Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law

Authors
Beets, I.A.M.*, Rösler, F., and Fiehler, K.

Affiliation
Experimental and Biological Psychology, Philipps University Marburg

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* Manuscript correspondence:
Iseult Beets
Philipps University Marburg
Department of Psychology
Gutenbergstrasse 18
35032 Marburg
Germany
Email: beets@staff.uni-marburg.de, iseult.beets@gmail.com
Phone: +49-6421-2823652
Abstract

Few studies have reported direct effects of motor learning on visual perception, especially when using novel movements for the motor system. Atypical motor behaviors that violate movement constraints provide an excellent opportunity to study action-to-perception transfer. In our study, we passively trained blindfolded participants on movements violating the two-thirds power law. Before and after motor training, participants performed a visual discrimination task, in which they decided whether two consecutive movements were same or different. For motor training, we randomly assigned the participants to two motor training groups or a control group. The motor training group experienced either a weak or a strong elliptic velocity profile on a circular trajectory which matched one of the visual test stimuli. The control group was presented with linear trajectories unrelated to the viewed movements. After each training session, participants actively reproduced the movement in order to assess motor learning. The group trained on the strong elliptic velocity profile reproduced movements with increasing elliptic velocity profiles while circular geometry remained constant. Furthermore, both training groups improved in visual discrimination ability for the learned movement as well as for highly similar movements. Participants in the control group, however, did not show any improvements in the visual discrimination task, nor did participants who did not acquire the trained movement. The present results provide evidence for a transfer from action to perception which generalizes to highly related movements and depends on the success of motor learning. Moreover, under specific conditions, it seems to be possible to acquire movements deviating from the two-thirds power law.
Introduction

Looking at other people performing an action can help one to acquire new motor skills, such as learning to perform a handstand, and even abstract skills like learning to work with a new computer program. However, can motor skills affect visual perception as well?

The common coding theory (Hommel et al. 2001; Prinz 1997) posits that the final stages of perception and the initial stages of action control share a common representational domain, where planned actions are represented in the same format as perceived events. The idea that perception affects action, including ‘observational learning’, has been supported by many studies (Hecht et al. 2001; for an overview see McCullagh et al. 1989). On the other hand, if perception and action share the same codes, it is predicted that changes in these codes due to motor learning, should lead to corresponding changes in perceptual skills (Hecht et al. 2001; Prinz 1997; for a review see Schütz-Bosbach and Prinz 2007). Only few studies have examined the effects of action on perception, probably due to problems in avoiding perceptual experience which immediately emerges from action performance (Wolpert and Ghahramani 2000).

The question whether action-to-perception transfer is possible, regained interest after the discovery of mirror neurons in monkeys which fire during the execution of an action but also during the mere observation of the same goal-directed action (di Pellegrino et al. 1992; Gallese et al. 1996). Indirect neurophysiological measures have supported the idea that such a mirror neuron system also exists in humans (for an overview see Rizzolatti et al. 2001). This suggests that the brain internally simulates an action during the observation of others’ actions (Jeannerod 1994, 2001) which may yield action understanding (Gallese et al. 1996). An internal model, which merges motor and perceptual experience, is suggested to play a role in the anticipation of action effects (Wolpert and Ghahramani 2000; Wolpert et al. 1995; for an overview about biological movement perception see Giese and Poggio 2003). In summary,
there is converging evidence that the motor system is involved in action perception. As a consequence, changes in the motor system should elicit changes in perception.

In recent years, some studies have already demonstrated a direct influence of action on perception. Hecht and colleagues (2001) showed effects of action-to-perception transfer using a timed movement task in which participants practiced cyclical movements while being blindfolded. Performance in a subsequent visual perception task was significantly enhanced for the trained movement. Using functional magnetic resonance imaging (fMRI), brain structures involved in motor-related processes have been observed to be active during the mere visual perception of movements (Engel et al. 2008; Reithler et al. 2007). These brain areas were more active during the perception of trained than untrained movements suggesting a stronger resonance effect. Accordingly, expert dancers showed greater activity in premotor and parietal brain regions when they watched their own dance style compared to another dancing style (Calvo-Merino et al. 2005). To rule out that this effect was due to differences in visual experience, the authors conducted a follow-up study where they presented gender-specific ballet moves. In line with the previous results, enhanced activity was found when male and female ballet dancers viewed moves of their own motor repertoire (Calvo-Merino et al. 2006).

Further evidence for a tight link between action and perception comes from studies investigating motor constraints. Biological movements, i.e., movements humans are able to execute, are subjected to certain constraints. For example, curvature and velocity are inversely related, i.e., at points of low curvature, absolute velocity is high and vice versa. The two-thirds power law states that the instantaneous velocity $V$ depends on the radius of the curvature $R$ of the trajectory: $V = KR^{\beta}$ where $K$ is a constant which depends on the tempo of the trajectory. The name of the two-thirds power law has been derived from the original literature in which the exponent was expressed as $1-\beta$ in which $\beta$ lies around $2/3$. The value of
exponent $1 - \beta$ thus equals $1/3$ (Lacquaniti et al. 1983; Viviani et al. 1997; Viviani and Schneider 1991; Viviani and Stucchi 1992) and is here further referred to as $\beta$. This law has been shown to be effective in motion perception as well. The velocity of a dot travelling along an elliptic path was only perceived to be uniform if the movement path and its velocity profile obeyed the two-thirds power law (Viviani and Stucchi 1992). Movement anticipation also seems to rely greatly on the two-thirds power law (Flach et al. 2004). In line with these results, it was found that people are very sensitive to violations of the two-thirds power law (i.e., when velocity does not correspond with the curvature), and that even slight violations can be detected easily from natural movements (Bidet-Ildei et al. 2006). Moreover, it has been shown that motor-related brain areas (including primary motor cortex, premotor cortex, and supplementary motor areas) were much more active during movement perception in which the two-thirds power law was obeyed (Casile et al. 2010; Dayan et al. 2007), which supports the idea that the motor system resonates more strongly when movements which lay in our own motor repertoire, are perceived.

So far, most studies investigating action-to-perception transfer applied long-term skill learning with visual feedback (e.g. Calvo-Merino et al. 2005, 2006) or learning of specific movement trajectories under the use of explicit memory (e.g. Reithler et al. 2007). To rule out that visual experience of the movement or explicit motor learning mainly contribute to the transfer of action to perception, non-visual learning of an a-typical movement that does not belong to the person’s motor repertoire provides an excellent alternative. Casile and Giese (2006) followed this approach. They actively trained participants to execute a gait pattern in which their arms moved with an a-typical phase shift of $270^\circ$. During training, participants were blindfolded and received haptic and verbal feedback. There were four anchor points along which participants learned the relative positions of their hands. After motor training, visual recognition (i.e. hit-rate) of the learned movement was higher than before training. In this study, however, only 2 participants were able to learn the a-typical arm movement.
In the present study, we investigated action-to-perception transfer by applying a highly standardized passive motor training of hand movements violating the two-thirds power law. Thus, we presented atypical movements which do not belong to the human motor repertoire. Blindfolded participants were trained on a fixed number of trials using a movement manipulandum. Such a passive motor training ensured a standardized training procedure without additional visual or verbal feedback. Motor training was executed over the course of four consecutive days on a movement exhibiting consistent properties. The trajectories were all circular and featured a velocity profile belonging to a vertical ellipse. Movements along a circle would normally be executed with a constant velocity due to constant curvature. Combining a circular geometry with an elliptic velocity pattern leads to an atypical relationship of geometry and velocity. We repeatedly measured improvement in motor learning by a movement tracking system during active reproduction blocks. Before and after motor training, participants performed a visual discrimination task to assess whether learning of a specific movement skill improved visual perception. To test whether training effects on visual discrimination performance before and after training were due to learning of one specific novel movement; and not to motor training in general, a control group was tested who were trained to execute simple linear trajectories unrelated to the viewed movements of the visual discrimination task.

We demonstrate that successful learning of a novel movement improves visual discrimination ability of the learned movement as well as highly similar movements. In contrast to previous studies (Viviani 2002; Viviani et al. 1987; Viviani and Mounoud 1990), but similar to findings of Wann et al. (1988), the typical curvature-velocity relation as predicted by the two-thirds power law, seems to be altered after motor training.
Materials and Methods

Participants

Fifty-one healthy, right-handed participants took part in the experiment. Seven participants were excluded from further analyses because performance deviated more than 2 standard deviations from the norm in the visual pre-test or in any of the measured motor parameters (4 due to the visual pre-test; 2 due to motor performance; 1 due to both). Thus, the sample consisted of forty-four participants (9 male, 35 female) between the ages of 19 and 30 years (mean age, standard deviation: 22.8, ± 2.9 years). They performed the experiment over four consecutive days. All participants had normal or corrected-to-normal vision. Naïve participants were recruited from the Philipps-University Marburg, and were compensated with course-credits or money for their participation. The experiment was performed in accordance with the ethical standard laid down in the Declaration of Helsinki (2000).

Apparatus

A programmable movement manipulandum with two degrees of freedom (x- and y-plane) driven by two servo motors and controlled by LabVIEW (http://www.ni.com/labview) induced passive arm movements in the horizontal plane. The trajectory was circular, but the velocity varied over the trajectory according to the applied velocity profile. Participants sat facing the workspace and grasped the vertical handle of the motion device with a precision grip using their right thumb and index finger (Fig. 1A). A chin rest was used to keep body posture constant during each motor training session. The chair and chin rest were adjusted individually to assure a comfortable and stable position during motor training sessions.
As the movement manipulandum does not enable decoupling from the servo motors, its handle cannot be moved freely. Therefore, active movement reproduction was done in a separate room (due to space limitations) by sliding a smooth cuboid plastic device (width x length x height: 96mm x 65mm x 35mm) freely over a horizontal plane surface. The vertical handle on this device was comparable with that of the movement manipulandum. Movement trajectories were recorded with an ultrasound motion recording device (ZEBRIS CMS20, Zebris Medical GmbH, Isny im Allgäu, Germany). The data were sampled with 50Hz and analyzed offline. Participants were blindfolded during passive motor training and during the active movement reproduction blocks.

< Insert Figure 1 about here>

**Procedure**

Participants were randomly assigned to two experimental groups, or to the control group. One experimental group was trained on a trajectory with a circular geometry (geometric eccentricity, $\Sigma_g = 0$) with a velocity profile simulating an extremely elongated vertical ellipse (dynamic eccentricity, $\Sigma_d = -.92$). The other experimental group was trained on a trajectory with a circular geometry ($\Sigma_g = 0$) with a velocity profile simulating a weakly elongated vertical ellipse ($\Sigma_d = -.71$). In the following, we refer to the two experimental groups as *extreme elliptic condition* and *weak elliptic condition*. Twelve participants (2 male, 10 female; mean age, standard deviation: 24.3, 2.6 years), were allocated to the extreme elliptic condition and nineteen (3 male, 16 female; mean age, standard deviation: 23, 2.8) to the weak elliptic condition. Thirteen participants (4 male, 9 female) were assigned to the control group (mean age, standard deviation: 21.5 ± 2.6 years). They were passively trained on a linear movement along the body midline ($y$-plane) using the movement manipulandum.
The eccentricity parameter is conventionally applied in the movement literature (e.g. Viviani et al. 1997; Viviani and Stucchi 1989), and is used to describe the elongation of an ellipse. We distinguish here between geometric and dynamic eccentricity. The geometric eccentricity describes the shape of the trajectory. The dynamic eccentricity describes the velocity profile of the trajectory. In all of our manipulations, the geometric eccentricity is set at 0 (for visual and passively presented movements). This means that each trajectory has a circular shape. The factor which is varied in our manipulations is the dynamic eccentricity, which was laid over these circular trajectories. The eccentricity, $\Sigma$, is defined as $\Sigma = [1 - (A_{xg} / A_{yg})^2]^{1/2}$, where $A_{xg}$ and $A_{yg}$ denote the horizontal and vertical axes of the ellipse, respectively. The x-y ratio is $A_{xg} / A_{yg}$, which thus denotes the width and the height of the ellipse (that is simulated by the velocity profile). The eccentricity of the velocity profiles of vertical ellipses is conventionally set to be negative throughout this paper (c.f. Viviani et al. 1997). For example, an ellipse with a width ($x$) of 4 cm and a height ($y$) of 10 cm. would have an x-y ratio of 0.4. The eccentricity of this ellipse would thus be -0.92. The trained trajectories in the weak and extreme elliptic conditions always had a circular geometry, while the velocity profiles belonged to ellipses with an eccentricity of -0.71 (x-y ratio = 0.7) in the weak elliptic condition, and an eccentricity of -0.92 (x-y ratio = 0.4) in the extreme elliptic condition. Note that the dynamic x-y ratio depicts the ratio between minimum and maximum speed in the velocity profile of the trajectory.

Polar plots of the geometry (dotted line) and velocity profiles (solid line) for the passively trained stimuli are depicted in Fig. 2. The dotted line depicts the geometry of the movement which is strictly circular due to the constant radius of curvature. The solid line illustrates the velocity profile which is inconsistent with the geometry. The radius of curvature of the solid line is low at the top and bottom portions of the movement, indicating the minimum velocity at these parts of the trajectory (see also fig. 2C in Viviani et al. 1997).
corresponding velocity profiles are illustrated in Fig. 4A (weak elliptic condition) and 4B (extreme elliptic condition).

To verify that participants in the experimental groups violated the curvature-velocity relation normally seen in circle drawing, we compared the unnatural movements acquired during motor training with natural circle drawing. To this end, an additional natural-movement-group (2 male, 4 female; mean age, standard deviation: $24.6 \pm 2.7$ years) was asked to actively produce circular trajectories while moving the cuboid plastic device over a horizontal plane surface (2 blocks of 15 movements; equivalent to data obtained in 1 motor training session in the other groups) without visual feedback.

All participants of the experimental groups and the control group performed a visual discrimination test before (pre-test) and after (post-test) motor training (Fig. 1B). The experiment was performed on four consecutive days. The visual test was accomplished on the first and the last day and took about 1.5 hours. Motor training was performed each day, which lasted about half an hour. Thus, the first and last experimental session took 2 hours in total and the second and third experimental session about half an hour.

Visual pre- and post-test followed the same experimental protocol (Fig. 1C). They consisted of 288 trials each, organized into six blocks. Between blocks, there was an obligatory 3-minute break. In each trial, two stimuli were presented consecutively with a short interval, upon which the participant indicated whether both movements were identical (“same”) or different. Participants were instructed to press “different” only when they were sure that both movements were different. Buttons for “same” and “different” responses were counterbalanced across participants. To avoid inconsistent eye movements, participants were instructed to keep their eyes on the fixation cross located at the center of the screen.
Each trial started with a fixation cross for 1000 ms. Within the last 300 ms a tone was presented indicating the onset of the first stimulus (3100 ms) in which one movement cycle was presented. Then, a fixation cross appeared for 1800 ms followed by the second stimulus (3100 ms). The stimuli were a white dot on a black background moving along circular trajectories centered in the middle of the screen. Participants had to respond as quickly and as accurately as possible. Responses could be given from the beginning of the second stimulus until 2000 ms after second stimulus presentation end. When participants did not answer within the requested time, the next trial was initiated, and the trial was counted as incorrect. No feedback about their responses was given.

Visual stimuli were divided into categories belonging to 3 prototypes. Identical to the kinaesthetic stimuli generated by the movement manipulandum, the geometry of movements of all prototypes was circular ($\Sigma_g = 0$), but varied in the velocity profile. Prototype P0 had a velocity profile belonging to a circle ($\Sigma_d = 0$). The velocity of this prototype was thus constant. Because the geometry and the velocity both belong to a circle, curvature and velocity matched, the two-thirds power law was obeyed. The velocity profile of prototype P-.71 corresponded to a weakly elongated vertical ellipse ($\Sigma_d = -0.71$; identical to the eccentricity presented in the weak elliptic training condition). The velocity was thus relatively high at the sides of the circular trajectory, but relatively low at the top and bottom of the circle. Because the velocity profile was slightly different from the geometry, i.e., curvature and velocity did not match, the two-thirds power law was weakly violated. The velocity profile of prototype P-.92 corresponded to an extremely elongated vertical ellipse ($\Sigma_d = -0.92$; identical to the eccentricity presented in the extreme elliptic training condition). The velocity was thus very high at the sides of the circular trajectory, but very low at the top and bottom of the circle. Because the velocity profile clearly differed from the geometry, the two-thirds power law was strongly violated. The weak and extreme elliptic visual prototypes were thus identical to the movements trained in the weak and extreme elliptic conditions during the
motor training, respectively. To summarize, P0 obeyed the two-thirds power law (the curvature and the velocity is constant over the trajectory); P-.71 violated the two-thirds power law weakly (the geometric curvature is constant, but the velocity is distributed as if it were a weakly elongated ellipse); and P-.92 featured an extreme violation of the two-thirds power law (the geometric curvature is constant, but the velocity is distributed as if it were an extremely elongated ellipse). The velocity profile of both P-.71 and P-.92 can be seen in Fig. 4A and 4B (black line). The velocity profiles of comparison stimuli lay around these prototypical profiles; the ones with stronger eccentricities (i.e., more different from 0) exhibited a larger discrepancy between minimum and maximum velocity, and vice versa.

In half of the trials (48 per prototype), one of the three prototypes was presented with the same prototype (“same” trial). In the other half of trials, the prototype was presented with one of its comparison stimuli (“different” trial). Comparison stimuli laid at .30 (“far”; less alike) or .15 (“near”; more alike) from each prototype (expressed in dynamic x-y-ratio \(^1\)). The comparison stimuli either had more elliptic or less elliptic velocity profiles than the prototype which could differ in two degrees, i.e., near (small deviation from the prototype) or far (large deviation from the prototype). The two-thirds power law was obeyed only in P0 (dynamic x-y ratio = 0), and all other prototypes and all comparison stimuli violated the two-thirds power law to smaller or greater extent. For example, the prototype P-.92 has an x-y ratio of 0.4; an extremely elongated ellipse, and will thus have comparison stimuli with equally deviating x-y ratios (cf. de’Sperati and Viviani 1997), i.e., 0.10 and 0.25 (i.e., more extremely elongated ellipses), and 0.55 and 0.7 (i.e. less extremely elongated ellipses compared to P-.92). Each comparison stimulus appeared with equal probabilities, i.e., 12 trials per comparison stimulus and prototype. Thus, the visual stimulus set consisted of 15 different dot movements. The order of prototype, trial type (same or different), and comparison stimulus (far or near) were semi-randomized, i.e., the number of trial type occurrence was held constant over blocks.
After the visual pre-test, participants were passively trained on the movement according to their assigned condition. Due to the unnatural movement type which cannot be freely produced, we could not obtain a pre-training baseline. One motor training block consisted of 80 movement cycles on the motion device which were interrupted by 1000 ms breaks. The participants’ task during motor training was to pay attention to both the shape and velocity distribution of the perceived movement, and to imagine performing the movement actively. No information was given about movement parameters. In order to assess effects of motor learning, passive motor training was followed by an active movement reproduction block. Participants were instructed to reproduce the previously felt movement for 15 movement cycles as accurately as possible regarding movement shape and velocity. Analogous to the manipulandum, participants stopped between every movement cycle. Overall, they performed 160 movement cycles on the motion device and 30 movement cycles of active movement reproduction per motor training session. The nature of the reproduced movements was very consistent within each reproduction session. The same procedure was maintained for participants in the control group (the linear movement data were not analyzed).

**Stimuli**

Visual and motor stimuli were programmed in Matlab 2007a (http://www.mathworks.com). Coordinates (155 per movement) were refreshed every 20 ms. Presentation 11.0 (http://www.neurobs.com) was used to control the course of visual stimuli as well as passive-movement stimuli generated on the motion device. Both types of stimuli rotated clockwise along a circular path with a duration of 3100 ms and the same start and end location. Exactly one rotation was completed in this time. Thus, each stimulus consisted of one movement cycle only. The paths of both visual and motor stimuli were always circular, but their velocity profile varied, depending on which ellipse the velocity profile simulated.
The dynamic eccentricity defined the distribution of the coordinates along the circular path through which the motion device, or the point light, traveled. The calculation and generation of the coordinates was performed in Matlab 2007a. We followed the same approach as in Viviani and Stucchi (1989). The speed of the motion device, or the point light, was defined by the distance between two consecutive coordinates, i.e., the time needed to travel from one coordinate to the next was always 20ms. Thus, the coordinates in which speed was higher lay further apart, and vice versa. The two-thirds power law was only obeyed when the dynamic eccentricity was zero and thus matched the geometric eccentricity. The more the dynamic eccentricity deviated from zero, the more the two-thirds power law was violated, and the greater the variability among the distances between coordinates was (thus featuring unequal velocity distributions).

The movement stimuli started at about 20 cm from the body midline. For the weak and extreme elliptic condition, the stimuli had a fixed radius of 80 mm (perimeter of 502.4 mm) and a variable velocity profile (see Procedure) with an average velocity of 0.16 m/s. For the control group, the motion device moved the participants’ hand back and forth along a linear trajectory with a length of 200 mm and an average velocity of 0.13 m/s. Movement duration was kept identical between the experimental groups and the control group, i.e., 3100ms. Visual stimuli were presented on the center of a 16” screen (85 Hz; 1024 x 768 pixels) located about 50cm from the participant at eye-height. They consisted of a moving white dot (diameter: 0.23°) on a black screen. The diameter of the circular trajectory was 3.18°. Exactly one rotation was shown per stimulus.

**Movement data pre-processing**

Movement data pre-processing was executed in Java (Eclipse 3.3.2). Movement trajectories acquired during the active movement reproduction session were first fragmented
into separate movement cycles (15 per reproduction block, i.e., 30 per reproduction session) and then smoothed using a weighted moving average filter that weighted data point \( x_i \) with 0.3; \( x_{i+1} \) with 0.25; and \( x_{i+2} \) with 0.1, to minimize amplitude and phase distortion (Winter 1990). Then, \( x \) and \( y \) coordinates and angular velocity \( \nu \) (in °/s), the radius (in mm) per movement cycle and the deviation from radius of each movement cycle per time point were calculated to assess geometry. The pre-processed data were exported to SPSS for statistical analyses with a spatial resolution of 1 mm² and a temporal resolution of 20 ms. Note that the tangential velocity was calculated for curvature-velocity relationship only by using Matlab (see below).

**Statistical analyses**

*Visual discrimination data.* We calculated \( d' (Z_{\text{hits}} - Z_{\text{false alarms}}) \) and response bias (criterion, \( C = \frac{Z_{\text{hits}} + Z_{\text{false alarms}}}{2} \)) per prototype and comparison stimulus to obtain a measure of visual discrimination ability, which is more reliable than hit-rate or percentage correct, because effects of response bias are excluded (Swets and Picket 1982; Macmillan and Creelman 2005). Especially here, where the instruction was to only press “different” when participants were sure that there was a difference, we expected the response bias to be significantly shifted toward “same” answers. Therefore, \( d' \) was used as it is independent of response bias (Tanner and Swets 1954; Swets and Picket 1982; Macmillan and Creelman 2005). Comparison stimuli with identical distances and opposite directions (e.g. 0.15 and -0.15) were collapsed for each prototype to obtain \( d' \) per distance and prototype. The visual data as measured by \( d' \) did not violate the assumption of a normal distribution, as indicated by the Kolmogorov-Smirnov test \( (P > 0.2 \text{ in all stimulus types}) \). Data could therefore be tested with parametric tests. Statistical tests for the experimental groups and the control group consisted of planned comparisons t-tests per prototype, in which we were interested in the
difference between visual discrimination before (pre-test) and after (post-test) motor training. To assess whether discrimination ability varied over different grades of two-thirds power law violation, and to assess response bias, a repeated measures analysis of variance (ANOVA) with factor prototype (3) and comparison stimulus distance (2) was conducted for the visual pre-test among all participants. Post-hoc t-tests examined differences between prototypes and were adjusted for multiple comparisons using Bonferroni correction.

Movement reproduction data. Effects of motor learning were examined on movement variability, geometry, velocity, and the curvature-velocity relationship. An example of movement data of one representative participant is shown in Fig. 3.

Movement variability was defined as the standard deviation (SD) of the 15 movement cycles within each reproduction block. Deviation from circular geometry was assessed by the averaged deviations (in %) from radius per time point taken per session. To obtain the dynamics of each movement, duration of movement data was first standardized on the duration of the movement produced by the motion device (3100 ms) by extrapolation. Then, the two maxima and the minimum \( v \) (angular velocity) were sought, which had to occur at 780 ms and 2320 ms for the maxima and at 1560 ms for the minimum, according to the movement of the motion device (= ideal time points). A time window of + / - 200 ms around the ideal time points was applied to allow for some movement variance. The ratios were calculated with the following formula: \( (\text{min} / \text{max}_1) + (\text{min} / \text{max}_2) / 2 \), where ‘\( \text{min} \)’ represents the minimum velocity of the velocity profile, and ‘\( \text{max} \)’ is the maximum velocity of the velocity profile. This formula therefore indicates how elliptic the velocity profile is. The more extreme the difference between minimum and maximum speed (i.e., the smaller the ratio), the more elliptic the velocity profile was. Note that this measure is used later on to express \( x-y \) ratio of the velocity profile (i.e., it describes the shape of the ellipse the velocity profile belongs to). This measure was used to determine whether the participant followed a biphasic, i.e. a
vertically elliptic, velocity profile. In this case, the value had to be $< 1$ to verify that the value at the location of the expected minimum was smaller than the value at the location of the expected maxima.

To determine how well participants learned to reproduce the given velocity profile, we took the root mean squared error measure (RMSE) between the produced and the trained velocity profile curve. This was done by taking the root of the mean squared difference between these curves per time point: $\sqrt{\sum (C_t - C_p)^2}$ with $C$ is the velocity value of the trained curve ($C_t$) and the velocity value of the produced curve ($C_p$). A smaller RMSE indicates a smaller error from the trained velocity curve. This is a common measure in the motor training literature to indicate motor learning (e.g. Hodges and Franks 2000, 2002; Siengsukon and Boyd 2009).

In order to investigate whether the curvature-velocity relationship deviated from the naturally occurring value, we calculated the logarithmic radius of curvature and the logarithmic tangential velocity for each trajectory per time point using Matlab 2007a. The slope between these parameters estimated by linear regression is the value $\beta$ of the formula $V = KR^\beta$, which normally lies around $\frac{1}{3}$.

For all movement parameters, the mean over both movement reproduction blocks was taken to obtain a value for one motor training session (i.e. 2 times 15 movements). To test for learning effects over training sessions, a repeated measures ANOVA with factor session (4) was performed for all movement parameters. Statistical tests were 2-sided.

<Insert Figure 3 about here>
Results

The aim of this study was to investigate how non-visual motor learning of a movement which violates the two-thirds power law, influences visual perception. First, we will show whether it is possible to learn such a movement. Second, we examine the results of the visual perception baseline (pre-test) to determine if discrimination ability varies over different grades of two-thirds power law violation. Finally, we compare the results of the visual discrimination task before and after motor training to test the effect of motor learning on visual perception. The statistics mean and standard deviations are reported separately for the movement parameters in Table 1 and 2, and the results of the visual discrimination task in Table 3 and 4.

Progress in motor learning

As shown in Fig. 4, participants in the extreme elliptic condition produced biphasic velocity profiles during movement reproduction sessions, which correspond to a vertical ellipse (Fig. 4A). In the weak elliptic condition, however, only 11 participants produced a biphasic elliptic velocity pattern (‘learners’) (Fig. 4B), while the other 8 showed a bell-shaped or tri-phasic velocity profile (‘non-learners’) (Fig. 4C). Because learning of a vertical elliptic velocity profile was important to show effects of action on perception, the non-learners were analyzed as a separate group. Precisely, participants were classified as learners when they produced a mean velocity profile with a dynamic $x$-$y$ ratio $\leq 1$, which corresponds with an eccentricity of a vertical ellipse. Participants in the natural movement group produced a bell-shaped velocity profile (Fig. 4D). Due to stops between movement cycles and the constant geometric curvature, we expected this type of velocity profile which is normally seen in point-to-point reaching movements (Abend et al. 1982; Harris and Wolpert 1998). $X$-$y$ ratios of non-
learners lied around 1 and did not differ from the natural movement group \( F_{(1,12)} = 0.434; P = 0.523 \). In contrast, \( x-y \) ratios of learners were significantly smaller than 1 after the first motor training day and differed significantly from the natural movement group \( F_{(1,15)} = -14.421, P < 0.01 \). \( x-y \) ratios also differed significantly between learners and non-learners \( F_{(1,17)} = 14.557, P < 0.01 \). Trajectories of participants in the extreme elliptic condition also had \( x-y \) ratios significantly smaller than 1 and differed significantly from the natural movement group \( F_{(1,16)} = 72.224, P < 0.001 \) and from the learners in the weak elliptic condition \( F_{(1,21)} = 13.629; P < 0.01 \).

Movement variability. Movement variability (Fig. 5A) significantly decreased over the motor training sessions in the extreme elliptic condition \( F_{(3,33)} = 6.374, P < 0.01 \). In the weak elliptic condition, movement variability significantly decreased for learners \( F_{(3,30)} = 9.106, P < 0.001 \), but not for non-learners \( F_{(3,21)} = 2.015, P = 0.143 \).

Circular geometry. In both conditions, mean deviation of the radius of each movement from the circular trajectory (Fig. 5B) did not change significantly over sessions (extreme elliptic condition \( F_{(3,33)} = 0.823, P = 0.491 \); weak elliptic condition - learners \( F_{(3,30)} = 0.376, P = 0.771 \); weak elliptic condition - non-learners: \( F_{(3,21)} = 0.422, P = 0.739 \)), suggesting that the shape of trajectories remained circular. To test whether circular geometry deviated from the geometry observed during natural circle drawing, the produced geometry of the experimental conditions was tested against the natural-movement-group revealing no difference (extreme elliptic condition \( F_{(1,16)} = 1.221, P = 0.286 \); weak elliptic condition –
learners \([F_{(1,15)} = 0.460, P = 0.508]\); weak elliptic condition – non-learners \([F_{(1,12)} = 0.419, P = 0.530]\).

\(<\text{Insert Figure 5 about here}>\)

**Velocity.** To assess how well participants learned the velocity distribution, the RMSE between the passively trained velocity profile curve and the actively produced velocity profile curve was calculated (see Fig. 4). A significant decline was observed in the extreme elliptic condition \([F_{(3,33)} = 3.426, P < 0.05]\), indicating a decreased error. In the weak elliptic condition (learners), no significant change was found \([F_{(3,30)} = 0.093, P = 0.857]\).

**Curvature-velocity relationship.** To assess whether the curvature-velocity relationship was distorted by drawing circles with elliptic velocity profiles, a regression analysis was calculated between the logarithm of the radius of curvature and the logarithm of the tangential velocity. This yields the exponent \(\beta\) of the formula describing the two-thirds power law \(V = KR^\beta\) in which \(\beta\) lies around \(\frac{1}{3}\). The mean of exponent \(\beta\) was significantly smaller than \(\frac{1}{3}\) in both experimental conditions (extreme elliptic condition: \([t_{(11)} = -3.730, P < 0.01]\); weak elliptic condition – learners: \([t_{(10)} = -3.826; P < 0.01]\)). In the natural-movement-group, \(\beta\) did not differ from \(\frac{1}{3}\) \([t_{(5)} = -0.715, P = 0.507]\) (see Table 2). To investigate whether the power-law relation emerged from greater variation in curvature around the stops between each movement cycle; each trajectory was split into quarters of which the exponent was calculated. In the natural movement group, the exponent did not differ from \(\frac{1}{3}\) in any of the quarters. When the second and third quarter were collapsed and were compared with the collapsed first and last quarter (i.e., movement initiation and ending), the exponent lay closer to \(\frac{1}{3}\) in the middle of the movement than in the beginning and the end of the movement \([t_{(5)} = 4.364, P <\)
suggesting that the power law relation was stronger in segments where no stops occurred. In the experimental conditions, the exponent was significantly smaller than $\frac{1}{3}$ in the first three quarters of the trajectory. The middle and the beginning and end quarters did not differ [extreme elliptic condition: $t_{(11)} = 1.385, P = 0.194$; weak elliptic condition: $t_{(10)} = 0.248, P = 0.809$]. This suggests that the variation in curvature due to imperfections of drawing a circle was constant throughout the movement cycle and that the curvature-velocity relation was not influenced by stops between movement cycles.

R-squared, which is the explained variance of the cloud of dots in the logarithm of the radius of curvature against the logarithm of the tangential velocity, did not deviate from natural circle drawing in the extreme [$F_{(1,16)} = 1.850, P = 0.193$], nor in the weak elliptic [$F_{(1,15)} = 0.009, P = 0.927$] condition, suggesting that the reliability of the prediction of $\beta$ by linear regression was similar to natural circle drawing. Data of two representative participants who participated in one experimental condition and in the natural-movement-condition are shown in Fig. 6. The figure shows different movement characteristics depending on the condition.

Visual discrimination performance

Baseline performance: Visual pre-test. We tested participants’ ability to discriminate between differences in the velocity profiles when a dot moves along a circular trajectory with constant velocity (circular prototype) which follows the two-thirds power law or with a velocity profile which violates the this movement constraint weakly or extremely (weak and extreme elliptic prototypes, respectively). Fig. 7A illustrates baseline level performance in
visual discrimination ability (d’) per prototype averaged across all participants. We observed a
significant difference between the three prototypes [main effect prototype: $F_{(2,86)} = 23.261$, $P$
< 0.001]. Post-hoc t-tests showed that the more elliptical the dynamic eccentricity of the
prototype was, the better it was discriminated from nearby eccentricities [extreme > weak: $t_{(43)}$
= 4.414, $P < 0.001$; extreme > circular: $t_{(43)} = 5.971$, $P < 0.001$; weak > circular: $t_{(43)} = 2.498,$
$P < 0.05$]. We analyzed whether discrimination ability depended on the distance of the
comparison stimuli from the prototype (near vs. far). As expected, performance on
comparison stimuli lying far from the prototype and thus are most different were
discriminated significantly better than comparison stimuli near to the prototype [$F_{(1,43)} =
294.475$, $P < 0.001$] (Fig. 7B).

Response bias. Due to our instruction that participants should press “different” only
when they were sure that a difference was present, we expected participants to tend to answer
more frequently with “same” (C > 0). Indeed, we found that the bias was significantly greater
than zero [$t_{(44)} = 12.745$; $P < 0.001$]. The “same” responses occurred more often for difficult
discriminations in which the comparison stimulus was lying near to the prototype [$F_{(1,43)} =
458.184$, $P < 0.001$], and less for prototypes which had stronger dynamic eccentricities [$F_{(2,86)}$
= 17.613; $P < 0.001$]. These results thus suggest that the amount of “same” responses
increases as the task difficulty increases. Between pre- and post test, we found an increase in
response bias [$F_{(1,43)} = 14.007$; $P < 0.01$]. However, there was no interaction between pre-post
and condition [$F_{(3,40)} = 1.257$; $P = 0.302$], suggesting that the change in criterion between
visual pre- and post test did not differ between conditions.

<Insert Figure 7 about here>
Effects of motor learning on visual perception. Here we tested whether motor training of a circular trajectory with a varying velocity profile affects people’s ability to visually discriminate between different velocity profiles of a moving dot. Fig. 8 depicts visual discrimination scores before and after motor training for participants of the experimental groups and the control group. Participants who were trained in the extreme elliptic condition showed a significant improvement in the visual post- compared to visual pre-test for the trained extreme elliptic prototype P-.92 \( [t(11) = 2.420, P < 0.05] \), marginally for the non-trained prototype P-.71 \( [t(11) = 2.046; P = 0.065] \) and not for P0 \( [t(11) = 0.847, P = 0.415] \) (Fig. 8A). Learners in the weak elliptic condition (Fig. 8B) significantly improved their visual discrimination ability for the trained prototype P-.71 \( [t(10) = 2.229, P < 0.05] \), and for P-.92 \( [t(10) = 3.225, P < 0.01] \), but not for P0 \( [t(10) = -0.163, P = 0.873] \). In contrast, no changes in discrimination ability were observed for non-learners in the weak elliptic condition [P0: \( t(7) = 1.083, P = 0.315 \); P-.71: \( t(7) = 0.471, P = 0.652 \); P-.92: \( t(7) = -0.281, P = 0.787 \)] (Fig. 8C). Consistently, participants in the control group, who underwent motor training on a non-related linear movement, did not show any changes on visual post- compared to pre-test [P0: \( t(12) = 0.206, P = 0.840 \); P-.71: \( t(12) = 0.776, P = 0.453 \); P-.92: \( t(12) = 0.343, P = 0.738 \)] (Fig. 8D).
Discussion

The aim of this study was to investigate the effect of action on perception by motor training of a movement without visual feedback that violates the two-thirds power law. First, we examine whether such an a-typical movement which is assumed not to be present in the motor repertoire, could be learned without visual feedback. Second, we test whether non-visual motor training could improve visual discrimination ability of the specific trained movement. We demonstrate that people are able to learn a-typical movements in which curvature and velocity do not match; exhibiting deviations from the two-thirds power law. Successful motor learning of this novel movement improved visual perception of the trained movement and highly similar movements. However, action-to-perception transfer was not present if no motor learning occurred.

Progress in motor learning

We show that people generate circular hand movements with an elliptic velocity profile after passive motor training. Motor training led to significant changes in the velocity distribution toward the trained velocity profile of the produced movement without affecting the geometry. It thus seems to be possible to execute movements in which velocity and geometry do not match according to the two-thirds power law. This finding is in contrast with previous studies on manual tracking of predictable (Viviani and Mounoud 1990) and unpredictable two-dimensional movements (Viviani et al. 1987), and in a study in which participants had to reproduce a movement which was imposed on the right arm, with the left arm (Viviani et al. 1997). These studies demonstrated that it is nearly impossible to produce movements violating the two-thirds power law. In the Viviani and Mounoud (1990) and Viviani et al. (1987) studies, participants had to manually track a visual stimulus which
followed the trajectory of an extremely elongated ellipse. In half of the trials, the velocity profile did not correspond to the trajectory (two-thirds power law violation). Additionally, the orientation of the ellipse and the speed of the trajectories were varied. This wide variation of the presented stimuli together with a short training time could have prevented participants from motor learning. The use of consistent stimuli over the experiment is very likely to be an important factor in motor learning of such an a-typical movement. It is therefore possible that our training which used one consistent violation of a movement constraint over a longer time period could yield participants to generate movements at variance with the two-thirds power law. Another contributing factor may be that we used passive training on the same hand which was used for reproduction; in contrast to Viviani et al. (1997). In this way, many consistent movement cycles could be learned in order to execute them later on with the same hand. Moreover, it has been found that the two-thirds power law does not hold for all movements, and that there can be significant deviations from the law when subjects perform movements at their chosen rate or when movements are simple and harmonic (Viviani and Flash 1995; Wann et al. 1988). Wann et al. (1988) suggested that conformity with and departures from the two-thirds power law can be better explained by their modification of the minimum-jerk model. Other findings have implied that the two-thirds power law seems to be a by-product of a movement system that favors smooth trajectories with minimum variance rather than it is a primary movement-generating principle (e.g. Gribble and Ostry 1996; Harris and Wolpert 1998; Schaal and Sternad 2001; Todorov and Jordan 1998).

The exponent values in our data are in agreement with these latter studies (Viviani and Flash 1995; Wann et al. 1988) that found deviations of the two-thirds power law. Here, we find that strong elliptic velocity profiles could be produced without affecting the geometry of the movement, which implies a different relation between geometry and velocity as proposed by the two-thirds power law. As a consequence, the exponent describing the curvature-velocity relation was different from $\frac{1}{3}$, while this was not the case in natural circle drawing.
In our experiment, the possibility to execute this movement at the own pace may have led to the finding that people are able to produce movements deviating from the two-thirds power law (Wann et al. 1988). However, to further substantiate this finding, a baseline measurement with which the movements after training could be compared is needed. In contrast to previous studies, movements were always interrupted by stops after each cycle. This procedure was employed to guarantee that stimuli used in the motor training and the visual discrimination test were presented in an equal manner. Although these stops did not seem to affect the two-third power law relation as observed by drawing natural circles (i.e., the exponent was 0.31 and did not significantly deviate from $\frac{1}{3}$), it might have affected movements which had circular geometry with an elliptic velocity profile.

While the kinaesthetic presentation of movement stimuli led to the required biphasic velocity profile in the extreme elliptic condition in all cases, only a subset of participants in the weak elliptic condition was able to feel and reproduce this movement. This finding suggests that the stronger the movement violates the two-thirds power law the easier it is to identify and to acquire. According to the post-experimental interview, just over half of the participants in the weak elliptic condition were able to perceive a slight elliptic velocity profile. The others reported that the velocity profile appeared constant to them over the whole trajectory. In the extreme elliptic condition, however, all participants detected the given elliptic velocity distribution. Moreover, the velocity profiles produced in the extreme elliptic condition improved over sessions, while this improvement over sessions was not observed in participants who acquired the movement type in the weak elliptic condition. The reduced training success over sessions observed in the weak elliptic condition might be caused by a floor effect, i.e., there was less room for improvement in the weak than in the extreme elliptic condition due to the less pronounced differences between minimum and maximum velocity (i.e., more ambiguity).
In both conditions in which participants were trained to execute the extreme and the weak elliptic velocity profile, active movement reproduction variability decreased over training sessions. This was not observed in a group which did not acquire the movement type. Decreases in movement variability demonstrate an increase in movement consistency reflecting greater motor control (Jordan et al. 2009). Based on the Haken-Kelso-Bunz (HKB)-model, increasing fluctuations, i.e. greater standard deviation, in relative phase between limbs is regarded as a loss of stability in intra-limb coordination (Haken et al. 1985).

In summary, a-typical combinations of curvature and velocity may be learned in the same way as learning unusual phase shifts in bimanual coordination (Zanone and Kelso 1992, 1997).

Visual perception baseline

We found that participants were more accurate at discriminating moving dots whose motion violated the two-thirds power law. Visual discrimination was even superior for strongly compared to weakly violated movement constraints despite the use of comparison stimuli which deviated from the visual prototype in discrete $x$-$y$ ratio steps. The two-thirds power law has also been explained to be an effect of constant affine velocity (Pollick and Sapiro 1997). The constant velocity which is perceived in movements complying with the two-thirds power law can thus be explained by the constant affine velocity that these movements feature. Any other functions which are not affine invariant are thus perceived as non-uniform (Pollick and Sapiro 1997). The degree of non-uniformity (or non-smoothness) may have been used as a marker to discriminate these types of motion in our study.

Effects of motor learning on visual perception

...
In line with previous studies which found an effect of action on visual (Brown et al. 2007; Hecht et al. 2001) and auditory (Repp and Knoblich 2007) perception, visual perception significantly improved by motor training. Since we aimed to double-dissociate the effects of learning a-typical movements on visual perception (in contrast to other studies) we tested participants on two different movements. Consistent with previous studies (Casile and Giese 2006; Reithler et al. 2007), we find a significant improvement in visual perception of the trained movement, but in addition, we find that training can transfer to highly similar movement types. Although training of both movement types led to improved visual discrimination ability of the trained movement type, this effect seemed to transfer to the non-trained, elliptic prototype, but not to the unrelated, circular prototype. This suggests that the information of one movement type may have been used to discriminate highly related movement types as well. The transfer effect seemed to be stronger in the group which was trained on the weak elliptic velocity profile, which may be due to a higher level of fine-tuning to the movement caused by the ambiguity of the stimulus. It remains an issue for future research to further determine how action-to-perception transfer generalizes across different types of action.

The present study extends previous findings demonstrating action-to-perception transfer for different a-typical movements applying a highly standardized motor learning procedure. We trained participants on a movement which violates a common motor constraint, the two-thirds power law, instead of using pre-defined movement trajectories (e.g., Engel et al. 2008; Hecht et al. 2001; Reithler et al. 2007). Thus, we could assure that participants had no visual experience of the applied movement and that motor learning led to an acquisition of a motor representation (defined by geometry and dynamics) rather than a mere use of memorizing trajectories. In contrast to the previous study which also trained on a-typical movements violating a motor constraint (Casile and Giese 2006), we used passive motor training. Thereby, we could ensure that participants acquired the novel movement in a
highly standardized manner and could achieve training success in most of our participants. Taken together, this study provides reliable evidence that motor learning affects visual perception.

We show that successful motor learning is a necessary requirement for action-to-perception transfer. Participants who were not able to actively execute the trained movement did not improve in the visual discrimination task. This suggests that even when low-level sensory experience of the novel movement was present, improvements in visual perception depended upon successful motor learning of the specific movement. Moreover, learning of movements unrelated to the visually perceived stimuli did not lead to perceptual improvements either. Thus, our findings support the tight link between action and perception (e.g. Prinz 1997; Schütz-Bosbach and Prinz 2007) especially in the case of action-to-perception (Hecht et al. 2001).

A possibility which cannot be fully excluded by the present data is that improvement in visual perception may have been affected by increased attention for the trained movement during the visual discrimination task. Motion processes are supposed to be ‘low-level’ and stimulus driven (Werkhoven et al. 1993, 1994). Evidence is accumulating, however, that it is mediated by attention (Cavanagh 1992) and that motion capture may be better conceived as a ‘high-level’ process involving active attention (Culham and Cavanagh 1994; Wohlschläger 2000). Our motor training may thus have led to increased attention paid to the learned stimulus, rather than that the increased visual discrimination performance was due to mnemonic effects.

Conclusion

Our results reliably demonstrate that non-visual motor learning of a novel movement improves visual perception of the trained movement and highly related movements. Moreover, action-to-perception transfer seems to be dependent on the successful acquisition
of the trained movement. In line with some previous studies, the typical curvature-velocity
relation as predicted by the two-thirds power law seems to be susceptible to changes after
motor training.
Footnotes

1. The x-y ratio of an ellipse represents the minor divided by the major axis of an ellipse. Comparison stimuli were calibrated at x-y ratio distances (cf. de’Sperati and Viviani 1997). The expression of elliptic eccentricity has a non-linear relation to x-y ratios. At greater elliptic eccentricities, the x-y ratios decrease disproportionally. X-y ratios were thus used to ensure that dynamic elliptic eccentricities would differ according to what their geometric ellipse would look like. The stimuli for the other two prototypes had the following x-y ratios: the circular prototype “0”: x-y ratio = 1; its comparison stimuli: 0.85, 0.70 (horizontal and vertical); the weak elliptic prototype “-.71”: x-y ratio = 0.7; its comparison stimuli: 0.4, 0.55, 0.85, 1; the extreme elliptic prototype “-.92”: x-y ratio = 4; its comparison stimuli: 0.1, 0.25, 0.55, 0.7.

2. The reason we did not time-standardize data for movement variance calculations was that variations in movement duration / timing also play a role in this parameter and should thus be included. As time standardization does not influence calculations on movement geometry (deviation from radius), it is preferable to use the original data. Time-standardization in the Java program took place just before smoothing data.
Acknowledgments

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References


FIG. 1. Experimental protocol. A: Movement manipulandum by which participants were trained on a movement with a circular path (see solid line), but with a velocity profile of a weakly (light dotted) or an extremely (dark dotted) elongated ellipse. B: Experimental procedure over the 4 days. “V Pre” is visual pre-test; “V Post” is visual post-test; MT is motor training session (consisting of 2 passive training and 2 active reproduction blocks). C: Trial procedure for the visual discrimination task. ISI: inter-stimulus interval; ITI: inter-trial interval. During stimulus 2 and the response screen, participants could respond. Dotted lines in stimuli represent circular movement paths; striped lines represent the elliptic velocity profiles. The size of the icons here are arbitrary and do not correspond to real sizes in the experiment.

FIG. 2. Polar plots of geometry and velocity profiles in both kinesthetically presented movement trajectories. The radius of the striped line represents the radius of the trajectory (geometry); the radius of the solid line represents the varying radius of curvature of the corresponding simulated ellipse (velocity profile). Note that at points of low radius of curvature (where the line is located inwards), velocity is low. A: the extreme elliptic condition (Σd = -.92); B: the weak elliptic condition (Σd = -.71). Starting and ending point of all stimuli was at 270°.

FIG. 3. Example data of one representative participant in the extreme elliptic condition during the third day. Data points reflect the means over one reproduction block (= 15 movements). Left: geometry of the movement trajectory (data are not time-standardized). Each dot represents the (x, y) coordinates (every 20ms). Mean deviation from radius here was 4.62 %. Right: Velocity over time of the movement trajectory (data are time-standardized). The ratio between minimum and maximum speed (x-y ratio simulated by the velocity profiles) here was 0.324 (i.e. dynamic eccentricity = -0.946).

FIG. 4. Velocity profiles per condition per session. A: Extreme elliptic condition. B: Weak elliptic condition (learners). C: Weak elliptic condition (non-learners). D: Natural movement condition. Thick black line indicates the trained velocity profile; yellow to dark-red lines (see legend) indicate produced velocity profiles per session. Note that in the movement only condition, data for only one session exist.

FIG. 5. Movement variability and geometry. A: Movement variability expressed in standard deviation (SD) between movements per active reproduction session. B: Geometry of trajectories expressed in per cent deviation from radius per session. See legend for each condition. Error bars represent standard error (SE).
FIG. 6. Curvature-velocity relationship. A and B represent data of one participant (JR) who participated in the natural movement (A), and in the extreme elliptic condition (B). C and D represent data of a different participant (CN) who participated in the natural movement (C), and in the weak elliptic condition (D). On the x-axis the logarithm of the radius of curvature is plotted against the logarithm of the velocity (m/s) on the y-axis. The four sessions were taken together here for illustratory purposes (over which the slope was calculated). For data analyses, the slope ($\beta$) and R-square were only calculated per session.

FIG. 7. Baseline visual discrimination ability (visual pre-test in all experimental conditions). A. $D'$ per prototype on visual pre-test collapsed for all comparison stimuli. B. $d'$ for all three prototypes for ‘near’ (0.15; dark grey) and ‘far’ (0.30; light grey) comparison stimuli from the concerning prototype. Error bars represent standard error.

FIG. 8. Visual discrimination ability before and after motor training. Light grey bars indicate discrimination ability ($d'$) on visual pre-test; black bars indicate discrimination ability ($d'$) on visual post-test. A. performance in extreme elliptic condition. B. performance in learners of the weak elliptic condition. C. performance in non-learners of the weak elliptic condition. D. performance in the visual control condition. Error bars represent standard error; the asterisk indicates a significant difference with $P < 0.05$ between visual pre- and post-test.
<table>
<thead>
<tr>
<th>Training Condition</th>
<th>Movement variability</th>
<th>Geometry (x-y ratio)</th>
<th>Dynamics (x-y ratio)</th>
<th>Velocity (RMSE)</th>
<th>Session</th>
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Values are Mean ± SD. ‘Movement variability’ is the standard deviation (SD) between movement trajectories in millimetres. The geometry is expressed in deviation from radius in per cent. The velocity profile is expressed in dynamic x-y ratio (minimum / maximum velocity). Velocity (RMSE) is the root of the mean squared deviation between the trained velocity profile curve and the reproduced velocity profile curves. Note that the control group only produced 2 times 15 movements, so data exist only for session 1.
Table 2. *Curvature-velocity relationship.*

<table>
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<th>Exponent $\beta$</th>
<th>R-squared</th>
<th>Session</th>
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<td>0.28 ± 0.06</td>
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<td></td>
<td>0.29 ± 0.05</td>
<td>0.85 ± 0.04</td>
<td>3</td>
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<td></td>
<td>0.29 ± 0.05</td>
<td>0.83 ± 0.09</td>
<td>4</td>
</tr>
<tr>
<td>Weak elliptic condition –</td>
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<td>learners</td>
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<td>0.88 ± 0.05</td>
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<td>0.27 ± 0.05</td>
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<td>4</td>
</tr>
<tr>
<td>Natural movement group</td>
<td>0.31 ± 0.07</td>
<td>0.88 ± 0.04</td>
<td>1</td>
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</tbody>
</table>

Exponent $\beta$ of the formula $V = KR^\beta$, as indicated by the slope between the logarithm of the radius of curvature and the logarithm of the tangential velocity, and R-squared of the cloud of dots. Values are Mean ± SD.
Table 3. Visual discrimination ability ($d'$) on visual pre- and post-test per prototype and comparison stimuli (CS).

<table>
<thead>
<tr>
<th>Training Condition</th>
<th>Visual Pre-test</th>
<th>Visual Post-test</th>
<th>CS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P 0</td>
<td>P -.71</td>
<td>P -.92</td>
</tr>
<tr>
<td>Baseline all participants</td>
<td>0.40 ± 0.30</td>
<td>0.59 ± 0.32</td>
<td>0.87 ± 0.34</td>
</tr>
<tr>
<td></td>
<td>0.05 ± 0.32</td>
<td>0.36 ± 0.35</td>
<td>0.47 ± 0.34</td>
</tr>
<tr>
<td></td>
<td>0.75 ± 0.34</td>
<td>0.81 ± 0.35</td>
<td>1.27 ± 0.46</td>
</tr>
<tr>
<td>Extreme elliptic condition</td>
<td>0.36 ± 0.24</td>
<td>0.52 ± 0.30</td>
<td>0.91 ± 0.24</td>
</tr>
<tr>
<td></td>
<td>0.00 ± 0.18</td>
<td>0.26 ± 0.34</td>
<td>0.48 ± 0.25</td>
</tr>
<tr>
<td></td>
<td>0.71 ± 0.36</td>
<td>0.78 ± 0.33</td>
<td>1.33 ± 0.34</td>
</tr>
<tr>
<td>Weak elliptic condition – learners</td>
<td>0.43 ± 0.43</td>
<td>0.60 ± 0.32</td>
<td>0.72 ± 0.41</td>
</tr>
<tr>
<td></td>
<td>0.02 ± 0.53</td>
<td>0.40 ± 0.30</td>
<td>0.39 ± 0.33</td>
</tr>
<tr>
<td></td>
<td>0.84 ± 0.39</td>
<td>0.81 ± 0.39</td>
<td>1.05 ± 0.55</td>
</tr>
<tr>
<td>Weak elliptic condition – non-learners</td>
<td>0.38 ± 0.28</td>
<td>0.61 ± 0.35</td>
<td>0.85 ± 0.59</td>
</tr>
<tr>
<td></td>
<td>0.05 ± 0.26</td>
<td>0.29 ± 0.42</td>
<td>0.57 ± 0.52</td>
</tr>
<tr>
<td></td>
<td>0.67 ± 0.32</td>
<td>0.84 ± 0.38</td>
<td>1.38 ± 0.56</td>
</tr>
<tr>
<td>Visual Control group</td>
<td>0.36 ± 0.34</td>
<td>0.48 ± 0.23</td>
<td>0.99 ± 0.78</td>
</tr>
<tr>
<td></td>
<td>-0.03 ± 0.51</td>
<td>0.29 ± 0.31</td>
<td>0.60 ± 0.65</td>
</tr>
<tr>
<td></td>
<td>0.75 ± 0.54</td>
<td>0.67 ± 0.32</td>
<td>1.38 ± 0.95</td>
</tr>
</tbody>
</table>

Values ($d'$) are Mean ± SD. ‘Mean’ in the CS column is mean $d'$ over both comparison stimuli. Significant increases in $d'$ on post-test are marked in bold. One asterisk indicates $P < 0.05$; two asterisks indicate $P < 0.01$. 
Table 4. *Criterion (bias) of visual pre- and post-test per prototype and comparison stimuli (CS).*

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<tr>
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<td></td>
<td>P 0</td>
<td>P-.71</td>
<td>P-.92</td>
</tr>
<tr>
<td>Baseline all participants</td>
<td>0.67 ± 0.42</td>
<td>0.38 ± 0.29</td>
<td>0.44 ± 0.37 x</td>
</tr>
<tr>
<td></td>
<td>0.85 ± 0.47</td>
<td>0.49 ± 0.30</td>
<td>0.63 ± 0.40 x</td>
</tr>
<tr>
<td></td>
<td>0.48 ± 0.40</td>
<td>0.27 ± 0.30</td>
<td>0.24 ± 0.36 x</td>
</tr>
<tr>
<td>Extreme elliptic condition</td>
<td>0.78 ± 0.47</td>
<td>0.46 ± 0.28</td>
<td>0.66 ± 0.32 0.96 ± 0.56</td>
</tr>
<tr>
<td></td>
<td>0.96 ± 0.51</td>
<td>0.59 ± 0.30</td>
<td>0.88 ± 0.37 1.17 ± 0.67</td>
</tr>
<tr>
<td></td>
<td>0.60 ± 0.44</td>
<td>0.33 ± 0.28</td>
<td>0.45 ± 0.28 0.75 ± 0.50</td>
</tr>
<tr>
<td>Weak elliptic condition – learners</td>
<td>0.61 ± 0.28</td>
<td>0.44 ± 0.25</td>
<td>0.46 ± 0.32 0.97 ± 0.46</td>
</tr>
<tr>
<td></td>
<td>0.81 ± 0.25</td>
<td>0.54 ± 0.26</td>
<td>0.63 ± 0.36 1.17 ± 0.44</td>
</tr>
<tr>
<td></td>
<td>0.40 ± 0.33</td>
<td>0.34 ± 0.26</td>
<td>0.29 ± 0.30 0.77 ± 0.50</td>
</tr>
<tr>
<td>Weak elliptic condition – non-learners</td>
<td>0.83 ± 0.23</td>
<td>0.42 ± 0.22</td>
<td>0.42 ± 0.44 1.14 ± 0.63</td>
</tr>
<tr>
<td></td>
<td>0.98 ± 0.27</td>
<td>0.56 ± 0.19</td>
<td>0.62 ± 0.52 1.34 ± 0.72</td>
</tr>
<tr>
<td></td>
<td>0.68 ± 0.19</td>
<td>0.28 ± 0.26</td>
<td>0.21 ± 0.40 0.95 ± 0.54</td>
</tr>
<tr>
<td>Visual Control group</td>
<td>0.52 ± 0.53</td>
<td>0.23 ± 0.34</td>
<td>0.22 ± 0.31 0.61 ± 0.55</td>
</tr>
<tr>
<td></td>
<td>0.71 ± 0.65</td>
<td>0.32 ± 0.34</td>
<td>0.41 ± 0.29 0.78 ± 0.52</td>
</tr>
<tr>
<td></td>
<td>0.32 ± 0.46</td>
<td>0.13 ± 0.37</td>
<td>0.02 ± 0.36 0.43 ± 0.58</td>
</tr>
</tbody>
</table>

Values are Mean criterion \((z_{hits} + z_{false alarms}) / 2\) ± SD. ‘Mean’ in the CS column is mean criterion over both comparison stimuli.
Day 1: Vpre  MT
Day 2:  MT
Day 3:  MT
Day 4:  MT  Vpost
--- Geometry  --- Velocity profile

A

B  

radius of curvature
Velocity profile

- (0) circular
- (-0.71) weak elliptic
- (-0.92) extreme elliptic

**Visual Pre-test**  **Visual Post-test**

A

B

C

D