attached to the wrist, upper arm, and the shoulder of the dominant arm as well as to the chest at the collarbone proximal to that arm. The subjects were further fitted with a wrist brace, which prevented wrist motion. The subsequent analysis used data only from the wrist sensor, designating it as the end effector or working point. The positions and orientations of these four sensors were measured using the Polhemus Liberty electromagnetic spatial tracking system (Polhemus Electronics, Colchester, VT). Because the accuracy of this system drops significantly in the presence of metallic objects, the experiments were performed outdoors, far from any metals (the surroundings, including the ground, were carefully tested with a metal detector). The chair and stands used for the experiment were composed entirely of wood and plastic, respectively (the absence of metals was again ascertained with a metal detector). The subjects further removed any metallic items they were carrying before the experiment began.

These strict noise-reduction measures were necessary to make sure that the power law would not originate from measurement noise, following the criticism of Maoz et al. (2006). There it was demonstrated that white and other types of noise can induce power-law compliance in non-power-law signals, if the noise levels after smoothing roughly equal the mean displacement between consecutive samples in the measured data. The Liberty system’s specifications suggest a static position accuracy of 0.76 mm. We tested the dynamic accuracy of this system by moving a 1.2-m-long rigid wooden stick, with sensors firmly attached to it, around the working area at approximately the same distance from the magnetic field source as the subjects would move and analyzing the SD of the distance between
sensors. The system’s measurement error was judged to be about 1 mm before smoothing and at most 0.3 mm after smoothing (see following text). The system’s measurement error after smoothing was therefore well below the average displacement between consecutive samples, which is always > 1 mm. This effectively ensures that any power laws subsequently computed would not be an artifact of measurement noise.

Data were collected at 240 Hz and stored on an IBM Thinkpad A31p laptop running Windows XP. The software designed to record the movements was developed using the Liberty’s software development kit. It notified the experimenter of any data loss or accuracy problems in real time. The very few problematic trials that were encountered were immediately aborted and rerecorded.

**Experimental procedure**

The experiment was composed of six blocks. A different shape was traced in each block. These shapes, illustrated in Fig. 1, were the double-bent ellipse (DBE), figure eight (FE), large bent ellipse (LBE), left-to-right helix (LRH), spiral helix (SH), and small bent ellipse (SBE). Before each block, the subject was given a wire-frame model of the shape. She or he would then practice tracing the shape in a continuous manner (except for the LRH and SH, in which subjects reached back to the shapes’ starting point after completing each trace) until feeling confident in the ability to correctly trace the shape.

The subjects were instructed to draw at a natural pace within their comfortable working area. They were further informed that the overall size and proportions of the shapes were up to them. This was to keep their movements as natural as possible. Before they started moving, the subjects closed their eyes to eliminate visual feedback of their moving arm. They verbally signaled to the experimenter when they were ready for data recording to begin. Recoding then actually began only after the participant reached a stable pace, to eliminate motion-initiation effects, which might result in nonstereotypical trajectories. A recording trial lasted for 20 s, but the subject was requested to stop moving only after \( \approx 25 \) s to avoid motion-termination effects. Three trials were executed in each block. Participants were encouraged to rest their arms between trials for as long as they felt necessary.

Therefore overall the database of movements consists of 8 (subjects) \( \times 6 \) (blocks or shapes) \( \times 3 \) (trials per shape) = 144 recording trials.

**Data processing**

The 3D trajectories were tested for missing data points using the sample index provided by the Liberty system. Missing samples (very rare and at most seven consecutively, i.e., always resulting in time gaps < 30 ms) were interpolated with cubic splines. The motion data were approximated with splines using the Matlab (The MathWorks) implementation of the GCVSPL package for generalized, cross-validatory spline smoothing and differentiation (Woltring 1986). This method is suited for nonstationary additive noise and nonequispaced time stamps, both of which are characteristic of our measurement system. The 1-mm measurement error (see earlier text) was used to compute the appropriate tolerance for these splines. The quantities of speed \( v \), curvature \( \kappa \), and torsion \( \tau \) could then be calculated by analytically differentiating these splines. Extensive simulations that we performed with the Liberty’s characteristic noise suggest that for shape-tracing trajectories such as ours, torsion is calculated to an accuracy of about 10% of the signal’s magnitude, whereas speed and curvature are calculated to within 2–3% error.

Processing of the data involved examining whether the predicted relationship between the speed, curvature, and absolute value of torsion in Eq. 7 was obtained. There were two initial considerations in examination of this relationship. The first was whether parts of the movement were planar. In regions where a movement is rather planar, the torsion was approximately zero and the relationship between speed, curvature, and torsion, as presented in Eq. 7, becomes ill-defined. A second consideration is that subjects tend to trace 3D paths whose signed torsion is composed of negative and positive regions. Taking the absolute value of this torsion (as in Eq. 7) thus gives rise to physically unrealizable cusps at locations that are transition regions between positive and negative values for signed torsion. These nonrealizable transition regions must be omitted before any correspondence between speed, curvature, and torsion can be examined. To deal with the planar regions and the torsion cusps we placed a threshold of 2 m\(^{-1}\) on the value of absolute torsion for the fitting procedures of power laws described in the following text, effectively using only data that had absolute torsion values of \( \approx 2 \) m\(^{-1}\) for power-law fitting. This threshold value was the lowest one that enabled us to considerably eliminate not only the planar regions of the movement but also the transition regions of the cusps. Overall, 79% of the data samples had a corresponding torsion value above the threshold and were maintained for the power-law fitting.

The 3D trajectories of all experimental trials were sliced into discrete repetitions using a semiautomatic method, the results of which were examined manually. This slicing procedure eliminated any slow drifts of the drawing pattern in space due to the blindfolded manner of execution. These repetitions are the elemental units of analysis in this study; therefore all power-law fitting (see following text) was carried out globally, encompassing an entire repetition. The perimeter of each repetition was further computed as the sum of the Euclidean distance between consecutive samples of that repetition (i.e., the integral of the path of that repetition). Last, the measure of the nonplanarity of each repetition that we used was the square root of

\[
\text{nonplanarity} = \sqrt{\text{Euclidean distance between consecutive samples}}
\]

4 Similar singularities and cusps in power-law relationships have been noted for the planar two-thirds power law at inflection points (e.g. Viviani and Flash 1995). There, such regions were also discarded.

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**Fig. 1.** Models of the different paths (or shapes) used in the experiments. DBE, double bent ellipse (or bent oblate limacon); FE, figure eight (asymmetric lemniscate); LBE, large bent ellipse; LRH, left-to-right helix (right-to-left for left-handed subjects); SH, left-to-right spiral helix (again, right-to-left for left-handed subjects); and SBE, small bent ellipse.
the smallest eigenvalue of the covariance matrix for that repetition, following Schaal and Sternad (2001).

**Fitting the power laws to the data**

Two power-law comparisons were carried out. In the first, the 2/3-PL and 1/6-PL are compared against each other as well as against the power law

\[ v = a \left( \sqrt[3]{\kappa^2 + \tau^2} \right)^{-\frac{1}{3}} \]  

This power law, introduced by Gielen et al. (2008), suggests that the speed is proportional to the total curvature, i.e., \( \sqrt[3]{\kappa^2 + \tau^2} \), to the power of \(-1/3\). We name it the one-third total-curvature power law and designate it 1/3-Tot-pl. In this first power-law comparison only the best-fit speed gain factor \( a \) (in the least-squares sense) of each of Eqs. 1, 7, and 8 was calculated using linear regression.

In the second power-law comparison, exponents of the power laws were not taken as fixed constants, but rather the least-squares-error speed gain factor and exponents were sought together. In other words, the method was based on simultaneously finding the gain factor and exponents that minimize the squared error between the experimentally measured speed and the speed predicted according to Eqs. 9–12 in the following text (using the curvature and torsion computed from the experimental data).

More formally, instead of the two-thirds power law we have

\[ v = a \kappa^\beta \]  

We name this the curvature power law and denote it by the acronym k-PL. Similarly, instead of the 1/6-PL we have

\[ v = a \kappa^b \tau^\gamma \]  

It is termed the curvature–torsion power law and is often denoted kT-PL in the following text. We also maintain a constrained version of the curvature–torsion power law

\[ v = a \left( \kappa \sqrt{\frac{\tau}{\sqrt{\kappa^2 + \tau^2}}} \right)^\beta \]  

which is named the constrained curvature–torsion power law because of the constraint between its curvature and torsion values. It is denoted c-kT-PL in the following text. This constraint was imposed so that we would have a version of the curvature–torsion power law with the same number of free parameters as the rest of the free-exponent power laws, which makes their comparison simpler. Last, instead of the one-third total-curvature power law, there is

\[ v = a \left( \sqrt[3]{\kappa^2 + \tau^2} \right)^\beta \]  

which we name the total-curvature power law and denote Tot-kPL. These seven power laws are summarized in Table 1.

**Fitting the free-exponent power laws required the use of nonlinear regression to find the best-fit exponents. For each of Eqs. 9–12 we did the following: taking the log of both sides of the equations, the approximate least-squares regression values were calculated with linear regression in this log-space. These values then served as starting points for the subspace trust region nonlinear regression method (Coleman and Li 1994, 1996). This resulted in a best-fit solution for the speed gain factor and exponents, which was double-checked using an exhaustive regional search with iteratively increasing resolution.**

The \( R^2 \) goodness-of-fit statistic (Rao 1973) of linear and nonlinear regression was used to compare among the power laws’ fits to the data. This statistic measures how successful a fit is in explaining the variance of the data (in our case the movement speed) or what ratio of the data variance is explained by the fit (to one of the power laws). It is also named the square of multiple correlation coefficient and the coefficient of multiple determination. More formally, for some predictor data sequence (independent variable) \( x \), \( R^2 \) is the square of the correlation between the response values (dependent variable) \( y \) and the response values predicted by the fit (or the model) \( \hat{y} \). Quantitatively

\[ R^2 = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y})^2} \]

where \( \bar{y} \) is the mean over all \( y_i \). Therefore formally \( R^2 \leq 1 \) and can be zero. However, negative \( R^2 \) scores are actually possible for nonlinear regression only. This arises from the fact that for linear regression \( \sum (y_i - \hat{y}_i)^2 \leq \sum (y_i - \bar{y})^2 \) because, by the definition of linear regression, if some trend is found in the data \( \sum (y_i - \hat{y}_i)^2 < \sum (y_i - \bar{y})^2 \) and thus \( R^2 > 0 \), whereas if no trend is found in the data \( \hat{y}_i = \bar{y} \) for all \( i \), and thus \( \sum (y_i - \hat{y}_i)^2 = \sum (y_i - \bar{y})^2 \) and \( R^2 = 0 \).

**RESULTS**

All subjects were presented with the same set of templates for practice, one for each shape (see Fig. 1). The template was removed before movement onset, leaving the subjects free to trace out their subjective interpretation of the template. Indeed, intersubject variations for each shape were considerable, as can be appreciated from Fig. 2.

**Comparing the 2/3-PL, 1/6-PL, and 1/3-Tot-k-PL**

We initially compared the 2/3-PL, 1/6-PL, and 1/3-Tot-k-PL (see Eqs. 1, 7, and 8, respectively). Figure 3 illustrates the speed prediction of the various power laws versus the experimentally measured speed. We calculated the predicted tangential hand speed of the 2/3-PL, 1/6-PL, and 1/3-Tot-k-PL for six sections of movement, one for each shape. As is apparent, the speed profile of the 1/6-PL is

**TABLE 1. Summary of the seven power laws discussed in text, with their acronyms and formulas**

<table>
<thead>
<tr>
<th>Name</th>
<th>Acronym</th>
<th>Formula</th>
<th>Equation Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Two-thirds power law</td>
<td>2/3-PL</td>
<td>( v = a \kappa^{-\frac{1}{3}} )</td>
<td>(1)</td>
</tr>
<tr>
<td>One-sixth power law</td>
<td>1/6-PL</td>
<td>( v = a \kappa^{-\frac{1}{2}} )</td>
<td>(7)</td>
</tr>
<tr>
<td>One-third total-curvature power law</td>
<td>1/3-Tot-k-PL</td>
<td>( v = a (\sqrt{\kappa^2 + \tau^2})^{-\frac{1}{3}} )</td>
<td>(8)</td>
</tr>
<tr>
<td>Curvature power law</td>
<td>k-PL</td>
<td>( v = a \kappa^b )</td>
<td>(9)</td>
</tr>
<tr>
<td>Curvature-torsion power law</td>
<td>kT-PL</td>
<td>( v = a \kappa^b \tau^\gamma )</td>
<td>(10)</td>
</tr>
<tr>
<td>Constrained curvature-torsion power law</td>
<td>c-kT-PL</td>
<td>( v = a (\kappa \sqrt{\tau/\kappa^2 + \tau^2})^\beta )</td>
<td>(11)</td>
</tr>
<tr>
<td>Total-curvature power law</td>
<td>Tot-k-PL</td>
<td>( v = a (\sqrt{\kappa^2 + \tau^2})^\beta )</td>
<td>(12)</td>
</tr>
</tbody>
</table>
usually closest to that of the measured speed and the 1/3-Tot-κ-PL is typically farthest from it.

More rigorous statistical analysis suggests that the trends observed in Fig. 3 are borne out over the entire movement database. Table 2 gives the $R^2$ statistic of the fit between the speeds predicted by each of the 2/3-PL, 1/6-PL, and 1/3-Tot-κ-PL against the experimentally measured speed (Supplemental Tables S1–S3 give the $R^2$ statistic of these power laws for each subject and shape). On average, the 1/6-PL explains 17% more of the experimentally measured speed variance than does the 2/3-PL and 38% more of the variance than does the 1/3-Tot-κ-PL.

When pooled over all subjects (naturally, always with an equal number of randomly selected samples from each subject), the $R^2$ scores of the 1/6-PL are significantly greater than those of the 2/3-PL for all shapes except LRH (one-way ANOVA and multiple-comparison test of means using Tukey’s honestly significant difference [HSD] criterion, $P < 0.04$ for LBE and $P < 0.001$ for DBE, FE, SH, and SBE) and greater than those of the 1/3-Tot-κ-PL scores for all shapes (one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, $P < 0.001$). The $R^2$ scores of the 2/3-PL pooled over all subjects are significantly greater than those of the 1/3-Tot-κ-PL for all shapes except FE and SH (one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, $P < 0.01$ for DBE and $P < 0.001$ for LBE, LRH, and SBE).

The average $R^2$ scores of the 1/3-Tot-κ-PL for LRH and SBE in Table 2 are negative. As discussed in METHODS, this is because for these shapes the speed profile predicted by the 1/3-Tot-κ-PL explains the experimentally measured speed profile even worse than the average of that experimentally measured speed (Rao 1973).

**Comparing the κ-PL, κτ-PL, c-κτ-PL, and Tot-κ-PL**

We now compare the power laws again when best-fitting both the exponents and the speed gain factors. This tests how well the different power laws describe the movement data without restricting their exponents to the values prescribed in Eqs. 1, 7, and 8. We therefore also calculated the predicted tangential speeds from the κ-PL, κτ-PL, c-κτ-PL, and Tot-κ-PL (see Eqs. 9, 10, 11, and 12, respectively) and compared them to the speeds actually measured in the experiments. Six examples of these speed profiles are depicted in Fig. 4, one for each shape. As is apparent, the speed profiles of the c-κτ-PL and κτ-PL are usually closer to those of the measured speeds than to those predicted by the other power laws.

Once again, more rigorous statistical analysis suggests that the trends apparent in Fig. 4 are manifested over the entire movement database. Table 3 portrays the $R^2$ statistic of the fit between the speeds predicted by each of the κ-PL, κτ-PL, c-κτ-PL, and Tot-κ-PL against the experimentally measured speed for every shape, when pooled over all subjects (Supplemental Tables S4–S7 give the $R^2$ statistic of these power laws for each subject and shape). The κτ-PL explains 3% more of the experimentally measured speed variance than does the c-κτ-PL, 11% more than does the κ-PL, and 19% more of the variance than does the Tot-κ-PL, averaged over all subjects and shapes.

When pooled over all subjects (again, with an equal number of randomly selected samples from each subject), the $R^2$ scores of the κτ-PL are not significantly different from those of the c-κτ-PL for all shapes except SBE (two-way ANOVA and one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, respectively). Moreover, the $R^2$ scores of the c-κτ-PL are significantly greater than those of the κ-PL for four of the six shapes (DBE, FE, LBE, and SH; one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, $P < 0.01$ and not significantly different for the other two shapes (two-way ANOVA) as well as significantly greater than those of the Tot-κ-PL for four of the six shapes (DBE, FE, LBE, and SBE; one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, $P < 10^{-5}$) and not significantly different for the other two shapes (two-way ANOVA). Last, the $R^2$ scores of the κ-PL are significantly greater than those of the Tot-κ-PL for four of the six shapes (DBE, FE, LBE, and SBE; one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, $P < 0.04$ for DBE, FE, and LBE, and $P < 0.01$ for SBE and SBE; one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, $P < 0.01$) and not significantly different for the other

![FIG. 2. Three examples of one repetition from each of the shapes. For each shape a different set of 3 subjects was chosen at random to demonstrate intersubject differences. Axis limits are identical for all plots.](http://jn.physiology.org/)

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criterion, \(P < 0.001\), significantly smaller than the \(\text{Tot-}^{1/3}\)-PL for the SH (one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, \(P < 0.01\)), and not significantly different for the LRH (two-way ANOVA).

Pooling over all subjects and shapes (the last row of Table 3), we find that the \(R^2\) scores of the \(c^{1/3}\)-PL once more are not significantly different from those of the \(c^{1/6}\)-PL, whereas the scores of both these power laws are greater than the \(c^{2/3}\)-PL and \(\text{Tot-}^{1/3}\)-PL (one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, \(P < 10^{-10}\)). The \(R^2\) scores of the \(c^{2/3}\)-PL are also significantly greater than those of the \(\text{Tot-}^{1/3}\)-PL (one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion, \(P < 10^{-10}\)).

Summing up, when averaging not only over all subjects and shapes, but also for each shape separately, the \(c^{1/3}\)-PL and \(\text{Tot-}^{1/3}\)-PL share similar explanatory powers over our data set of movements, even though the first has an extra free parameter over the second. The \(c^{1/3}\)-PL explains the data just as well as, or significantly better than, the \(c^{2/3}\)-PL and the \(\text{Tot-}^{1/3}\)-PL for all shapes separately as well as overall on average. Last, the \(\text{Tot-}^{1/3}\)-PL has the overall worst explanatory power on our movement data set.

### Further investigation of speed–shape relations

At this point we focus our investigation on the \(c^{1/3}\)-PL. We already showed that the constrained version of the \(c^{1/3}\)-PL, the \(c^{1/3}\)-PL, which has the same number of free parameters as the \(2/3\)-PL and the \(\text{Tot-}^{1/3}\)-PL, explains the data better than

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**TABLE 2.** \(R^2\) values for the \(2/3\)-PL, \(1/6\)-PL, and \(1/3\)-Tot-\(\kappa\)-PL over the various shapes averaged over the entire pool of subjects (\(\pm 1SD\))

<table>
<thead>
<tr>
<th>Shape</th>
<th>(2/3)-PL</th>
<th>(1/6)-PL</th>
<th>(1/3)-Tot-(\kappa)-PL</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBE</td>
<td>0.49 ± 0.09</td>
<td>0.65 ± 0.07</td>
<td>0.39 ± 0.13</td>
</tr>
<tr>
<td>FE</td>
<td>0.26 ± 0.25</td>
<td>0.64 ± 0.13</td>
<td>0.27 ± 0.20</td>
</tr>
<tr>
<td>LBE</td>
<td>0.35 ± 0.25</td>
<td>0.56 ± 0.19</td>
<td>0.14 ± 0.49</td>
</tr>
<tr>
<td>LRH</td>
<td>0.45 ± 0.43</td>
<td>0.52 ± 0.30</td>
<td>-0.02 ± 0.66</td>
</tr>
<tr>
<td>SH</td>
<td>0.66 ± 0.11</td>
<td>0.75 ± 0.08</td>
<td>0.66 ± 0.14</td>
</tr>
<tr>
<td>SBE</td>
<td>0.42 ± 0.16</td>
<td>0.57 ± 0.15</td>
<td>-0.04 ± 0.36</td>
</tr>
<tr>
<td>Average</td>
<td>0.44 ± 0.12</td>
<td>0.61 ± 0.08</td>
<td>0.23 ± 0.24</td>
</tr>
</tbody>
</table>

The last row is the grand-averaging over all the shapes as well.
these two power laws. Because the $\kappa$-PL is a generalization of both the c-$\kappa$-PL and the 2/3-PL, it is the most flexible among these three power laws. Also, by definition as in practice, it fits the data just as well as, or better than, these other two. The Tot-$\kappa$-PL, with its relatively poor fit to the data, is no longer pursued.

Table 4 presents the mean and SD of the best-fit $\kappa$ and $\gamma$ exponent distributions for the $\kappa$-PL when pooled over all subjects (Supplemental Tables S8 and S9, respectively, give the best-fit $\beta$ and $\gamma$ values of the $\kappa$-PL for each subject and shape individually). Average $\beta$ and $\gamma$ values among the shapes in Table 4 range between $-0.39$ and $-0.28$ and $-0.15$ and $-0.08$, respectively. The mean values of $\beta$ and $\gamma$ over all subjects and shapes are $-0.32$ and $-0.12$, respectively. These values are not very far from the values of $-0.333$ and $-0.167$, which are congruent with movement at constant equi-affine speed.

Figure 5 presents the results presented in Table 4 in more detail, depicting the joint $\kappa$–$\gamma$ distribution histograms for all shapes. For each shape the $\beta$ and $\gamma$ values are pooled over all subjects, with an equal number of randomly chosen movement repetitions from each subject. (Empirical distributions can be derived from these histograms via normalization and vice versa, given the overall number of repetitions. The terms histogram and distribution will therefore be used interchangeably.)

Taken together, these results suggest that, when grand-averaging over all subjects and shapes, it may be appropriate to describe the speed–shape relations in our data as movement at constant equi-affine speed. Nevertheless, we now seek to delve deeper into the details and examine similarities and differences...
between the best-fit exponents of the $\kappa$-PL for each shape separately.

Rigorous statistical testing suggests that when comparing the $\beta$–$\gamma$ distributions of the various shapes, almost all distributions are significantly different in pairs. [Thirteen of the 15 pairs (87%) of all pairs, except FE–LBE and LRH–SBE, are significantly different. Hotelling’s multivariate extension to Student’s $t$-test was combined with one-way ANOVA and multiple-comparison test of means using Tukey’s HSD criterion on each variable separately, after a Bonferroni correction for multiple comparisons at $P < 0.05$. Performing the same test when raising the significance level to $P < 0.001$ results in just one more pair, DBE–SH, becoming nonsignificantly different.]

Further statistical testing suggests that whereas the intersubject variations in the power-law’s exponent values are small enough to be insignificant, the intershape variations of these exponents are greater and thus significant (mixed-model ANOVA suggests that whereas the means of the exponent values across the different shapes are not all similar, $P = 0.009$ for $\beta$ and $P = 4 \times 10^{-6}$ for $\gamma$, the means of the exponent values across the different subjects are likely the same, $P > 0.9$ for $\beta$ and $P > 0.29$ for $\gamma$; a further F-test suggests that the

<table>
<thead>
<tr>
<th>$\kappa$-PL</th>
<th>DBE $\beta$</th>
<th>FE $\beta$</th>
<th>LBE $\beta$</th>
<th>LRH $\beta$</th>
<th>SH $\beta$</th>
<th>SBE $\beta$</th>
<th>Average $\beta$</th>
<th>DBE $\gamma$</th>
<th>FE $\gamma$</th>
<th>LBE $\gamma$</th>
<th>LRH $\gamma$</th>
<th>SH $\gamma$</th>
<th>SBE $\gamma$</th>
<th>Average $\gamma$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta$</td>
<td>$-0.36 \pm 0.06$</td>
<td>$-0.29 \pm 0.04$</td>
<td>$-0.29 \pm 0.05$</td>
<td>$-0.29 \pm 0.06$</td>
<td>$-0.39 \pm 0.08$</td>
<td>$-0.28 \pm 0.03$</td>
<td>$-0.32 \pm 0.04$</td>
<td>$-0.15 \pm 0.03$</td>
<td>$-0.13 \pm 0.02$</td>
<td>$-0.12 \pm 0.04$</td>
<td>$-0.08 \pm 0.03$</td>
<td>$-0.15 \pm 0.04$</td>
<td>$-0.10 \pm 0.04$</td>
<td>$-0.12 \pm 0.03$</td>
</tr>
</tbody>
</table>

The last column is the grand average over all shapes as well as subjects.

**TABLE 4.** The average ($\pm$1SD) best-fit values of the $\kappa$-PL exponents for each shape averaged over all subjects

**FIG. 5.** Distributions of power-law exponents for the different shapes. Shown are the joint-distribution histograms of $\kappa$-PL’s $\beta$ and $\gamma$ exponents for the different shapes over all subjects, with an equal number of trials sampled from each subject. The color of the bars in the 3D histograms designates the number of occurrences of that bin (mirrored also in the height of the bar), as shown in the color bar on the bottom right. The number of samples in each histogram appears under the name of the shape.
variance of shapes is significantly greater than that of the subjects, \( P = 4 \times 10^{-4} \) for \( \beta \) and \( P = 0.03 \) for \( \gamma \). These differences suggest that the empirical \( \beta - \gamma \) joint distributions for each shape originate from different parent distributions. Put less technically, there tends to be a distinct \( \beta - \gamma \) distribution for each shape.

The above-cited results suggest the following: \( >60\% \) of the variance in spatial movement speed can be explained by the path being traversed at 3D constant equi-affine speed in 3D (i.e., according to the 1/6-PL; Table 2). Moreover, almost three quarters of spatial movement speed variance can be explained by relaxing the constant equi-affine speed constraint on the exponents of the \( \kappa-PL \) (Table 3), with the over-all-shapes and subjects exponent averages varying around values close to those predicted by spatial constant equi-affine speed movement. Nevertheless, this small variance of the exponent values among the different shapes is still significant and systematic.

As noted in the INTRODUCTION, a few studies demonstrated that for the planar case, the exponent of the \( \kappa-PL \) may change systematically with the path (Schaal and Sternad 1999; Wann et al. 1988). Of special interest is the study by Schaal and Sternad (2001), which investigates the 2/3-PL for unconstrained ellipse tracing in 3D space. They find that the fit to the planar \( \kappa-PL \) decreases with the increase in the global geometric parameters of perimeter and nonplanarity, both in terms of the exponent value deviating from \(-1/3\) and in terms of the \( R^2 \) score decreasing. They attribute this to nonlinearities inherent in mapping from joint to hand coordinates and to the smooth oscillatory nature of joint rotations. Yet we suspect that their observed deviations are due, at least in part, to their attempt to explain movement data that are inherently 3D with a power law resulting from planar constant equi-affine speed. Indeed, because their ellipses became less planar the divergence they measured from the two-thirds power law (i.e., from planar constant equi-affine speed) increased.

The fact that the spatial 1/6-PL and \( \kappa-PL \) both explain spatial movement data significantly better than the planar 2/3-PL and \( \kappa-PL \), respectively, seems to lend evidence in favor of our suspicion that Schaal and Sternad (2001) used the inappropriate planar equi-affine framework to account for their data, instead of a more suitable explanation in terms of spatial equi-affine speed. However, the small, yet systematic, variability of the power-law exponents with shape demonstrated in Table 4 suggests that the global geometric parameters of perimeter and nonplanarity might affect the \( \kappa-PL \) as well. We therefore decided to test the effect of the global-shape parameters of perimeter and nonplanarity on the fit of the \( \kappa-PL \) to the data in terms of exponent values and \( R^2 \) scores.

The correlation between the mean \( R^2 \) value of the power-law fit for each shape, given in Table 3, and the corresponding mean perimeter and nonplanarity values of these shapes, in Table 5, is insignificant (0.48 between the \( R^2 \) scores and the perimeter and \(-0.11 \) between the \( R^2 \) scores and the degree of nonplanarity, with corresponding \( t \)-test \( P \) values of 0.34 and 0.84, respectively). This suggests that the \( R^2 \) score of the fit of the \( \kappa-PL \) to the data does not decrease when the perimeter or nonplanarity increase, unlike the fit of the \( \kappa-PL \) to the data analyzed by Schaal and Sternad (2001).

We further wanted to test whether shapes with similar average perimeter and nonplanarity values (Table 5) tend to obtain similar average values of the exponents of the \( \kappa-PL \) (Table 4). We therefore defined a distance measure for the perimeter and nonplanarity values between all shape pairs as well as a distance measure for the exponents of the \( \kappa-PL \) between all shape pairs. We then tested whether these distances tended to covary—whether shapes separated by small perimeter–nonplanarity distances (i.e., shapes with similar average perimeter and nonplanarity values) tend to also be separated by small \( \beta - \gamma \) distances (i.e., tend to have similar average \( \beta \) and \( \gamma \) values).

We defined the distance measure between the mean \( \beta \) and \( \gamma \) exponents of every pair of shapes as the \( L_2 \) distance between corresponding pair of points in the \( \beta - \gamma \) plane. For example, if the mean \( \beta \) and \( \gamma \) exponent values for a pair of shapes are \( \beta_1 \) and \( \gamma_1 \), respectively, for the first shape and \( \beta_2 \) and \( \gamma_2 \), respectively, for the second shape, we define \((\beta_1 - \beta_2)^2 + (\gamma_2 - \gamma_1)^2 \) to be the \( \beta - \gamma \) distance between that pair of shapes. The distance measure between the perimeter and nonplanarity values of every pair of shapes was similarly defined as the \( L_2 \) distance between the corresponding pair of points in the perimeter–nonplanarity plane. For example, if the mean perimeter and nonplanarity of a pair of shapes are \( p_1 \) and \( n_1 \), respectively, for the first shape and \( p_2 \) and \( n_2 \), respectively, for the second shape, then \((p_2 - p_1)^2 + (n_2 - n_1)^2 \) is the perimeter–nonplanarity distance between that pair of shapes.

Because there are six shapes, there are 15 \((6 \times 5)/2\) shape pairs. The correlation between the \( \beta - \gamma \) distances and the perimeter–nonplanarity distances was found to be significant (0.74, with the corresponding \( t \)-test \( P \) value of 0.002), suggesting that shapes with similar average perimeter and nonplanarity values indeed tend to have similar average \( \kappa-PL \) exponents. We similarly examined whether shapes with perimeter and nonplanarity values alike have \( R^2 \) scores for the power-law fit that are alike. This time, however, we found no significant correlation (the correlation between the perimeter–nonplanarity distance and the \( R^2 \) distance is 0.44, with the corresponding \( t \)-test \( P \) value of 0.1, and for the \( \kappa-PL \) and 0.43, with the corresponding \( t \)-test \( P \) value of 0.11, for the 1/6-PL). This indicates that shapes with similar mean perimeter and nonplanarity values do not necessarily have \( R^2 \) scores that are alike and vice versa.

**DISCUSSION**

Under the hypothesis that the brain might use non-Euclidean geometry to plan and control movements, this study empiri-

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**Table 5. The perimeter and nonplanarity measures for each shape averaged over all subjects and repetitions (±1SD)**

<table>
<thead>
<tr>
<th></th>
<th>DBE</th>
<th>FE</th>
<th>LBE</th>
<th>LRH</th>
<th>SH</th>
<th>SBE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perimeter</td>
<td>2.350 ± 0.504</td>
<td>1.140 ± 0.224</td>
<td>1.531 ± 0.275</td>
<td>1.886 ± 0.844</td>
<td>2.929 ± 1.073</td>
<td>1.026 ± 0.142</td>
</tr>
<tr>
<td>Nonplanarity</td>
<td>0.051 ± 0.015</td>
<td>0.011 ± 0.002</td>
<td>0.061 ± 0.013</td>
<td>0.033 ± 0.012</td>
<td>0.053 ± 0.013</td>
<td>0.044 ± 0.005</td>
</tr>
</tbody>
</table>

The perimeter and nonplanarity for each subject separately are given in Supplemental Tables S10 and S11, respectively.
cally examines the idea that the hand may move at constant equi-affine speed when repetitively tracing 3D shapes. Whereas for the planar case constant equi-affine speed results in the two-thirds power law between drawing speed and curvature, constant spatial equi-affine speed entails a new power law, which we name the one-sixth power law between drawing speed, curvature, and torsion.

We have previously demonstrated that this new power law explains 3D scribbling movements rather well (Pollick et al. 2008). The results presented here suggest that the power law also explains 3D shape-tracing movements just as well and certainly significantly better than the two-thirds power law and another power law previously proposed for this purpose. If we allow the power-law’s exponents to take their best-fit values over each repetition of each shape, the power law again explains the data significantly better than the other power laws, with the average exponent values over all subjects and shapes not far from those consistent with movement at constant spatial equi-affine speed.

The inherent noisiness of the human motor system makes variability in end-effector motion inescapable, especially during unconstrained self-paced 3D movement. Moreover, our subjects traced their own subjective interpretation of complex spatial shapes (there was no visual feedback while drawing due to the blindfolded manner of execution), which resulted in considerable additional variability among the trajectories traced for each shape (see Fig. 2). Therefore given the differences among subjects for each shape as well as between consecutive repetitions of every shape for the same subject, the fact that a deterministic power law can capture almost three quarters of the variability of motion over the duration of an entire repetition of a complex shape (lasting ≥5 s) is noteworthy.

Most research on power laws of hand motion for shape-tracing is based on data containing at most two or three shapes; moreover, even studies that do cover a larger number of paths do not directly examine differences between the best-fit exponents over different shapes. Any such differences tend to be attributed to noise in the motor system or to other transitory irregularities in execution. Our data, which consist of hand movements along six different complex paths, enable us to study the differences in the curvature–torsion power-law’s exponents over this relatively large number of different shapes. We therefore decided to investigate these intershape differences more thoroughly, seeking to find some explanation for the observed differences.

The best-fit exponents of the curvature–torsion power law across the various shapes were shown to have small, though significant, differences among almost all shape pairs. This suggests that the amount of local influence of geometrical shape (characterized by curvature and torsion) on instantaneous movement speed slightly varies among shapes. Further analysis suggests that the combination of global geometrical parameters of shape perimeter and nonplanarity is significantly correlated with the power-law exponents of the different shapes—similar global geometric form translates into similar power-law exponents and vice versa.

Importantly, unlike the power-law exponents, the goodness of fit of the power law to the data (i.e., the $R^2$ score) is not influenced by global geometric parameters, such as the extent of the perimeter and the degree of nonplanarity. This indicates that the curvature–torsion power law, as it was formulated in Eq. 10, is broad enough to capture the shape-induced variability in speed–shape relations. Moreover, its grand-averaged exponent values over all shapes, as well as those for scribbling (Pollick et al. 2008), are in general accordance with constant spatial equi-affine speed. Nevertheless, origins of the deviations from constant equi-affine speed remain unclear and may well be due to anything from centrally controlled to epiphenomenal behavior. Further research is therefore required to give a fuller and more structured account of the observed results.

Some implications of this work

Evidence is mounting that movements at roughly planar constant equi-affine speed or, equivalently, movements that approximately obey the two-thirds power law originate from central (i.e., CNS-based) control and planning mechanisms. Single-cell monkey recordings demonstrate that population vector coding in the motor and premotor cortex obeys the two-thirds power law during motion execution (Schwartz 1994; Schwartz and Moran 1999, 2000). Moreover, a recent fMRI study in humans shows that motion perception seems to reflect this constraint and the brain’s response to this law of motion is much stronger and more widespread than that to other types of movement (Dayan et al. 2007). It therefore seems plausible to hypothesize that movements at roughly constant 3D equi-affine speed—like motion according to the curvature–torsion power law with its slightly different exponents for different shapes—may also stem from central mechanisms.

Under this assumption, our current results seem to suggest that when planning and controlling the execution of complex shapes, a major objective of the motor system might be to generate motion that is constant under the equi-affine framework. Moreover, this constant equi-affine speed motion seems to undergo fine-tuning of its local speed–shape relation, possibly according to global characteristics of the path, such as the perimeter and nonplanarity of the traced shape. Viewing scribbling movements as sequential temporal concatenation of various 3D segments, its planning, and execution may follow some average case shape-based exponent values, which our data suggest to be not very far from those compatible with constant equi-affine speed (see Table 4). This may explain why scribbling movements tend to conform to constant spatial equi-affine speed (Pollick et al. 2008).

The fact that speed varies with torsion as well as curvature may further explain, at least partially, the results of Schaal and Sterman (2001). There it was demonstrated that for ellipses traced freely in 3D space, the two-thirds power law is systematically violated with increased pattern size, which is also consistent with increased nonplanarity. This violation is manifested both in exponent values that depart from $-1/3$ and in a deterioration in the goodness of fit of the two-thirds power law to the data. Moreover, as planarity decreases torsion becomes more prominent. This caused their data to be increasingly incompatible with movement at planar constant equi-affine speed movement (i.e., to be incompatible with the $2/3$-PL). By
contrast, the goodness of fit of our movement data to the spatial constant equi-affine speed model does not deteriorate with the increase in perimeter or in nonplanarity. This provides further evidence for our claim that the corresponding increasing divergence of the data of Schaal and Sternad (2001) from the two-thirds power law is a result of their attempt to explain their 3D data with a model that is suitable only for the planar case, i.e., with constant planar equi-affine speed.

Future research directions

As detailed in METHODS, our subjects repetitively traced the various shapes of Fig. 1. These 20-s-long movement trajectories were then sliced into discrete repetitions of the shape (see Fig. 2 for some examples of repetitions). Each repetition was then fit with the various power laws. It should thus be borne in mind that for the above-cited analyses we used only one value for the speed gain factor ($\alpha$ in Eqs. 7 and 10) per movement repetition, which lasted $\approx5$ s. However, it was demonstrated that the speed gain factor of the two-thirds power law ($\alpha$ in Eq. 1) is merely piecewise constant when tracing complex planar shapes, with the shifts in the otherwise roughly constant speed gain factor occurring in the transitions between consecutive segments of the drawing movement (Viviani 1986; Viviani and Cenzato 1985; Viviani and Flash 1995). This means that such paths are traced with only piecewise constant equi-affine speed (Flash and Handzel 2007; Handzel and Flash 1999). Thus consecutive segments may invoke the use of different equi-affine speeds.

Nevertheless, additional claims that this segmentation may reflect central segmented control (Viviani 1986; Viviani and Cenzato 1985) were contrasted with results suggesting this segmentation to be epiphenomenal to continuous smooth minimum-jerk control at the hand level (Richardson and Flash 2002) or to nonlinear transformations of the forward kinematics of human arms that perform smooth multijoint rotations, which are governed by continuous control (Dounskaia 2007; Sternad and Schaal 1999). It will therefore be interesting to test what type of segmentation is implied by the one-sixth or curvature–torsion power laws and how much more of the variance in the speed profile might be explained by geometry under the assumption of movement segmentation. Furthermore, it would be intriguing to investigate the relation between any movement segmentation and the slight dependence of the curvature–torsion power-law exponents on shape.

The two-thirds power law was shown to possibly result from various planning strategies that favor smooth trajectories in hand- or joint space (Gribble and Ostry 1996; Richardson and Flash 2002; Schaal and Sternd 2001; Todorov and Jordan 1998; Viviani and Flash 1995; Wann et al. 1988). The minimum variance principle was also demonstrated to predict this power law, at least for simple elliptical trajectories (Harris and Wolpert 1998). It would therefore be important to test whether the curvature–torsion power law and any segmentation scheme it may imply can be derived from smoothness (or smoothness-compatible) criteria in joint- or hand-space. Moreover, it was recently suggested that the two-thirds power law might be at least partially due to correlated noise in the motor system (Maoz et al. 2006). It would thus be interesting to test whether similar results might be extended to the one-sixth or curvature–torsion power laws.

We have demonstrated that the global shape characteristics of perimeter and nonplanarity modulate the exponents of the curvature–torsion power law. However, more research is needed to establish to what extent these modulations in the speed–shape relations reflect central planning and to what extent they are a by-product of peripheral factors, such as muscle dynamics. Further research is also required to investigate which shapes and which other characteristics of movement, if any, systematically modulate the predicted spatial speed–shape relation derived from the assumption of constant spatial equi-affine speed. Other geometrical features that may possibly also influence the speed profile include, for example, orientation and ratios between the lengths of various segments in different directions. Average speed, bounds on maximum acceleration, and other kinematic parameters may also play a role, as may joint rotations, muscle flexion, gravity, and other dynamic factors. Optimal feedback control and the choice of task-relevant and task-irrelevant parameters (Todorov and Jordan 2002) may also modify speed–shape relations.

Last, we found a small dependence of the speed–shape relation on the global shape of the drawing, on the one hand, combined with an over-all-shapes general compliance of this relation with constant equi-affine speed, on the other hand. This dual behavior might indicate that although planar or spatial motion at constant equi-affine may be the primary governing principle for the corresponding drawing movements, it may not give a full and final account of the finer-grain intershape modulations in speed–shape relations. From the perspective of non-Euclidean geometry, the constant equi-affine framework might need refinement because it is possibly not broad enough to completely explain the intricacies of the functional organization of human sensorimotor space for the aforementioned drawing task.

Conclusions

Herein we have proposed and experimentally tested a model of instantaneous speed–shape covariation for hand movement, which stems from the notion of motion at constant spatial equi-affine speed. With a database composed of shape-tracing movements of six different geometrical paths, our results suggest that the model’s predictions fit the data rather well, with unconstrained spatial drawing movements slowing down not only in regions of high curvature but also in regions of high torsion (although to a lesser extent, as the model predicts). This model results in a power law that describes the relationship between spatial speed and geometry significantly better than the two-thirds and total-curvature power laws, enabling a more accurate speed profile prediction for a given path. We further demonstrated small systematic modulations of the power-law’s exponents, which were shown to depend, at least partially, on global geometric characteristics of the path. However, these exponents are in general accordance with constant spatial equi-affine speed when averaged over all shapes. This suggests that although local path geometry is the primary determining factor for instantaneous hand speed, via the constant equi-affine framework, this speed is also dependent, to a much lesser extent, on global geometric factors.

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REFERENCES
Gileadi CCAM, Disler TMH, Roozen LJ, Welten J. Coordination of gaze and hand movements for tracking and tracing in 3D. Cortex (July 11, 2008). [Epub ahead of print].