Movement paths in operating hand-held tools: tests of distal-shift hypotheses

Sandra Sülzenbrück and Herbert Heuer
IfADo—Leibniz Research Centre for Working Environment and Human Factors, Dortmund, Germany

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Sülzenbrück S, Heuer H. Movement paths in operating hand-held tools: tests of distal-shift hypotheses. J Neurophysiol 109: 2680–2690, 2013. First published March 13, 2013; doi:10.1152/jn.01101.2012.—Extending the body with a tool could imply that characteristics of hand movements become characteristics of the movement of the effective part of the tool. Recent research suggests that such distal shifts are subject to boundary conditions. Here we propose the existence of three constraints: a strategy constraint, a constraint of movement characteristics, and a constraint of mode of control. We investigate their validity for the curvature of transverse movements aimed at a target while using a sliding first-order lever. Participants moved the tip of the effort arm of a real or virtual lever to control a cursor representing movements of the tip of the load arm of the lever on a monitor. With this tool, straight transverse hand movements are associated with concave curvature of the path of the tip of the tool. When terminal visual feedback and when targets were presented for the hand, hand paths were slightly concave in the absence of the dynamic transformation of the tool and slightly convex in its presence. When targets were presented for the tip of the lever, both the concave and convex curvatures of the hand paths became stronger. Finally, with continuous visual feedback of the tip of the lever, curvature of hand paths became convex and concave curvature of the paths of the tip of the lever was reduced. In addition, the effect of the dynamic transformation on curvature was attenuated. These findings support the notion that distal shifts are subject to at least the three proposed constraints.

motor control; tool use; movement trajectories; visual feedback

HUMANS ARE HIGHLY PROFICIENT in tool use. According to a time-honored notion, the proficiency is based on the incorporation of the tool into the body schema (Head and Holmes 1911). In recent years this notion has been supported by different types of physiological and behavioral data (Berti and Frassinetti 2000; Cardinali et al. 2009, 2012; Iriki et al. 1996; Maravita and Iriki 2004; Yamamoto and Kitazawa 2001). When the body schema is extended by a hand-held tool, the effective part of the tool replaces the hand as the end effector. As a consequence, movement characteristics of the hand could become characteristics of movements of the tool. They could be shifted distally along the series of transformations that range from motor outflow to the movement of the hand and finally to the movement of the effective part of the tool (cf. Heuer and Massen 2012).

A strong version of the distal-shift hypothesis would posit that all characteristics of hand movements become characteristics of the effective part of the tool as soon as a tool is held. However, recent findings provide evidence against such a strong version. Rather, they suggest that the distal shift is subject to boundary conditions, for example, a proper use of the tool (cf. Maravita and Iriki 2004; Witt et al. 2005). In this report we aim to further the understanding of the boundary conditions for distal shifts. We propose and test three constraints: strategies, movement characteristics, and modes of control. These three constraints will be elaborated in turn.

The first constraint that we propose is the strategy constraint: distal shifts of movement characteristics are strategic rather than mandatory. This constraint follows from the assumption that the representation of the tool does not necessarily have to be integrated with the representation of the body but rather can be kept separate. The notion of a body schema is similar to the notion of an internal model of the transformations the brain has to deal with in motor control (cf. Heuer 1983; Wolpert and Kawato 1998). Within this computational framework, internal models of the intrinsic transformations of the neural, muscular, and skeletal structures of the body and the extrinsic transformations of tools have been distinguished conceptually and operationally (cf. Heuer 1983; Kluzik et al. 2008). With separate internal models of intrinsic and extrinsic transformations it should be possible to plan and control the outputs of both transformations selectively or even concurrently (cf. Van den Steen and Bongers 2011). Therefore the distal shift of movement characteristics could be strategic rather than mandatory.

The second proposed constraint is the constraint of movement characteristics: distal shifts occur for some movement characteristics but not for all of them. Movement characteristics can be classified as being controlled or uncontrolled (cf. Scholz and Schöner 1999). Controlled characteristics are likely those that have consequences for the achievement of task goals, whereas movement characteristics that are irrelevant for task goals are likely to be uncontrolled. Distal shifts could be limited to controlled characteristics and spare uncontrolled characteristics. For example, the end positions of movements aimed at a target should be well controlled because their deviations from the target positions matter in terms of performance. In contrast, the trajectories could take many different forms and may be uncontrolled. When a tool is used, a distal shift of the end positions is required—the end positions of the hand when no tool is used should become end positions of the effective part of the tool. In contrast, a distal shift of trajectory characteristics is not required by the task. In fact, Verwey and Heuer (2007) as well as Rieger et al. (2008) reported such findings. They studied rapid aiming with a nonlinear transformation of hand positions into positions of a cursor on a monitor. Whereas end positions of the hand were appropriately derived from the target positions defined for the cursor, the velocity profiles did not reflect the nonlinear transformation. Rather, the hand movements had basically the same velocity profiles as movements to directly presented targets.

The third constraint that we propose is the constraint of mode of control: distal shifts occur for certain modes of control.
but not for others. Control of the output of a transformation requires that the input is determined that results in a certain desired output. Formally this is an inversion of the transformation. It can be achieved by means of open-loop or closed-loop control (Jordan 1996). Closed-loop or feedback control requires that the output of the transformation is fed back during movement execution. Open-loop or feedforward control requires a sufficiently accurate (inverse) internal model of the transformation that maps the desired output to an appropriate input. In principle, for certain trajectory characteristics distal shifts could be different for closed-loop and open-loop control. For example, when the internal model of open-loop control only maps target positions for the tool to target positions for the hand (cf. Rieger et al. 2008; Verwey and Heuer 2007), closed-loop control could add trajectory characteristics such as (approximate) straightness of movements of the effective part of the tool (cf. Flanagan and Rao 1995; Wolpert et al. 1995). Therefore we assume that closed-loop control is more likely to be associated with a distal shift than open-loop control.

In the present experiments we test the validity of the three distal-shift hypotheses outlined, that is, of the three constraints proposed for the distal shifts of movement characteristics in tool use. In experiment 1 we test the first two hypotheses according to which distal shifts are strategic and restricted to certain movement characteristics such as target positions. In experiment 2 we test the third distal-shift hypothesis according to which distal shifts are confined to certain modes of control such as closed-loop control. We investigate these hypotheses for the distal shift of a particular trajectory characteristic, namely, the curvature of movement paths. The paths of point-to-point movements are often described as being approximately straight (Abend et al. 1982; Morasso 1981). Nevertheless, systematic and often small deviations from straightness have been reported (Atkeson and Hollerbach 1985; Desmurget et al. 1997, 1999). As in point-to-point movements, there are no task demands with respect to straightness or a particular curvature of movement paths; these are generally attributed to the minimization of various kinds of costs (e.g., Cruse and Bürkner 1987; Flash and Hogan 1985; Harris and Wolpert 1998; Hollerbach and Atkeson 1987; Todorov 2004; Uno et al. 1989; Van Thiel et al. 1998).

The costs for the controlled maintenance of a particular curvature of movement paths can be increased by adding a dynamic influence such as the dynamic transformation of a tool. One way to deal with variable dynamics, even when they are unpredictable, is to increase the impedance of the limb (Franklin et al. 2003). This can be achieved by way of cocontractions, which are associated with metabolic costs. However, if curvature were largely uncontrolled, limb impedance could be reduced so that curvature would become more strongly affected by the dynamic environment. Thus the influence of a dynamic environment can serve as a marker for the precision with which curvature is controlled.

We tested the constraints on the distal shift of curvature of transverse movements in the horizontal plane with a sliding first-order lever as a tool. Participants were asked to control a cursor on a computer screen to reach different target positions. While their hand moved the effector arm of a physically present or virtual two-sided lever, the cursor could either represent movements of the tip of the load arm of this lever or movements of the hand. Movements of the hand were always executed in a horizontal plane. Generally, rotations of the lever around the pivot (also known as the fulcrum), translations passing through the pivot point, as well as combinations of rotations and translations were possible.

The sliding first-order lever implements rather complex kinematic and dynamic transformations (cf. Heuer and Sülzenbrück 2009 for a detailed description). Its kinematic transformation, which is the relation between hand movements and the resulting movements of the effective part of the tool, has two main features. First, there is an inverse relation between directions of movements of the hand and of the tip of the lever for rotations, which is referred to as the fulcrum effect (Gallagher et al. 1998). Second, the relation between the amplitudes of hand movements and resulting amplitudes of the distal tip of the lever depends on direction (gain anisotropy). As a consequence, the direction of the tip of the lever does generally deviate from the direction of the hand. The dynamic transformation of the sliding first-order lever, which is the transformation of the net force exerted by the hand into the acceleration of the hand-held lever arm, consists primarily of a direction-dependent inertia. As a consequence of this inertial anisotropy, the direction of acceleration generally deviates from the direction of force.

For transverse movements the characteristics of the kinematic transformation of the sliding first-order lever are illustrated in Fig. 1. With this tool the path of the hand and the path of the tip of the lever have different curvatures, and only one of them can be straight. Two sets of combinations of start and target positions are shown. In one set the target amplitudes of the hand are constant, whereas those of the tip of the lever vary. In the other set the target amplitudes of the tip of the lever are constant and those of the hand vary. For the first set straight paths of the hand are shown, which result in concave curvature of the paths of the tip of the lever. For the second set straight paths of the tip of the lever are shown, which require convex curvature of hand paths.

**MATERIALS AND METHODS**

**Experiment 1**

In experiment 1 we tested the first two hypothesized constraints on distal shifts, namely, the strategy constraint and the constraint of movement characteristics. Specifically, we compared the curvature of the paths of transverse movements as they were produced without (noKin) and with (Kin) the kinematic transformation of the sliding first-order lever, referring to conditions where the cursor represented movements of the hand (noKin) or of the tip of load arm of the lever (Kin). We did so in two groups in which the dynamic transformation of the sliding lever was absent (noDyn) or present (Dyn), respectively. Thus there were four conditions that differed with respect to the absence versus presence of the kinematic transformation and with respect to the absence versus presence of the dynamic transformation. In the absence of the kinematic transformation targets were defined for the hand. Consistent with previous observations, we expected almost straight movement paths or a slight concave curvature (Haggard and Richardson 1996; Wolpert et al. 1994; Van Thiel et al. 1998) and only little or no influence of the absence versus presence of the dynamic transformation (Heuer and Sülzenbrück 2012). In the presence of the kinematic transformation targets were defined for the tip of the lever. Under the unconstrained distal-shift hypothesis, curvature characteristics of hand paths in the absence of the kinematic transfor-
Participants had to move a pen attached to a hold (diameter: 25 mm) in a horizontal plane across the digitizer. The hold, which was a plastic cylinder, served to keep the inserted pen in a position perpendicular to the digitizer plane. The hold of the pen slid on the surface of the digitizer and could not be tilted. Friction between the hold and the digitizer was minimized by attaching felt to the bottom of the hold. Participants grasped the hold with a precision grip involving the thumb, the index, and/or the middle finger of their right hand. The total mass of the pen and the hold was 0.075 kg. The lever was 355 mm long and had a mass of 0.370 kg; its moment of inertia was \((0.0061 + 0.370 \cdot r^2) \text{kgm}^2\), where \(r\) is the distance of the center of mass from the fulcrum. The position of the tip of the pen on the digitizer was recorded with a sampling rate of 60 samples/s. For participants of the Dyn group, this pen was attached to the end of the effort arm of the sliding lever, so that there was a position- and direction-dependent inertia. Participants of the noDyn group used the pen attached to the hold but detached from the lever. In this condition the inertia of the lever should become curvature characteristics of the paths of the tip of the lever in its presence. Under the constraint of movement characteristics, with the specification that a distal shift occurs only for end positions but not for path characteristics, hand paths in the presence of the kinematic transformation should remain essentially as they were without the transformation. However, they might become less strictly controlled so that the influence of the dynamic environment should be increased.

In the presence of the dynamic transformation targets were defined either for the hand (kinematic transformation absent) or for the tip of the lever (kinematic transformation present). According to the strategy constraint, distal shifts should occur only when appropriate for performance, that is, when targets are presented for the tip of the lever but not when they are presented for the hand.

**Methods.** PARTICIPANTS. Two groups of 12 right-handed participants each took part in the experiment. In the noDyn group, in which movements were performed without the dynamic transformation, there were six women and six men, aged 19–28 yr (mean: 23.8 yr; SD: 2.5 yr). In the Dyn group, in which the dynamic transformation was present, there were again six women and six men, aged 20–29 yr (mean: 23.2 yr; SD: 3.1 yr). All participants had given written informed consent prior to the start of the experiment. The experiment was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Behavioral studies like these that do not put any load on the participants are approved by the ethics committee of the Leibniz Research Centre for Working Environment and Human Factors without requiring an individual request for approval.

**APPARATUS.** The apparatus was the same as that described by Sülzenbrück and Heuer (2009, 2010, 2011, 2012). As depicted in Fig. 2, participants sat at a table and faced a 17-in. monitor (Iiyama ProLite, refresh rate 60 Hz, resolution \(1,280 \times 1,024\) pixels) at \(\sim 1\)-m distance from their eyes. Between the participant and the monitor a digitizer (Wacom Intuos 2) with the same resolution and an active area of \(324 \times 243\) mm\(^2\) was placed on the table. At the far end of the digitizer a vertical frame was attached. This frame carried the ball bearing of a sliding first-order lever. Participants were seated such that the fulcrum of the lever was roughly in their median plane. Throughout the experiment an opaque screen was placed 240 mm above the table surface to prevent participants from seeing their hand and the lever.

Fig. 2. Apparatus. Participants were placed in front of a table with a digitizer on it. A vertical frame was attached to the digitizer, holding the ball bearings of a sliding first-order lever. Participants were asked to slide a pen across the digitizer to control a cursor presented on a computer monitor. While in trials without the kinematic transformation of the lever (noKin) this cursor represented movements of the hand holding the effort arm of the lever, the cursor represented movements of the tip of the load arm of the lever with the kinematic transformation (Kin). When the pen was attached to the end of the effort arm of the lever, the dynamic transformation was present (Dyn); it was absent when the pen was detached from the lever (noDyn). An opaque screen prevented a direct view of the apparatus and the movements of the hand.
tool was fixed with the constant mass of the pen and the hold and therefore independent of position and movement direction.

TASK. Participants were instructed to move as quickly and as accurately as possible from a start location to a target location. At the beginning of each trial the current position of the tip of the lever or of the hand was presented on the monitor by a cursor, which was a filled red circle of radius 1 mm. Participants had to move the cursor to a start position, a filled white circle of radius 1.8 mm, by moving the pen forward or backward or to the left or right. When the cursor had reached the center of the start position (position tolerance was 1.2 mm) and had been held in that position for 1 s, the color of the start circle changed to green and a filled white circle (radius 1.8 mm) became visible on the monitor, representing the current target position.

In practice trials with continuous visual feedback, the red cursor was visible throughout the trial. When the cursor had reached the target position (position tolerance 1.2 mm), the color of the target changed to yellow. In trials with terminal visual feedback, the cursor disappeared when it left the tolerance range of 1.2 mm around the start position. Participants ought to stop moving and hold that position when they judged they had reached the target position. When hand velocity had been slower than 5 mm/s for 500 ms, the cursor reappeared on the screen for 1 s (together with the target) to provide information on movement accuracy. After another second, a new trial started.

The start and target positions are shown in Fig. 1, both for the hand and for the tip of the lever. All hand movements analyzed were from right to left. Return movements from left to right were performed in every second trial. In Fig. 1A, start-target configurations with the same amplitude (100 mm) of hand movements are shown with the corresponding end positions of the tip of the lever. Hand paths are illustrated as straight and paths of the tip of the lever as appropriately (concavely) curved. In Fig. 1B, start-target configurations with the same amplitude (100 mm) of movements of the tip of the load arm of the lever are shown with the corresponding end positions of the hand. Here the paths of the tip of the lever are illustrated as straight and the paths of the hand as appropriately (convexly) curved. For start-target combination 3, amplitudes of the hand and the tip of the (load arm of the) lever were identical because the load arm and the effort arm were of equal length. In the following, start-target combinations with the same amplitude of hand movements are referred to as a hand-same target set, while combinations with different amplitudes of hand movements are called a hand-different target set.

DESIGN. At the start of the experiment, participants received written instructions about the procedure. They were informed that the relation between cursor motion and hand movement could be that of a sliding first-order lever, and the functioning of such a lever was explained in detail and with reference to an illustration presented on the monitor.

The experiment comprised two test phases of four blocks with 56 trials each. The first two trials of each block were warm-up trials. Half of the remaining trials were test trials, and the other half were trials with return movements. In one test phase the cursor represented the position of the hand (noKin); in the other test phase the cursor represented the position of the tip of the lever (Kin). In the noKin condition the kinematic transformation of the lever was absent, whereas in the Kin condition it was present. Half of the participants in each group started with the noKin condition followed by the Kin condition. For the other half of the participants the order of conditions was reversed. Throughout all test trials participants received terminal visual feedback on the end location of the cursor. Before each test phase there were two practice blocks with 56 trials each, with continuous visual feedback being available in the first practice block and terminal visual feedback in the second practice block.

DATA ANALYSIS. The time series of the recorded Cartesian coordinates of the tip of the pen on the digitizer were low-pass filtered (4th-order Butterworth, 10 Hz, dual pass) and differentiated (2-point central difference algorithm). We determined the start and end of each movement by the tangential velocity being <3 mm/ms for 450 ms in a forward and backward scan, beginning at peak tangential velocity.

For each individual hand movement, movement time, amplitude, path length, and direction were determined. Movement amplitude was computed as the distance from initial to final position and path length as the total distance along the movement path. Movement direction was determined as the direction of the vector pointing from the initial to the final position. All movements were screened for outliers. A trial was removed from further analyses if it satisfied at least one of four criteria: 1) movement time was <200 ms or >5,000 ms, 2) hand amplitude was <10 mm or >300 mm, 3) path length of the hand was longer than three times the amplitude, or 4) absolute error of direction of the cursor was >40°. In total, 4,875 trials (24 × 216 trials minus 309 discarded trials) were analyzed. In the noDyn group the percentage of discarded trials was 5.2% (0.9–15.3% in individual participants); in the Dyn group the percentage of discarded trials was 6.8% (0–16.2%).

For all hand movements to each of the nine targets, separately for noKin and Kin conditions, mean movement time, end-point accuracy in terms of mean amplitude error and mean direction error, and mean curvature were computed for each participant. For the noKin condition trajectory combinations of the hand and of the cursor were identical. For the Kin condition mean curvature was also computed for cursor movements. Errors of direction and amplitude were the differences of the amplitude and direction of the hand movement from the direction and amplitude of each start-target vector. Curvature of each movement was defined as the difference between two directions, the mean direction of all measured positions in the middle 50% of the movement amplitude and the direction of the vector from initial to final position of the movement. The sign of the difference was chosen such that positive values indicate convex and negative values concave curvature. The individual means of movement time, amplitude and direction errors, and curvature were subjected to separate ANOVAs for the two target sets with same and different amplitudes of hand movements. One start-target combination (sequential in Fig. 1) was included in both analyses. Furthermore, average movement paths were computed after normalizing the duration of each movement.

Results. We present the average paths of the hand and thereafter focus on the results for curvature. Data on end-point accuracy of hand movements as well as movement time (mean values and SEs) are only briefly reported.

MOVEMENT PATHS. The average paths of the hand are displayed in Fig. 3. When the cursor represented hand movements (noDyn/noKin and Dyn/noKin conditions), almost straight hand paths were produced in the absence and in the presence of the dynamic transformation. If, however, the cursor represented movements of the tip of the lever, movement trajectories were curved. While in the noDyn/Kin condition curvature of hand paths was concave, curvature was convex in the Dyn/Kin condition.

Without the kinematic transformation (noDyn/noKin and Dyn/noKin conditions), movement end points were fairly accurate. In contrast, with the kinematic transformation (noDyn/Kin and Dyn/Kin conditions) amplitudes of hand movements were systematically inaccurate. They were too short when the effort arm was long and the visuomotor gain (ratio of the amplitude of the movement of the tip of the lever over the amplitude of the movement of the hand) was small, and they were too long when the effort arm was short and the visuomotor gain was large.

CURVATURE. The pattern of results observed for curvature is presented first, and information about the statistical relevance of these findings follows. Mean curvature of hand movements is shown in Fig. 4. The findings were essentially the same with both target sets. Without the kinematic transformation (noKin), curvature was close to zero both without (noDyn/noKin) and with (Dyn/noKin) the dynamic transformation. Nevertheless, there was a small and consistent influ-
ence of the dynamic transformation. With the kinematic transformation (Kin), in contrast, curvature of hand paths was stronger. Without the dynamic transformation (noDyn/Kin) paths of the hand had concave curvature, but with the dynamic transformation (Dyn/Kin) curvature was convex. Whereas concave curvature of hand paths served to increase the concave curvature of the movements of the tip of the lever compared with straight paths of the hand, convex curvature of hand paths served to reduce the concave curvature of the tip of the lever. Averaged across the two target sets, mean (concave) curvature of the paths of the tip of the lever was $-25.8 \pm 8.7^\circ$ and $-19.5 \pm 8.7^\circ$ in noDyn/Kin and Dyn/Kin conditions, respectively.

The curvature data were subjected to separate three-way ANOVAs for the two target sets with the between-participant factor dynamic transformation (noDyn vs. Dyn) and the within-participant factors kinematic transformation (noKin vs. Kin) and start-target combination (5 combinations; cf. Fig. 1). The variations of curvature were reflected in significant interactions of the factors dynamic transformation and kinematic transformation [$F(1,22) = 8.1$, $P < 0.01$ for hand-same target set and $F(1,22) = 8.8$, $P < 0.01$ for hand-different target set]. In addition, the main effect of the factor dynamic transformation was significant for both target sets [$F(1,22) = 13.1$, $P < 0.01$ and $F(1,22) = 12.9$, $P < 0.01$, respectively]. Separate contrasts between absence and presence of the dynamic transformation were significant both without the kinematic transformation [noDyn/noKin vs. Dyn/noKin; $F(1,22) = 5.5$, $P < 0.05$ for both target sets] and with the kinematic transformation [noDyn/Kin vs. Dyn/Kin; $F(1,22) = 11.3$, $P < 0.01$ and $F(1,22) = 11.6$, $P < 0.01$ for both target sets]. No significant effects of the start-target combination were found.

END-POINT ACCURACY AND MOVEMENT TIME. Movements were rather accurate when targets were specified for the hand, that is, in the absence of the kinematic transformation. Amplitude errors were on the order of only a few millimeters. In contrast, controlling the tip of the lever in the presence of the kinematic transformation was associated with larger amplitude errors (see Fig. 3). For both target sets, overshoots were found for the start-target combination with the shortest effort arm and the largest visuomotor gain (+38.1 ± 4.3 mm and +39.8 ± 3.0 mm for hand-same and hand-different target sets, respectively) and undershoots were found for the start-target combination with the longest effort arm and the smallest visuomotor gain (−19.6 ± 3.9 mm and −56.5 ± 5.2 mm). Direction errors were small but slightly larger in the presence than in the absence of the kinematic transformation (hand-same target set: 4.6 ± 2.2° vs. 2.7 ± 1.2°; hand-different target set: 4.5 ± 2.1° vs. 2.6 ± 1.2°).

Movement time was $1,790 \pm 241$ ms overall for the hand-same target set (ranging from 1,109 to 2,614 ms for individual participants) and $1,791 \pm 258$ ms for the hand-different target set (ranging from 1,132 to 2,664 ms for individual participants). There was no reliable effect of the dynamic transformation, but movement times were longer with than without the kinematic transformation [1,953 ± 236 ms vs. 1,627 ± 155 ms (hand-same) and 1,961 ± 245 ms vs. 1,621 ± 182 ms (hand-different)] for the two target sets.

Discussion. In experiment 1 we tested the first two hypothesized constraints on the distal shift of movement characteristics in tool use. For this purpose we analyzed trajectory characteristics, in particular path curvature, while using a hand-held sliding first-order lever. On average, curvature of hand movements was the same both without and with the kinematic transformation. Hand movements were almost straight, and when the lever was used the path of its tip exhibited the
associated strong concave curvature. There was in fact no indication that curvature of hand movements changed when the tool was used so that curvature of the tip of the lever could match the curvature of hand movements in the absence of the tool. Thus there was clearly no distal shift of path curvature when the sliding first-order lever was used. This finding is consistent with the proposed constraint of movement characteristics, according to which distal shifts are restricted to certain movement characteristics.

The distal shift of path curvature was absent not only in the presence of the kinematic transformation of the sliding lever but also when only the dynamic transformation was present, that is, when the physical lever was moved but targets were defined for the hand. This finding would be evidence in favor of the strategy constraint, according to which distal shifts are strategic rather than mandatory, but only if a distal shift had been observed in the presence of the kinematic transformation. However, the observation of essentially no distal shift of path curvature at all instead of a contrast between a distal shift when targets were defined for the tip of the lever and its absence when targets were defined for the hand does not allow such a conclusion. Thus with respect to this particular distal-shift hypothesis the findings of experiment 1 are inconclusive.

Even though on average hand movements had essentially the same curvature in the absence and in the presence of the kinematic transformation, in both conditions there was an influence of the dynamic transformation of the sliding lever. Without the dynamic transformation curve of hand paths was concave, corresponding to findings of Haggard and Richardson (1996), Wolpert et al. (1994), and Van Thiel et al. (1998). When the dynamic transformation was present, curvature of hand paths became convex. There are at least two reasons for this. First, for start and end positions to the right and left of the midsagittal plane the vectors of minimal resistance point into the corresponding directions. Second, with a simple rotation of the lever, which results in convex curvature of the movement of the hand, the inertial load remains constant throughout the movement. Thus with this movement strategy the complexities of variable inertia are avoided. However, without the kinematic transformation of the sliding lever, the influence of its dynamic transformation or—more generally—the influence of the dynamic context was much weaker than in the presence of the lever’s kinematic transformation. Thus without the kinematic transformation path curvature is more strictly controlled than with the kinematic transformation.

The present findings are consistent with the conclusion of Verwey and Heuer (2007) and Rieger et al. (2008) that the internal model of the kinematic transformation maps target positions of aimed movements for the effective part of the tool on target positions for the hand but not desired trajectory characteristics of the tool. Target positions matter for performance and should be controlled, whereas trajectory characteristics matter only little or not at all for performance and could be uncontrolled (or at least less strictly controlled). However, such considerations apply not only to movements of the effective part of a tool but also to movements of the hand when no tool is used. Nevertheless, the influence of the dynamic transformation was much weaker without than with the tool. Thus control of curvature seems to be more relaxed in the presence of the kinematic transformation than in its absence.

Along with the two proposed constraints tested in experiment 1, we hypothesize that the mode of control can also modulate the occurrence of distal shifts. The finding of a relaxed control of curvature in the presence of the kinematic transformation might be related to the fact that open-loop control was required to perform the task in experiment 1. In experiment 2 we therefore investigate the third proposed constraint on distal shifts, the constraint of mode of control.

**Experiment 2**

According to the findings of experiment 1, curvature of hand movements is more strictly controlled in the absence of the kinematic transformation of a tool than in its presence. The stricter control under at least some conditions suggests that curvature might play some role for performance. In fact, Harris and Wolpert (1998) showed by way of simulation that under the assumption of signal-dependent noise high levels of accuracy of aimed movements impose constraints on curvature. Intuitively it seems that higher levels of accuracy might be more possible with straight paths in a particular direction than with curved paths, the direction of which varies in the course of the movement. However, straightness of the path might matter only for high levels of accuracy, as observed in experiment 1 without the kinematic transformation of the tool but not for low levels of accuracy as observed with the kinematic transformation. In addition, or alternatively, control of curvature might be a matter of closed-loop control, whereas open-loop control is restricted to end positions. There is in fact some indication that end positions and trajectories might be controlled separately (e.g., Brown et al. 2003; DiZio and Lackner 1995; Heuer 1981; Sainburg and Wang 2002). In the absence of visual feedback, as in experiment 1, closed-loop control of the end effector (the effective part of the tool) is impossible when the kinematic transformation of the tool is present. The reason is that the output of the transformation, the position of the cursor on the monitor, can only be perceived visually. In contrast, in the absence of the kinematic transformation the position of the end effector (the hand) can also be perceived proprioceptively, not only visually. Thus closed-loop control of the end effector is possible, based on proprioceptive signals.

Based on these considerations, experiment 2 served to test the third constraint on the distal-shift hypothesis, the constraint of mode of control according to which distal shifts of certain movement characteristics such as path curvature are restricted to closed-loop control. The availability of visual feedback in the presence of the kinematic transformation of the tool and thus the possibility of closed-loop control should actually have a twofold effect on curvature under this hypothesis—in addition to more accurate movements of the tip of the lever. First, movements of the tip of the lever should become straighter overall, and the associated convex curvature of the hand paths should become stronger. Thus there should be at least a partial distal shift of curvature that could serve to support accurate movements. Second, the influence of the dynamic transformation on curvature should be attenuated, indicating a stricter control of distal curvature. To test these hypotheses, in experiment 2 there were again two groups in which the dynamic transformation of the sliding lever was absent (noDyn) or present (Dyn), respectively. In both groups the kinematic transformation was present, but in different conditions visual feedback was absent (noFb), as in experiment 1, or present (Fb).

**Methods.** PARTICIPANTS. Two groups of 12 participants each took part in the experiment. In the noDyn group there were six women and six men, aged 20–26 yr (mean: 23.4 yr; SD: 2.2 yr). In the Dyn group there were again six women and six men, aged 19–29 yr (mean: 24.1 yr; SD: 2.9 yr). All participants were right-handed and had given written informed consent.

APPARATUS, TASK, AND PROCEDURE. The apparatus, task, and procedure were the same as in experiment 1. A minor difference was that during test trials participants received no visual feedback at all. During each movement, these trials were identical to the terminal-feedback trials of experiment 1: the cursor disappeared from the monitor when the tolerance range around the start position was left but did not reappear when movement velocity had been slower than 5 mm/s for 500 ms.

DESIGN. Participants received written instructions about the procedure and were specifically informed about the transformation of a sliding first-order lever. The functioning of such a lever was explained in detail with reference to an illustration presented on the monitor. The instruction was followed by a practice phase of five blocks of 56 trials each. In all practice trials visual feedback was continuously presented. The 56 trials consisted of two warm-up trials followed by three
repetitions of random permutations of the nine start-target combinations shown in Fig. 1, each one followed by a trial with a return movement. The test phase consisted of five blocks of 40 trials each, the first 20 trials with continuous visual feedback (Fb) and the second 20 trials without visual feedback (noFb). In each set of 20 trials there were two warm-up trials and one trial for each start-target combination (followed by a trial with a return movement). Thus each of the start-target combinations shown in Fig. 1 was presented once per block in a pseudorandom order.

**DATA ANALYSIS.** Movements were analyzed in the same way as for experiment 1. Altogether 2,038 trials (24 × 90 trials minus 122 discarded trials) were included in the analyses. In the noDyn group 2.7% of the trials were discarded (0 – 8.9% in individual participants); in the Dyn group the percentage of discarded trials was 8.6% (0 – 32.2%).

**Results.** As for experiment 1, we present the average paths of the hand and thereafter focus on the results for curvature. Data on accuracy and movement time are only briefly reported.

**MOVEMENT PATHS.** Averaged movement paths of the hand are shown in Fig. 5. With continuous visual feedback (noDyn/Fb and Dyn/Fb conditions), movements were accurate. Curvature of the hand paths was convex both in the absence and in the presence of the dynamic transformation. Without visual feedback (noDyn/noFb and Dyn/noFb conditions), however, curvature was different in the absence and the presence of the dynamic transformation. In the noDyn/noFb condition the curvature of the hand paths was concave rather than convex, and in the Dyn/noFb condition it was convex. noDyn/noFb and Dyn/noFb conditions were equivalent to noDyn/Kin and Dyn/Kin conditions, respectively, of experiment 1. Not only curvature but also the pattern of overshoots and undershoots observed for the different start-target combinations was quite similar in the two experiments.

**CURVATURE.** In Fig. 6, mean curvature of the paths of the hand is displayed. The findings were essentially the same with both target sets. Without visual feedback (noFb) curvature was concave or convex, depending on the dynamic environment. Without the dynamic transformation (noDyn/noFb) paths of the hand had concave curvature, but with the dynamic transformation (Dyn/noFb) curvature was convex. Averaged across the two target sets, mean (concave) curvature of the paths of the tip of the lever was $-17.5 \pm 7.9^\circ$ and $-10.4 \pm 7.9^\circ$ in noDyn/Fb and Dyn/Fb conditions, respectively. Thus visual feedback resulted in a clearly straighter path of the tip of the lever in the absence of the dynamic transformation, but its effect was smaller in the presence of the dynamic transformation where the path of the tip of the lever was less curved anyway.

Individual curvatures of hand paths were subjected to two three-way ANOVAs for the two target sets with the between-participant factor dynamic transformation (noDyn vs. Dyn) and the within-participant factors visual feedback (noFb vs. Fb) and start-target combination (5 combinations; cf. Fig. 1). The variations of curvature that was somewhat smaller than without visual feedback. Averaged across the two target sets, mean (concave) curvature of the paths of the tip of the lever was $-28.7 \pm 8.5^\circ$ and $-12.5 \pm 8.5^\circ$ in noDyn/noFb and Dyn/noFb conditions, respectively. With visual feedback (Fb), curvature of the hand paths was convex both without and with the dynamic transformation of the lever. Nevertheless, there was a remaining influence of the dynamic transformation
gave rise to significant interactions of the factors dynamic transformation and visual feedback [F(1, 22) = 5.6, P < 0.05 for hand-same target set and F(1, 22) = 10.9, P < 0.01 for hand-different target set]. In addition, there were main effects of the factor visual feedback [F(1, 22) = 27.2, P < 0.01 and F(1, 22) = 36.8, P < 0.01 for the 2 target sets] and the factor dynamic transformation [F(1, 22) = 17.6, P < 0.01 and F(1, 22) = 16.7, P < 0.01 for the 2 target sets]. Separate contrasts of the dynamic conditions were significant both without visual feedback [noDyn/noFb vs. Dyn/noFb: F(1, 22) = 16.6, P < 0.01 and F(1, 22) = 20.4, P < 0.01 for both target sets] and with visual feedback [noDyn/Fb vs. Dyn/Fb: F(1, 22) = 10.3, P < 0.01 and F(1, 22) = 7.1, P < 0.05 for both target sets]. Curvature varied somewhat across the different start-target combinations, but these variations did not affect the basic findings on curvature as shown in Fig. 6. Therefore we do not report them in detail.

END-POINT ACCURACY AND MOVEMENT TIME. Movements were quite accurate with continuous visual feedback. Without visual feedback, overshoots were found for the shortest effort arm and the largest visuomotor gain (+35.7 ± 4.9 mm and +33.9 ± 3.4 mm for hand-same and hand-different target sets, respectively) while under- overshoots were found for the longest effort arm and the smallest visuomotor gain (−23.5 ± 3.4 mm and −47.5 ± 5.0 mm). Direction errors were small overall. Mean direction errors were 3.7 ± 1.9° for the hand-same target set and 4.0 ± 1.7° for the hand-different target set.

Movement time was 2,447 ± 228 ms for the hand-same target set (ranging from 1,813 to 3,365 ms for individual participants) and 2,410 ± 228 ms for the hand-different target set (ranging from 1,751 to 3,214 ms for individual participants). Movement time was longer with than without the dynamic transformation: 2,690 ± 323 ms vs. 2,203 ± 323 ms and 2,660 ± 322 ms vs. 2,159 ± 322 ms for the two target sets. The difference between dynamic conditions was slightly more pronounced in trials without visual feedback than in trials with continuous visual feedback: 633 ms vs. 341 ms and 762 ms vs. 238 ms for hand-same and hand-different target sets, respectively.

Discussion. In experiment 2 we tested the constraint of mode of control by exploring the role of continuous visual feedback for the distal shift of path curvature. Without continuous visual feedback the findings of experiment 1 were replicated. Curvature of hand paths was concave in the absence of the dynamic transformation of the tool and convex in its presence. Continuous visual feedback had a twofold effect. First, concave curvature of hand paths turned into convex curvature and convex curvature became stronger, whereas concave curvature of the paths of the tip of the lever became weaker. This is consistent with findings of Flanagan and Rao (1995) and Wolpert et al. (1995) for other kinematic transformations that also required curved hand movements to produce straight motions of a cursor. However, straightening of the path of the tip of the lever was clearly incomplete when compared, e.g., with the straight hand movements observed in experiment 1 in the absence of the kinematic transformation. Second, with continuous visual feedback the influence of the dynamic transformation was attenuated. However, the attenuation was not as strong as observed without the kinematic transformation in experiment 1.

The findings of experiment 2 are consistent with the proposed constraint of mode of control according to which distal shifts can be present for closed-loop control but absent for open-loop control. In addition, distal shifts can be gradual and are not necessarily an all-or-none phenomenon. Finally, the observation of a partial distal shift in this experiment throws a new light on the essential absence of a distal shift in experiment 1 when the tool was held but the targets were presented for the hand. These two findings, taken together, are in support of the strategy constraint according to which distal shifts are strategic rather than mandatory. The absence of mandatory shifts whenever a tool is held is consistent with the observation that changes of receptive fields of parietal neurons of macaques are observed only when a tool is actually used but not when it is held passively (see Maravita and Iriki 2004). Similarly, holding a sticklike tool affected distance judgments only when it was actually used but not when it was only held (Witt et al. 2005).

GENERAL DISCUSSION

Several recent findings on tool use have strengthened the notion that tools become integrated with the body schema (Berti and Frassinetti 2000; Cardinali et al. 2009, 2012; Iriki et al. 1996; Maravita and Iriki 2004; Yamamoto and Kitazawa 2001). When the effective part of a tool replaces the hand as the end effector of the segmental chain, movement characteristics of the hand should turn into characteristics of tool movements. Such a distal shift of movement characteristics is a natural consequence of the hypothesized control of the effective part of the tool rather than of the hand. In fact, distal control has become a major ingredient of recent theories of the control of action (cf. Hommel et al. 2001; Kunde 2006; Kunde et al. 2004; Prinz 1992, 1997).

Recent findings (cf. Witt et al. 2005) suggest that distal shifts are subject to boundary conditions. In the present experiments we investigated three constraints on distal shifts of a particular movement characteristic and a particular tool. The movement characteristic was the curvature of transverse aiming movements. Whereas the desired final position of such movements is defined by the task, for curvature this is not the case. The tool was a sliding first-order lever. For the present experiments two of its characteristics were important. First, for transverse movements, curvatures of the paths of the hand and the tip of the lever are different. Second, the tool has a dynamic transformation that affects curvature.

The results of the present experiments revealed a pattern of curvature variations that appears complex. However, its parts are consistent with a number of observations in previous studies. First, when targets are specified for the hand, that is, in the absence of the kinematic transformation of the tool, hand paths are almost straight even in the absence of continuous visual feedback. Without the dynamic transformation of the tool, there is a slight concave curvature, consistent with findings of Haggard and Richardson (1996), Wolpert et al. (1994), and Van Thiel et al. (1998). With the dynamic transformation we found a slight convex curvature. The effect of the dynamic transformation, the difference between the concave and convex curvatures, was quite small (cf. Heuer and Sülzenbrück 2012).

Second, when targets are specified for the tip of the lever, that is, in the presence of the kinematic transformation of the tool, hand paths remain straight on the average provided there is no continuous visual feedback. However, compared with targets specified for the hand, the influence of the dynamic transformation becomes more powerful: concave curvature in the absence of the dynamic transformation becomes stronger, and convex curvature in its presence becomes stronger as well. The stronger convex curvature of the path of the hand is accompanied by a smaller concave curvature of the path of the tip of the lever. The effect of the dynamic transformation on the curvature of hand paths in the absence of visual feedback has also been reported by Sülzenbrück and Heuer (2011) for movements in various other directions.

Third, when targets are specified for the tip of the lever and continuous visual feedback is available, the influence of the dynamic transformation is attenuated, but it remains stronger than when targets are specified for the hand. Perhaps even more important, paths of the hand become convexly curved in both the
presence and the absence of the dynamic transformation, and the concave curvature of the path of the tip of the lever is reduced. Even though the straightening of the path of the tip of the lever is less than perfect, the straightening is consistent with observations of Flanagan and Rao (1995) and Wolpert et al. (1995).

This pattern of results supports the notion of certain constraints on distal shifts of movement characteristics in tool use. First, no indication at all of a distal shift of path curvature was observed when the sliding first-order lever was held but targets were defined for the hand. In contrast, when targets were defined for the tip of the lever, paths of the effective part of the tool were straightened when continuous visual feedback was available. Distal shifts of movement characteristics are likely to be associated with distal shifts of the focus of attention. For example, Collins, Schicke, and Röder (2008) found increased attention on the effective part of the tool as well as on hand positions, with attention being generally higher at the tip of the tool. Reed et al. (2010) showed that increased attention to the effective part of the tool after training with the same tool only occurs if the effective part of the tool is functionally relevant for the executed action. Whether or not attention is directed to the effective part of the tool or to the hand should be under strategic control. Thus the present findings are consistent with the strategy constraint: distal shifts of movement characteristics are strategic rather than mandatory—at least for some movement characteristics.

Second, when targets were defined for the tip of the lever the final positions of hand movements were adjusted accordingly, whereas curvature of hand paths—averaged across dynamic conditions—remained unchanged as long as continuous visual feedback was available. The adjustments of the final hand positions were inaccurate, but they were clearly present. The inaccuracy is not that remarkable because the internal model of the kinematic transformation of a sliding lever is of limited accuracy in general (e.g., Sülzenbrück and Heuer 2009, 2010, 2011, 2012). Even for the simple transverse movements, the required learning of position-dependent visuomotor gains is likely a challenging task (cf. Bock and Burghoff 1997; Heuer and Hegele 2008). More important than the inaccuracy of the movement, that is, the limited accuracy of the distal shift of hand positions, is the complete absence of a distal shift of path curvature. In addition, there was a strong effect of the dynamic transformation on the curvature of hand movements. In fact, there is some evidence of a functional haptic neglect in the presence of a visuomotor transformation of a tool (Bernier et al. 2009; Heuer and Rapp 2012; Müsseler and Sutter 2009). These observations are consistent with the constraint of movement characteristics: distal shifts occur for some movement characteristics, but not for all of them.

Third, when continuous visual feedback was introduced, movement paths of the tip of the lever became straighter and the influence of the dynamic transformation was attenuated compared with the absence of visual feedback. Thus curvature becomes more precisely controlled again, but under these conditions control is based on the visual feedback of the position of the effective part of the tool. These observations are consistent with the constraint of mode of control. Distal shifts may be specific for the mode of control; in particular, they may be absent for open-loop control and (partially) present for visual closed-loop control.

The present findings offer insights into the nature of the internal model of the kinematic transformation of a tool. At least for movements aimed at a target, the internal model is confined to target positions and does not embrace trajectory characteristics (cf. Rieger et al. 2008; Verwey and Heuer 2007). This limitation may reflect a principle of economy in that only essential characteristics of desired movements of the effective part of the tool are mapped on corresponding characteristics of hand movements. Thus, in the absence of visual feedback and thus visual closed-loop control, curvature of the paths of the tip of the lever is largely uncontrolled. In addition, curvature of the paths of the hand is also largely uncontrolled because of haptic neglect in the presence of a visuomotor transformation. Therefore, curvature is particularly sensitive to the influence of the dynamic environment.

Each of the proposed constraints on distal shifts of movement characteristics in tool use is associated with a “why” question. The strategic nature of distal shifts implies the question of why strategic shifts occur under some conditions only. Our tentative answer is that distal shifts occur when the attentional focus is shifted to the effective part of the tool, and this again is associated with its proper use. The selectivity of distal shifts for certain movement characteristics implies the question of why only particular characteristics are shifted. Our tentative answer is that essential and controlled movement characteristics, which satisfy task demands, are shifted whereas others are neglected for the internal model for economic reasons. Finally, the difference between open-loop control and closed-loop control implies the question of why certain characteristics are shifted only when closed-loop control is possible. At least to some degree the straightening of movement paths is a straightforward consequence of closed-loop control of the position of the effective part of the tool.

The present findings demonstrate that distal shifts of movement characteristics do not necessarily reflect distal control but can also result from a particular dynamic environment. With the sliding first-order lever, the dynamic transformation serves to reduce curvature of the path of the tip of the lever for the transverse movements of the present experiments. Such an effect of the dynamic transformation on curvature, which reduces the effect of the kinematic transformation, is likely to occur also for other movement directions. It can at least contribute to observations of a smaller curvature of paths of the tip of the lever than of the hand (cf. Heuer and Sülzenbrück 2009).

Although the notion of tools being incorporated into the body schema has been supported repeatedly (Berti and Frassinetti 2000; Cardinali et al. 2009, 2012; Iriki et al. 1996; Maravita and Iriki 2004; Yamamoto and Kitazawa 2001), this idea has also been challenged by recent observations. For example, it has been argued that instead of being incorporated into the body schema, the use of tools changes the allocation of spatial attention (Holmes et al. 2007). Rieger (2012) draws a distinction between integration of a tool into the body schema and the addition of an internal model of the tool’s transformation (cf. Kluzik et al. 2008). According to her, there is essentially no evidence of integration at least for tools that are more complex than sticks. The present findings do not add such evidence. Instead they point to other factors that govern distal shifts of movement characteristics that make the effective part of the tool behave similar to the hand.
Referring to the previously mentioned limited accuracy of the internal model of the complex lever transformation (e.g., Sülzenbrück and Heuer 2009, 2010, 2011, 2012), it could be argued that especially such a complex tool as the sliding lever needs more time to be incorporated into the body schema and that with a less complex tool different results would have been obtained. Of course, longer training periods could perhaps change our pattern of results. At present, however, this remains an open question.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: S.S. and H.H. conception and design of research; S.S. and H.H. performed experiments; S.S. and H.H. analyzed data; S.S. and H.H. interpreted results of experiments; S.S. and H.H. prepared figures; S.S. and H.H. drafted manuscript; S.S. and H.H. edited and revised manuscript; S.S. and H.H. approved final version of manuscript.

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