Timing of continuous motor imagery: the two-thirds power law originates in trajectory planning

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Karklinsky M, Flash T. Timing of continuous motor imagery: the two-thirds power law originates in trajectory planning. J Neurophysiol 113: 2490–2499, 2015. First published January 21, 2015; doi:10.1152/jn.00421.2014.—The two-thirds power law, \( v = \gamma \kappa^{-1/3} \), expresses a robust local relationship between the geometrical and temporal aspects of human movement, represented by curvature \( \kappa \) and speed \( v \), with a piecewise constant \( \gamma \). This law is equivalent to moving at a constant equi-affine speed and thus constitutes an important example of motor invariance. Whether this kinematic regularity reflects central planning or peripheral biomechanical effects has been strongly debated. Motor imagery, i.e., forming mental images of a motor action, allows unique access to the temporal structure of motor planning. Earlier studies have shown that imagined discrete movements obey Fitts’s law and their durations are well correlated with those of actual movements. Hence, it is natural to examine whether the temporal properties of continuous imagined movements comply with the two-thirds power law. A novel experimental paradigm for recording sparse imagery data from a continuous cyclic tracing task was developed. Using the likelihood ratio test, we concluded that for most subjects the distributions of the marked positions describing the imagined trajectory were significantly better explained by the two-thirds power law than by a constant Euclidean speed or by two other power law models. With nonlinear regression, the \( \beta \) parameter values in a generalized power law, \( v = \gamma \kappa^{-\beta} \), were inferred from the marked position records. This resulted in highly variable yet mostly positive \( \beta \) values. Our results imply that imagined trajectories do follow the two-thirds power law. Our findings therefore support the conclusion that the coupling between velocity and curvature originates in centrally represented motion planning.

motor imagery; motor control; trajectory planning; two-thirds power law; equi-affine geometry

EXECUTION OF HUMAN MOVEMENT requires consideration of geometry (movement path) and timing (velocity profile along this path). The concept of geometric invariance is important in unraveling how the central nervous system selects specific paths and timing. The influence of path geometry on timing is well captured by the two-thirds power law (Lacquaniti et al. 1983), \( \omega = C \kappa^{2/3} \), relating angular speed \( \omega \) to curvature \( \kappa \). This law is an example of invariance, because motion satisfying this law has constant equi-affine speed (Flash and Handzel 1997; Pollick and Shapirio 1996). Other geometries may play a role in movement generation (Bennequin et al. 2010), but equi-affine geometry is the most robust example of invariance and is found in smooth pursuit eye movements (de’Sperati and Viviani 1997), full body locomotion (Hicheur et al. 2005), leg motions (Ivanenko et al. 2002), speech (Tasko and Westbury 2004), and visual perception of motion (Viviani and Stucchi 1992). Here we use an equivalent formulation of the two-thirds power law, \( v = \gamma \kappa^{-\beta} \), relating speed \( v \) with curvature \( \kappa \), with exponent value \( \beta = 1/3 \), and \( \gamma \) a constant named the velocity gain factor.

Does the two-thirds power law indicate invariance in motor plans? The two-thirds power law may derive from biomechanics (the low-pass filtering properties of muscles; Gribble and Ostry 1996), it may be a by-product of oscillatory movement generators in joint space (Schaal and Sernad 2001) or of limb dynamics. Alternatively, it may arise from the intrinsic encoding of trajectory planning within the central nervous system. This latter view is supported by the encoding of kinematic features of hand trajectories in the size and direction of the population vector reflecting the activities of neural populations within various cortical areas (Schwartz and Moran 1999). Additionally, visual perception of the motion of dots moving along elliptical trajectories while obeying the two-thirds law evokes larger and stronger brain responses than perception of movements complying with other laws of motion (Dayan et al. 2007; Meirovitch et al. 2015). These findings support a central origin of this law in both motion planning and perception.

Motor imagery as a tool for deciphering the motor plan. Motor imagery is the mental simulation of a movement without executing it. We assume (following Jeannerod 1995) that motor imagery is functionally equivalent to the covert part of movement generation without overt execution. This functional equivalence is supported by imaging studies showing similar brain activation patterns during motor imagery and execution (Hétu et al. 2013; Lotze et al. 1999; Sharma and Baron 2013). It implies that the rules governing the kinematics of movement generation should apply to motor imagery (cf. Fitts’s law in Decety and Jeannerod 1995). While total durations of imagined and generated movements are similar (see Guillot et al. 2012 for review but also Rodriguez et al. 2008), little is known about the timing profiles and the role of invariances such as the two-thirds power law in motor imagery.

To examine whether imagined movements comply with the two-thirds power law, Papaxanthis et al. (2012) recently compared global movement durations of imagined and executed movements. The imagined movement durations were correlated with the accumulated path curvature but not with the number of curved regions along the imagined template. Here we introduce a more direct paradigm for examining the kinetics of imagined movements. We show that their speed profiles are similar to those of executed movements and are captured by the two-thirds power law. Our findings support central origins for the two-thirds power law, and our methods may open a new frontier in addressing the timing and geometry of continuous movements during motor imagery.

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METHODS

Imagine, stop, and report—a paradigm for recording imagined motion. We designed a novel experimental paradigm specifically to extract the properties of imagined movements. Our basic method involved stopping the subjects at arbitrary times during an imagined drawing motion and asking them to report the imagined locations of their hand. By studying the dynamically evolving hand positions throughout imagined movements, our paradigm allowed us to examine not only the durations of complete imagined movements but also their speed profiles.

During the experiment on imagined motion each subject imagined drawing a given cyclical template on a tablet for one training session and four recording sessions, each comprising 30 trials. To prevent influence of prior execution on the imagery task, subjects were instructed to never actually draw the shape prior to the completion of the imagery part of the experiment.

Subjects were instructed to imagine a constant pace of 3–4 s per lap, to avoid actually moving their right hand (the one they imagined to be moving), and to discard any trial if they were uncertain of its quality, e.g., the fluency of imagery.

The trials in the main imagery experiment comprised a complex task (Fig. 1B) that allowed extraction of the duration and extent of the full cycles of the imagined trajectories, as well as of particular segments within them. The subjects watched the template displayed on the tablet with a red dot marking the start of the cycle. An auditory cue marked the start of each trial. The subjects closed their eyes and imagined a clockwise movement at a constant pace. Each time the imaginary movement passed through the red dot, the subjects pressed a key with their left hand. Another high-pitched auditory cue sounded at a random interval after the first cue. The subjects memorized the imagined hand position at that time and continued the imagined movement, again pressing the key with the left hand each time a cycle was completed. Two more laps after the second auditory cue, a third, longer auditory cue was played and the subjects stopped the imagined movement and opened their eyes. The subjects marked on the screen the memorized position that their imaginary trace had reached at the time of the second auditory cue, unless they failed to memorize this position or made some mistake in the imagery process. In this case, the subjects marked a box on the upper right corner of the screen to discard this record. Each trial was followed by a short rest period.

In this experiment, the subjects were required to memorize the imagined position at the time of the second auditory cue over two laps. We conducted another version of the experiment to control for the involvement of memory. This version differed in that, on hearing the second auditory cue, subjects immediately opened their eyes and marked the imagined position of their hand on the tablet, without continuing the imagined motion. To indicate the difference between the two experiments, we denote the main experiment as MEM and the control experiment that lacked the long memorization period as NO MEM.

Normalization and correction of recorded imagery data. Unlike standard experimental imagery procedures, in which only one duration and arc length measurement are recorded for each trial, our MEM experiment gathered three durations and their three corresponding arc lengths for each complex trial (Fig. 1C). The durations measured included the durations of two full cycles of imagined movement (marked $T_p$ and $T$) and the duration of a specific segment contained within the second lap (marked $\tilde{t}$), which started at the fixed red dot and ended at the time of hearing the high-pitched auditory cue. For the full laps the matching arc length was simply the constant full lap length (marked $S$), and for the specific segment the arc length was measured along the curve between the fixed red dot marking the start position and the location that the subject marked on the tablet at the end of the trial (marked $s$).

In the NO MEM procedure the second lap was not complete, as the subject stopped the imagery immediately after hearing the auditory cue and did not complete the lap containing the specific segment. Therefore, in the NO MEM experiment only $\tilde{t}$ and $T_p$, but not $T$, were recorded.

To overcome the dependency of segment duration on the gain factor $\gamma$ (see DISCUSSION for details), we normalized the segment duration with respect to the total duration of the same lap, marking it as $\tilde{t} = \frac{\tilde{t}}{T}$. We also normalized the segment duration with respect to the total duration of the prior lap and marked it as $\tilde{t}_p = \frac{\tilde{t}}{T_p}$. We further normalized the segment arc length with respect to the total lap arc length and marked it as $\tilde{s} = \frac{s}{S}$. These normalizations were performed for each trial separately; thus we did not need to assume that the gain factor $\gamma$ had the same values in different trials. Measured $\tilde{s}$ and $\tilde{t}$ values for six subjects are shown in Fig. 2.

Note that $\tilde{t}$, $\tilde{t}_p$, and $\tilde{s}$ are all cyclical with period 1, because our analysis considered only movements from the last passage through the starting point to the hand location imagined by the subject when he/she heard the second auditory cue. By default, the values of $\tilde{t}$ fell within the range of $[0,1]$. The $\tilde{s}$ values also fell within the range of $[0,1]$, with rare exceptions (<6% of all trials). When subjects marked a location on the tablet in the vicinity of the red dot, i.e., the point at which $\tilde{s} = 0$, which is also the point at which $\tilde{s} = 1$, we had to decide whether to include the reported values as located closer to $\tilde{s} = 0$ or to $\tilde{s} = 1$. Our decision was based on the value of $\tilde{t}$. By default, we
selected the first option and reported \( \tilde{s} \) as being closer to 0. Only when the value of \( \tilde{t} \) was larger than 0.75 did we choose to report the value of \( \tilde{s} \) as being closer to 1. This procedure ensured that of the two possible interpretations of the data the one selected had the \( \tilde{t} \) and \( \tilde{s} \) values closer to each other.

To avoid ambiguity in interpreting the location of the marked positions around the self-intersection points of the limaçon paths, we removed all marked data points within a 1-cm radius around these points.

**Recording actual motions and questionnaires.** The second part of the experiments included actual movement recordings. The subjects traced trajectories on the tablet, following the template previously used for imagery. Two sessions of the drawing task were recorded, each session comprising six trials of six laps each (overall 72 repetitions).

The subjects were instructed to draw as continuously and as smoothly as possible, without changing pace, and not to pay attention to the accuracy of their drawing. They rapidly traced the shapes with their right hand and with their eyes open and used their left hand to press a key each time the pen passed through the red dot marking the start position.

Data were taken from the six trials of the second session, discarding the first two laps and the last lap of each trial (we also manually removed 1 lap of a single subject because of an extreme deviation from the template). This left 18 laps for each subject.

The subjects were also asked to take the Edinburgh questionnaire, measuring right-handedness (Oldfield 1971), the MIQ-RS questionnaire, measuring movement imagery ability (Gregg et al. 2010), and a follow-up questionnaire in which the subjects reported whether they actually moved any body part during the imagery task. The actual drawing trials, the follow-up questionnaire, and the MIQ-RS questionnaire were always administered after completion of the imagery task.

**Participants, settings, and templates.** Forty-five healthy subjects (19 men and 26 women, ages 18–33 yr) participated in the 3-h experiment that included imagery recording, actual drawing, and answering questionnaires. The experimental procedure was approved by the local Ethics Committee, and written informed consent was obtained from all subjects.

Subjects sat in front of a WACOM tablet (142 Hz sampling rate) placed on a 100-cm-high table. The tablet’s surface was tilted 65° from the horizontal plane. Subjects adjusted the chair height, the distance from the tablet, and the keyboard location to a comfortable position. They held a pen in their right hand, and their left hand was placed on the keyboard. Templates displayed on the tablet (see Fig. 1A) included two limaçons with ratios of 1:3 (L13) and 2:3 (L23) between the arc lengths of their inner (smaller) and outer (larger) loops, scaled by a factor of 1.7 compared with the limaçons used in Viviani and Flash (1995), and an ellipse (ELL; with major axis of 14 cm and minor axis of 3.5 cm with major axis tilted at 45° to the x-axis). A red mark was displayed on the figural forms (on the top right extremity of ELL and on the rightmost extremity of the limaçons) to indicate the starting point of each cycle.

Data of subjects who failed to comply with one of the requirements were eliminated as follows: subjects who discarded >40 data points, leaving <80 valid data points; subjects whose MIQ score was lower than 4, indicating poor imagery skill; or subjects whose LQ score was <0.7, indicating not being fully right-handed. One subject failed to perform the task. After elimination of the data of these subjects, the remaining data comprised 7, 7, and 7 MEM subjects and 3, 5, and 5 NO MEM subjects for the L13, L23, and ELL templates, respectively, and an additional outlier subject for the L23 template, whose results were not included in the statistical analysis and are reported separately.

**Actual motion during imagery.** A primary concern when examining motion imagery is whether the subject also produced some correlated...
but unreported movement. Subjects performed the experiments with eyes closed and with the right hand resting in a fixed position on the table. This ensured that they did not produce any large hand movements. We emphasized to the subjects the need for kinesthetically imagining their right hand moving, as opposed to visually imagining it. In a follow-up questionnaire only 6 of the 34 subjects reported moving their right hand during the imagery trials (always reporting a total movement amplitude smaller than 5 cm). However, all subjects reported moving either the head or the closed eyes at least once during imagery, and one subject reported moving the leg, while another reported moving the tongue.

Behavioral (Papaxanthis et al. 2012) and MRI (Chiew et al. 2012; Raffin et al. 2012) studies have shown that imagery activity does not give rise to activity in the arm muscles. Eye movements are naturally coupled with imagined hand movements (Heremans et al. 2008), but they have no effect on the temporal properties of the imagined movements (Gueugneau et al. 2008). Hence, many motor imagery experiments have not used EMG or EOG measurements for well-performed imagery tasks (Rodriguez et al. 2008, 2009). Relying on these observations, we focused on natural imagery production, disregarding any secondary muscular effects that may have arisen during imagery.

Statistical analysis of distributions. Unlike our drawing data, our imagery data were sparse, containing not more than 120 data samples per subject. The sparseness prevented reconstruction of speed profiles as the numeric derivative of the normalized location profile. Instead, we examined the distributions of marked locations, represented by the \( \hat{s} \) parameter. In the distributions of marked locations along a curve (see Fig. 2 for several individual subjects’ data points and distributions), the number of markings within each bin indicated the speed of the imagined movement; the probability of stopping within a specific bin was directly related to the time the subject spent imagining the movement within this bin. This time is inversely related to the speed of the imaginary movement within this bin. Hence, the speed profiles of the imagined movements can be inferred from these distributions.

Qualitatively, for the generalized power law model, \( v = \gamma \kappa^{-\beta} \), positive \( \beta \) values (such as the two-thirds power law, \( \beta = \frac{1}{3} \)) predict that more markings will occur during the more curved segments of a template, where the movement is slower. Quantitatively, each value of the exponent \( \beta \) predicts a unique distribution for each template. Therefore, to examine the validity of different power laws, we examined how well the predicted power law distributions described measured distributions of imagery and drawing data.

Using the measured data, we extracted the distribution of both \( \tilde{t} \) and \( \hat{s} \) within bins covering the range of \([0.05,0.95]\). For each studied power law we calculated the predicted distributions of \( \hat{s} \) based on this law of motion. The measured distribution of \( \tilde{t} \) established a specific distribution of the predicted values of \( \hat{s} \), calculated by using the normalized speed profile defined by this law of motion. Integrating this speed profile gave a prediction of an \( \hat{s} \) value for each value of \( \tilde{t} \) and, hence, a distribution of \( \hat{s} \) values for each distribution of \( \tilde{t} \) values. The observed and modeled distributions of \( \hat{s} \) for six subjects are shown in Fig. 2.

We compared the measured distribution of \( \hat{s} \) for each subject with the corresponding distribution of the predicted \( \hat{s} \) (based on the subject’s measured \( \tilde{t} \) values), using the \( \chi^2 \) goodness of fit test for each law of motion studied here.

For each law of motion we calculated its log likelihood value,

\[
\text{LL} = \sum_i d_i \ln P_i
\]

where \( d_i \) is the number of observed data points in bin \( i \), \( P_i \) is the number of data points predicted by the model for this bin, and the summation is across all bins.

To qualitatively compare the extent to which each of two laws of motion matched the measured data, we derived the log of the likelihood ratio for the two predicted distributions for each subject, calculated as the difference

\[
\ln \lambda = \text{LL}_{\text{alternative}} - \text{LL}_{\text{null}}
\]

where \( \lambda \) is the likelihood ratio stating how well the alternative model outperforms the null model. The likelihood ratio test was performed by comparing \( \lambda \) to a \( \chi^2 \) distribution with 1 degree of freedom.

We used a similar process for the comparison of an alternative model to several null models, where each comparison was made between the alternative model and the most likely of the null models.

We also compared log likelihood values of several models using repeated-measures ANOVA, which demonstrated which power laws were more likely than others. Conformity with normal distributions was tested with Shapiro-Wilk tests, and post hoc analysis using \( t \)-tests was corrected with the Fisher least significant difference (LSD) method.

Statistical analysis of speed profiles as power laws. In addition to the analysis of the distributions of the marked locations we examined the dependency of \( \hat{s} \) on \( \tilde{t} \) within an imagined movement. We considered models of normalized speed \( \tilde{v} = \frac{\partial \hat{s}}{\partial \hat{t}} \) as power laws of the form \( \tilde{v} = \gamma \kappa^{-\beta} \). We wished to estimate \( \beta \), which is the only free parameter of this model (because \( \int_0^1 \tilde{v} \, \text{d}\hat{t} = 1 \) so \( \gamma \) is uniquely determined). We defined an error term, the cyclic mean squared error (CMSE), in \( \hat{t} \) to be

\[
\text{CMSE}(\hat{t}, \hat{s}) = \sum d(f_{\text{model}}(s_i, t_{\text{data}}), t_{\text{data}})^2
\]

where \( f_{\text{data}}, f_{\text{data}} \) are the measured data points, \( f_{\text{model}}(x) \) is a function calculating predicted \( f \) values for given \( f \) values and for a given value of \( \beta \), and \( d(x,y) = \min(1-x, 1 - 1x - y) \) is the cyclic distance (used because of the cyclic nature of our variables). Nonlinear regression estimated the \( \beta \) value that minimized the CMSE error, along with the confidence intervals for \( \beta \) based on \( \alpha = 0.05 \).

This procedure for extracting \( \beta \) values for each whole shape was used for both the imagery and drawing data. We studied the extracted \( \beta \) values using a repeated-measures two-way ANOVA, comparing imagery and drawing across the studied templates. Conformity with normal distributions was tested with Shapiro-Wilk tests, sphericity violations were corrected by the Greenhouse-Geisser method, and post hoc analysis using \( t \)-tests was corrected with the Fisher LSD method.

For the data from drawing the limaçon shapes we also used the extracted \( \beta \) values along with the durations \( T \) to calculate the gain factor \( \gamma \). The \( \beta \) values, as well as the gain factor values, were compared for pairs of matching small and large loops comprising the limaçon laps with a Wilcoxon signed-rank test.

RESULTS

Distribution of subjects’ marked locations. A distribution of marked locations corresponds to an imagery speed profile, the number of data points in each bin being inversely proportional to the imagery speed within this bin (see Statistical analysis of distributions). Qualitatively, the two-thirds power law predicts that more markings will occur during the more curved segments of a template. Quantitatively, each value of the exponent \( \beta \) in the power law model \( \tilde{v} = \gamma \kappa^{-\beta} \) predicts a unique distribution. Therefore, we examined how well the predicted power law distributions described measured distributions of imagery and drawing data in order to infer evidence of the validity of different power laws.

Figure 2 presents imagery data points and distributions of \( \hat{s} \) for six subjects, while Fig. 3 presents the grouped resampled distributions of \( \hat{s} \), for both imagery and drawing data of the
Fig. 3. Group distributions of \( t \). A resampled distribution of \( t \) values (Obs Density), such that \( t \) distribution was uniform for grouped data for imagery and drawing of MEM subjects. Also shown are predicted distributions for movement according to the two-thirds power law (model \( \beta = \frac{2}{3} \)) and for movement with a constant Euclidean speed (model \( \beta = 0 \)) assuming a uniform distribution of \( t \). The distributions of \( t \) and \( \beta \) were resampled such that the \( t \) distribution became uniform. This eliminated the random effect of the \( t \) distribution from the presented \( \beta \) distribution. These distributions were compared to the predicted distributions of \( t \) for the 2 power laws with the assumption that \( \beta \) was uniformly distributed. This resampling, i.e., the process of randomly selecting 1 data point [a pair \((t, \beta)\) with \( t \) within the bin], was repeated 10,000 times for each bin of the \( t \) variable, and the resulting \( \beta \) values were collected in a histogram for each template.

MEM subjects. Note that in both figures the number of peaks and their locations match those predicted by the two-thirds power law; the subjects’ tendency to move more slowly in the more curved segments of each shape was evident from their tendency to stop more often while passing through the curved regions of the shape.

We tested whether observed distributions matched distributions predicted by model power laws, using \( \chi^2 \) goodness of fit tests. For the grouped data of the MEM subjects for each shape, the observed grouped \( t \) distribution, and also the observed grouped \( \beta \) distribution, were not uniform (\( \chi^2 \) goodness of fit resulted in \( P \leq 0.001 \), checking for 18 bins of size 0.05 covering the range \([0.05, 0.95]\)). Therefore, for each shape we used the values of \( t \) as inputs to the two power laws with \( \beta \) values of 0 and \( \frac{2}{3} \), corresponding to the constant-speed and two-thirds power law models, respectively. For neither of the two power law models did the predicted distribution of \( \beta \) match the observed distribution of \( \beta \) (for each group of subjects imagining 1 of the 3 templates, a \( \chi^2 \) goodness of fit test on the group distribution resulted in \( P < 0.001 \) for each of the \( \beta \) values, with the method described above). The mismatch between model and observation is visible in Fig. 3 and possibly indicates the noisy nature of the imagery data. To conclude, the \( \chi^2 \) goodness of fit tests showed that neither of the two power laws perfectly matched our data set.

Next, we compared different power laws to each other using likelihood ratio tests, which do not require a perfect match of one model but can indicate which of two (or more) imperfect models is better for describing the observed distributions. We tested whether the \( \beta = \frac{2}{3} \) model outperforms the null \( \beta = 0 \) model, obtaining significantly positive results for the majority of subjects for each of the templates (Table 1 summarizes the MEM \( t \) data, the MEM \( \beta \) data, and the NO MEM \( \beta \) data). This shows that for most subjects the two-thirds power law described our imagery data better than the constant-speed model. This result proved significant for all subject groups based on Fisher’s combined probability test, which gave a significant overall effect \((P < 0.001)\) for each group of subjects performing a shape, for the MEM \( t \), for the MEM \( \beta \), and for the NO MEM data separately. Hence, the effect of curvature on the subjects’ marked positions, indicating their imagery movement speed, was robust, persisting independently of the choice of a normalization procedure (whether by dividing \( t \) by \( T \) or by \( T_p \)) and independently of the effect of memory. Using a Pearson correlation test, we examined the correlation between the total imagery score and the \( P \) values derived from the likelihood ratio test. There was no significant correlation between the two scores. Similar tests applied to the visual and the kinesthetic imagery scores also showed no significant correlations \((P > 0.4\) for each of the 3 scores).

Table 1. Single-subject results of likelihood ratio test

<table>
<thead>
<tr>
<th>Shape</th>
<th>( P &lt; 0.05 )</th>
<th>Invalid*</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>MEM, ( t )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L13</td>
<td>4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>L23</td>
<td>5</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>ELL</td>
<td>5</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>MEM, ( \beta )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L13</td>
<td>6</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>L23</td>
<td>3</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>ELL</td>
<td>6</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>NO MEM, ( \tilde{t} )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L13</td>
<td>2</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>L23</td>
<td>4</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>ELL</td>
<td>3</td>
<td>0</td>
<td>5</td>
</tr>
</tbody>
</table>

Summary of single-subject results of the likelihood ratio tests on imagery data. For each shape we counted in how many subjects the two-thirds power law model described the distribution of their marked locations better than the constant speed model \((P < 0.05)\), calculated for 14 bins covering the range \([0.05, 0.95]\). Analysis of 3 data sets is shown in 3 corresponding rows. The MEM, \( t \) row shows results for the MEM subjects, with time normalized with respect to the same lap. The MEM, \( \beta \) row shows results for the same MEM subjects, with time normalized with respect to the previous lap. The NO MEM, \( \tilde{t} \) row shows results for the NO MEM subjects with time normalized with respect to the previous lap (this was the only option for the NO MEM subjects, since they did not complete the lap in which they were stopped by the beep). For most subjects the two-thirds power law was a more suitable description of their movement than a constant speed law. *For 2 subjects the test failed because of a technical problem arising when bins that were predicted to be empty according to the movement law were not empty in the measured data; the likelihood ratio test forces a zero division.
We then tested whether this model preference merely reflected a tendency toward positive β values or indicated the use of a more precise value, that of $\beta = \frac{1}{3}$. We used a similar likelihood ratio test for distributions to compare how well the MEM $\tilde{t}$ data fitted the second-power law of motion ($\beta = \frac{1}{2}$), but now compared with the best of three alternative models ($\beta = \frac{1}{3}, 0, -\frac{1}{3}$). For the MEM experiment, for three of the seven subjects of L13, the test gave statistically significant results ($P < 0.05$), indicating that the $\beta = \frac{1}{2}$ law outperformed all other models in describing these subjects’ distributions. This was also the case for three of the seven subjects of L23 and for three of the seven subjects of ELL.

An ANOVA test was used to group the individual results comparing the four power law models across multiple subjects. We extracted log likelihood values for each MEM subject’s data for each of the four models ($\beta = \frac{1}{3}, 0, -\frac{1}{3}$) (see Fig. 4). When a specific model yielded a likelihood value of 0 for any particular subject, to avoid having to take the logarithm of such likelihood value we assigned the minimal likelihood value of the other models to this model. For one subject all four models gave 0 likelihood values, and he was assigned four identical log likelihood values; the mean log likelihood values of the other subjects who imagined moving along the same template were averaged over all four models. The log likelihood values conformed with a normal distribution (Shapiro–Wilk tests yielded $P > 0.40$ for each of the 4 power law models). A one-way repeated-measures ANOVA was applied to the log likelihood values comparing the four power law models. We found a main effect of the $\beta$ parameter [$F(3) = 6.6040, P < 0.001$]. The mean log likelihood values were $-183.8, -177.7, -182.1, -187.4$ for $\beta = \frac{1}{3}, 0, -\frac{1}{3}$, respectively. Post hoc analysis using paired-sample $t$-tests (corrected with the Fisher LSD method) resulted in the two-thirds power law model, $\beta = \frac{1}{3}$, having the highest log likelihood among all four models ($P = 0.008, P = 0.050$, which is nearly significant, $P < 0.001$ for comparisons with $\beta = \frac{1}{2}, 0, -\frac{1}{3}$, respectively). The $\beta = \frac{1}{2}$ model was indistinguishable from the $\beta = 0$ model ($P = 0.448$) but almost significantly higher than the $\beta = -\frac{1}{3}$ model ($P = 0.012$). The $\beta = 0$ model had significantly higher log likelihood values than the $\beta = -\frac{1}{3}$ model ($P = 0.021$). Thus we concluded that the two-thirds power law explained the imagery distributions better than the other three kinematic models. The worst-performing model was the negative $\beta$ value model.

**Quantitative analysis of power laws for drawing and imagery.**

So far we had only analyzed distributions of the marked location $\tilde{x}$ variable. This analysis did not regard a basic property of our data set, namely, the coupling between time, $\tilde{t}$, and position, $\tilde{x}$, in the measured data set (see Fig. 2). Thus, to complement the analysis in the previous section, we employed a procedure that allowed a more precise extraction of the $\beta$ values. This used an alternative method of nonlinear regression, which took advantage of this coupling of time and location to reconstruct a speed profile. We performed the nonlinear regression procedure on the drawing and imagery data of each subject, obtaining optimal $\beta$ values as well as confidence intervals based on $\alpha = 0.05$ (Fig. 5 gives individual subject data; Table 2 summarizes mean group results). There was no correlation between $\beta$ values of the MEM drawing and imagery results (Fig. 6).

The optimal $\beta$ values of the MEM subjects conformed with a normal distribution (Shapiro-Wilk tests yielded $P > 0.1$ for each set of imagining or drawing $\beta$ values extracted for all subjects executing the same template) and were analyzed by repeated-measures ANOVA. We compared all subjects on the three shapes (shape, a between-subject variable), testing the $\beta$ values of imagery and drawing for each subject (imagery, a within-subject variable). Sphericity violations were corrected by the Greenhouse-Geisser method. A main effect of shape was found [$F(1,18) = 9.167, P = 0.002$]. No main effect of imagery was found [$F(1,18) = 0.016, P = 0.900$]. There was...
and for the L23 shape $T_{H11005}$ 0.002.

The effects found for the MEM experiment persisted without accompanied by high within-subject variability, as seen in the subjects (SD 0.45, a high between-subject variability that was found nothing extraordinary in her drawing data, which had an optimal value of 0.29.

<table>
<thead>
<tr>
<th></th>
<th>L13</th>
<th>L23</th>
<th>ELL</th>
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<tbody>
<tr>
<td>Imagery</td>
<td></td>
<td></td>
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<tr>
<td>MEM</td>
<td>0.33 (SD 0.15)</td>
<td>−0.04 (SD 0.45)</td>
<td>0.71 (SD 0.20)</td>
</tr>
<tr>
<td>NO MEM</td>
<td>0.18 (SD 0.25)</td>
<td>0.11 (SD 1.19)</td>
<td>0.79 (SD 0.18)</td>
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<tr>
<td>Drawing</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>MEM</td>
<td>0.38 (SD 0.16)</td>
<td>0.32 (SD 0.08)</td>
<td>0.28 (SD 0.03)</td>
</tr>
<tr>
<td>NO MEM</td>
<td>0.33 (SD 0.16)</td>
<td>0.39 (SD 0.06)</td>
<td>0.33 (SD 0.03)</td>
</tr>
</tbody>
</table>

Mean and SD of the $\beta$ values extracted with nonlinear regression (see Statistical analysis of speed profiles as power laws) for drawing and imagery. Each value represents the group value for the corresponding set of subjects.

To understand how $\beta$ values differ among shapes we performed separate one-way ANOVAs for the imagery and drawing conditions of the MEM subjects. No significant difference among the shapes was found for drawing [$F(2,18) = 1.658$, $P = 0.218$], and group optimal $\beta$ means were 0.38 (SD 0.16) for the L13 subjects, 0.31 (SD 0.08) for the L23 subjects, and 0.28 (SD 0.03) for the ELL subjects. For imagery we found a significant difference among the shapes [$F(2,18) = 11.029$, $P = 0.001$], which a Tukey post hoc analysis attributed to a difference between the $\beta$ values of subjects who performed the L23 and ELL shapes ($P = 0.001$). The group optimal $\beta$ means were 0.33 (SD 0.15) for the L13 subjects, −0.04 for the L23 subjects (SD 0.45), a high between-subject variability that was accompanied by high within-subject variability, as seen in the confidence intervals), and 0.71 (SD 0.20) for the ELL subjects.

We examined the control NO MEM subjects to see whether the effects found for the MEM experiment persisted without memorization. The mean optimal $\beta$ values followed a similar pattern. While for drawing they were 0.33 (SD 0.16) for the L13 subjects, 0.39 (SD 0.06) for the L23 subjects, and 0.33 (SD 0.03) for the ELL subjects, for imagery they were 0.18 (SD 0.25) for the L13 subjects, 0.11 (SD 1.19) for the L23 subjects, and 0.79 (SD 0.18) for the ELL subjects. Both the noisiness of the L23 subjects and the high $\beta$ values of the ELL shape appear unrelated to the memorization required in the main MEM task.

Finally, we report the results of the subject excluded from the statistical analysis. The eighth subject performing the L23 template had only 80 valid data points, without any samples of imagery $\hat{r}$ values in the interval [0.76, 0.96]. The likelihood values of all four power laws examined were 0 for her imagery data, rendering the study of this subject’s distributions uninformative. The nonlinear regression process yielded an optimal $\beta$ value of $-2.65$, which was an extreme outlier, and including it along with the optimal $\beta$ values of the L23 MEM subjects caused their $\beta$ values to lose their normal distribution. We found nothing extraordinary in her drawing data, which had an optimal $\beta$ value of 0.29.
imated $\beta$ values for the power law strongly tended toward positive values (Fig. 5). Our results thus suggest that the source of the two-thirds power law lies in the motion planning stages and that this law is not solely a by-product of motor execution. Similar conclusions have been reached by, e.g., Dayan et al. (2007), Schwartz and Moran (1999), Papaxanthis et al. (2012), and Meirovitch et al. (2015).

How $\beta$ is calculated determines the obtained values. As noted by Schaal and Sternad (2001), using nonlinear regression to extract the $\beta$ values (as we did here) gives results that diverge from $\beta = \frac{1}{3}$ more than using a linear fit in the log-log space (as in Viviani and Flash 1995). Thus our method of nonlinear regression is stricter than the standard methods in the motor control literature. These are inapplicable to our sparse imagery data, which do not include well-sampled velocity profiles. As different methods yield different estimations of the $\beta$ values, a systematic comparison of these methods is still necessary but is outside the scope of the present work.

Imagery results support a central origin for the two-thirds power law. The curvature-velocity relation for movement execution can be well quantified as a power law, as shown originally by Lacquaniti et al. (1983). It is crucial to determine to what extent the exponent of the power law, $\beta$, truly equals $\frac{1}{3}$, because $\beta = \frac{1}{3}$ implies a constant equi-affine speed, suggesting that movement is planned in an equi-affine invariant manner. For production data the specific values of $\beta$ vary with age, coming closer to $\frac{1}{3}$ in adults (Viviani and Schneider 1991). Our nonlinear regression analysis of drawing gave mean group $\beta$ values ranging from 0.28 to 0.39.

The distributions of the subjects’ marked positions here demonstrate that there is a similar curvature-velocity relation for imagery, and, indeed, the two-thirds power law ($\beta = \frac{1}{3}$) explained the data better than other power laws ($\beta = \frac{2}{3}, 0, -\frac{1}{3}$). Further quantification of this relation using nonlinear regression analysis gave positive mean $\beta$ values for the group, indicating that subjects did imagine slower movements in the more curved regions of each template. However, the resolution of the data did not allow a precise determination of $\beta$ values giving the best description. The curvature-velocity relation persisted in the control NO MEM experiment, where memory played a less important role, supporting our initial assumption that the memorization in this task was not a major factor, except perhaps for its effect on the variance of results.

Commonalities and differences between imagery and execution. The subjects’ variability of $\beta$ values for imagery (see Quantitative analysis of power laws for drawing and imagery; Fig. 5) cannot be explained by their drawing $\beta$ values, because there was no correlation between them (Fig. 6). This lack of correlation may result from increased variability in the imagery data. It is possible that the drawing data were more stereotypical and showed greater invariance because of the subjects’ greater proficiency in drawing versus imagery. On one hand, visual and proprioceptive feedback, absent during motor imagery, may give rise to better-controlled and less variable behavior (Hoff and Arbib 1993; Todorov and Jordan 2002). On the other hand, motor noise may be the cause of a significant portion of movement variability (Van Beers et al. 2004) and is likely to be more influential during motor execution than during imagery.

The major mechanism underlying motor imagery may involve a simulation process giving rise to motor predictions (Blakemore and Sirigu 2003). Forward models allow anticipation of the movement outcomes of internal motor commands even in the absence of overt motor execution. Therefore, an internal anticipatory model of a preplanned action may allow prediction of movement progress in space and time (Wolpert and Flanagan 2001), and this planned motion can be made accessible via the reporting of motor imagery. Characteristics common to motor imagery and execution may therefore indicate which aspects of the movement are ingrained in the feedforward commands. Differences between imagined and actual movements may indicate what aspects of the observed behavior are likely to be governed by other mechanisms, such as specific mechanical properties of the task and motor system that are not represented by the feedforward models, and unanticipated external perturbations and feedback corrections.

Alternative explanations of the two-thirds power law in motor imagery. Gribble and Ostry (1996) suggested that the two-thirds power law may reflect smoothing by the low-pass filtering properties of muscles. Such smoothing properties affect actual movement production but are unlikely to affect imagery. Therefore, similar to the increased brain activation during observation of motion obeying the two-thirds power law (Dayan et al. 2007; Meirovitch et al. 2015), the timing effects observed for motor imagery in our study probably do not solely reflect these biomechanical muscle properties. These properties, however, may explain some of the differences between our imagery and drawing results.

Alternatively, the two thirds-power law could result from actions comprised of oscillatory movements in joint space (Schaal and Sternad 2001). This could account for our findings only if subjects used a mental representation for imagery that fully described the joint angles of the kinematic chain of the arm. Subjects would also have to apply an internal simulation of the forward kinematics transformations from joint to end-effector motion along the prescribed path.

Movement dynamics may be represented to some extent in motor imagery. The durations of imagined movements, like those of executed movements, depend not only on movement kinematics but also on the inertial properties of the arm, which vary with arm configuration and are affected by external loads applied to the arm (Papaxanthis et al. 2002). The inertial properties of the arm appear better represented in motor imagery in adults than in children (Crognier et al. 2013). Therefore, we cannot completely rule out the possibility that a simulated model of movement dynamics yields the observed two-thirds power law behavior for imagined movements. We hope that future studies will determine to what extent motor imagery represents motion dynamics and joint space kinematics in addition to end-effector movement kinematics.

Real-virtual isochrony and the two-thirds power law. Durations of motor imagery and production are often positively correlated. This correlation, termed “real-virtual isochrony” in the imagery literature (not to be confused with “isochrony” in the motor control literature) is quite robust, but with some exceptions arising either from lack of proficiency or from an inherent difference between well-performed imagery and execution (see Guillot et al. 2012). The cases where real-virtual isochrony fails may provide useful information on the differences between planning and execution. Rodriguez et al. (2009) report an example where the speed profiles of movement imagery for straight reaching movements did not follow the
bell-shaped characteristics of the actual movements. They emphasized that this discrepancy was probably a characteristic of imagined movements of simple, automatic tasks like reaching and not of the more complex, attention-demanding tasks such as used here. Indeed, in our imagery data the basic temporal properties of production did persist, although for the ELL template, which is simpler than the limaçon templates, a mismatch between the β values of imagery versus drawing tasks did appear.

Challenges in recording continuous imagery motion. Comparisons of the total durations of imagined movements, used extensively in the imagery literature, are limited when it comes to describing the instantaneous kinematics of continuous trajectories. In previous motor imagery studies, during each trial the experimenters recorded only the geometric characteristics of the paths being drawn and the total durations of imagined movement along those paths. The speed profiles of the imagined movements cannot be constructed from these data, unless some simplifying assumptions are made.

The generalized power law model of the form \( v = \gamma \kappa^{-\beta} \) is the natural model in the context of power laws. This model has two free parameters. Therefore, for any shape with known curvature profile the measured total duration of the imagined motion must satisfy the equation \( T = \int dt = \int \frac{1}{v} ds = \gamma \int \kappa^\beta ds \).

For a known value of \( T \) this equation allows determination of the value of only one of the two parameters, \( \beta \) and \( \gamma \). Inside a relatively simple movement it can be assumed that \( \gamma \) is constant, but its value may change between different templates. For instance, Viviani (1986) showed that velocity gain factors \( \gamma \) for elliptical trajectories were dependent on their perimeters and speeds of execution. Hence, when the only available data are the total movement duration of the entire shape, it is not possible to infer the values of the exponent \( \beta \).

The alternative approach used here relies on reconstructing the entire speed profile by using multiple queries on the distance traveled during the imagined movement and using within-shape normalization. This normalization exploits the fact that the ratios between the durations needed to travel different distances along the same path do not depend on the value of the velocity gain factor \( \gamma \) but only on the value of the exponent \( \beta \). Therefore, we do not need to assume anything about the velocity gain factor \( \gamma \), except for the weak assumption that it is constant within each cycle of imagining a specific template, and we can extract the values of the \( \beta \) exponent.

Analyzing motor imagery, Papaxanthis et al. (2012) recently convincingly reported that the increase in the total duration of imagined movements is correlated with their cumulative turning angle, \( \int \kappa ds \). Unfortunately, even if one does assume a constant gain factor \( \gamma \), the following reasons show that these observations alone do not provide sufficient evidence for a compliance of imagined movements with a generalized power law.

First, the generalized power law model predicts an infinite speed in regions of zero curvature. Therefore, straight trajectory segments, included in the analysis of Papaxanthis et al. (2012), should be avoided when examining compliance with the power law. Second, for circular segments, any real value of the \( \beta \) exponent (including 0 and negative values) will yield a positive correlation between the duration of the movement and the cumulative turning angle (which is proportional to the arc length of the circular segment). Hence, the value of the exponent \( \beta \) can only be determined if the value of the gain factor \( \gamma \) is known. Third, movement through cusps and inflection points cannot be accounted for by a simple power law model.

In our opinion, these technical yet important limitations have not been sufficiently dealt with in previous studies. Nevertheless, the main novelty of the present work does not lie in any technical matter but rather in the fact that our paradigm allows examination of the speed profiles of complex continuous motions. We hope that future studies of motor imagery, in addition to reporting comparisons of durations of actual and imagined movements, will reveal in detail the qualitative and quantitative factors governing speed profiles of imagined movements. For example, one direction that may guide future studies of motor imagery is the examination of imagined movements using the framework developed by Bennequin et al. (2009). This suggests that movement duration and compositionality arise from cooperation among Euclidian, equi-affine, and full affine geometries.

Does imagery show the segmentation of movement execution? It is commonly assumed that movement is planned and executed as a composition of elementary units (Flash and Hochner 2005; Morasso and Mussa-Ivaldi 1982; Polyanov et al. 2009; Viviani 1986). Given the sparseness of our samples it was difficult to examine segmentation for our imagery data, but we could examine it in our drawing data. One indication of segmentation in the actual drawing of limaçons is that different values of the gain factors \( \gamma \) and of the \( \beta \) values derived for the different loops (see Segmented structure of the limaçon drawing data, after Viviani and Flash 1995). Bennequin et al. (2009) described a qualitatively similar segmentation effect, where two distinct linear trends emerged for regions of different curvature in the log \( v \) vs. log \( \kappa \) plot for drawing an ellipse. Such segmentation patterns require more than a single power law for the description of an entire shape. Experimental methods must be improved to investigate how well segmentation models apply to motor imagery. Nonetheless, in the absence of both muscle smoothing effects and the influence of corrections through feedback, motor imagery may allow examination of whether trajectory planning is indeed inherently segmented.

Further application of motor imagery to the study of continuous motion. The consistence of motor imagery observations with Fitts’s law (Decety and Jeannerod 1995) and our findings on the two-thirds power law raise the question of the possibility of identifying regularities and invariants of motion planning through motor imagery studies. Motor control theories describing both the task space and the joint space have much to benefit from imagery studies examining both timing and geometry of imagined motion. Characterization of motion structure, particularly identification of motion primitives, seems plausible with similar imagery paradigms. Imagination studies of kinematics may also allow distinguishing between movement characteristics arising from trajectory planning (feedforward processes) and properties arising from execution, such as online feedback-based error corrections.

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AUTHOR CONTRIBUTIONS
Author contributions: M.K. and T.F. conception and design of research; M.K. performed experiments; M.K. analyzed data; M.K. and T.F. interpreted results of experiments; M.K. prepared figures; M.K. drafted manuscript; M.K. and T.F. edited and revised manuscript; M.K. and T.F. approved final version of manuscript.

REFERENCES
Papaxanthis C, Schiappati M, Gentili R, Pozzo T. Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass. Exp Brain Res 143: 447–452, 2002.