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Abstract

Goal-directed movements performed in a virtual environment pose serious challenges to the central nervous system because the visual and proprioceptive representations of one's hand position are not perfectly congruent. The aim of the present study was to determine whether the vision of one's hand or upper arm, compared with that of a cursor representing the tips of one's index finger and thumb, optimizes the planning and modulation of one's movement as the cursor nears the target. The participants performed manual aiming movements that differed by the source of static visual information available during movement planning and the source of dynamic information available during movement execution. The results revealed that the vision of one's hand during the movement planning phase results in more efficient online control processes than when the movement planning was based on a virtual representation of one's initial hand location. This observation was seen regardless of the availability of online visual feedback during movement execution. These results suggest that a more reliable estimation of the initial hand position results in more accurate estimation of the position of the cursor/hand at any one time resulting in more accurate online control.

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Every day, most individuals perform reaching movements either to touch the "start" button of their computer or to move a cursor on a computer screen to reach an icon. In both cases, one must first determine the initial location of his or her hand or that of the cursor and target. The central nervous system (CNS) appears to use this information to determine a movement vector and issue a series of motor commands (Ghilardi et al. 1995; Gordon et al. 1994b). As the movement progresses toward the target, afferent information ensures the correction of planning errors resulting from any misperceptions of the hand/cursor (Vindras et al. 1998; Vindras et al. 2005) or the target localization (Desmurget et al. 2005; Prablanc and Martin 1992), any biomechanical factors affecting initial limb inertia (Gordon et al. 1994a; Mackrous and Proteau 2007), or any noise in the planning (Meyer et al. 1988; Schmidt et al. 1979) and execution processes (van Beers et al. 2004).

Although apparently very similar to a manual aiming task, the cursor-aiming task described above poses some interesting challenges to the CNS. First, in a manual aiming task, the seen and felt positions of one's limb provide direct, comparable information to the CNS concerning the starting point of the movement. This correlation does not occur in a cursor-aiming task for which the seen position of the cursor might represent conditions such as the tip of the index finger or the position of a computer mouse. Veilleux and Proteau (2011) recently showed that seeing one's upper limb prior to movement initiation resulted in smaller endpoint bias and variability than when the initial position of one's limb was represented by a cursor. Interestingly, the smaller endpoint variability observed in the former condition largely resulted from a sharp reduction in the movement variability between the peak deceleration and end of the initial impulses of the movement. Veilleux and Proteau proposed that tight coupling of the visual and proprioceptive information concerning the origin of the movement vector results in an accurate and reliable internal representation of one's hand on the starting base. In turn, as the starting position of

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the hand becomes more accurately defined, the CNS can better predict its course toward the target, leading to a more efficient modulation of the movement as the hand nears the target (Bourdin et al. 2006; Desmurget and Grafton 2003).

The aim of the present study was to determine what source of visual information prior to movement execution optimizes the modulation of one's movement when visual feedback is either available or unavailable as the hand nears the target: the vision of just the hand or the vision of the entire arm? In addition to its theoretical importance, this question is of interest because a better understanding of how visual and proprioceptive feedback are optimally combined could lead to the optimization of virtual and video systems that are used in different learning and rehabilitation settings.

One may only need to see his/her hand at the starting position to optimize movement planning and control these processes because the felt and seen position of the movement vector origin are congruent. Graziano, Cooke, and Taylor (2000) reported the presence of bimodal neurons in the primate posterior parietal cortex that receive both visual and proprioceptive input regarding the position of the arm. These neurons discharged when the initial position of the monkey upper limb was represented by a fake stuffed arm positioned in a natural anatomical position but not when the upper limb was represented by paper triangles. One possible explanation is that these bimodal neurons do not discharge when the position of one's hand is represented by a cursor, resulting in a suboptimal integration of visual and proprioceptive information relative to the position of the hand. Alternatively, the optimization of movement planning and control might not be due to the vision of the hand itself but rather the vision of the entire upper limb. With respect to the latter idea, Sober and Sabes (2005) showed that the availability to the participant of a virtual representation of his/her arm gives more weight to the visual information for the movement planning and control processes than does the representation of hand position by a cursor. Thus, the representation of the hand/arm position by a cursor on the computer screen may result in the loss of relevant visual information relative to arm configuration.

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To fulfill the aim of this study, participants performed reaching movements towards one of three visual targets. Prior to movement onset, participants in the first group had a visible cursor on the starting base without any other additional visual feedback relative to the hand or arm position. Participants in the second group could see the position of both the cursor and their hand, but not that of their forearm and arm. In contrast, the participants in the third group could see both the cursor and their entire upper limb prior to movement onset. For each group, the cursor remained visible or was occluded after the movement initiation was detected. The results could then be used to determine whether the presumed more accurate/reliable representation of one's hand when it is visible at the starting position produces a more efficient modulation of the latter part of one's movement.

Method

Participants

Forty-two undergraduate students, aged between 20 and 25 years old, were recruited in the Département de kinésiologie from the Université de Montréal. The participants had no previous experience with these experimental tasks. All participants reported normal or corrected to normal vision. The Health Sciences Ethics Committee of the Université de Montréal approved this study.

Task and apparatus

The participants had to perform a manual aiming task in which they moved a computer's mouse-like device on a horizontal surface from a fixed starting position toward three possible targets. The apparatus (Figure 1) consists of a table, two-degree-of-freedom manipulandum, computer screen, headrest, semi-reflecting mirror, cardboard, and light source.

Each participant sat close to the table so that his or her body rested along its leading edge. The tabletop was covered by a piece of Plexiglas over which the manipulandum and a starting base were affixed. The manipulandum consisted of two pieces of rigid Plexiglas (43 cm) joined at one end by an axle. One of its free ends was fitted with a second axle encased in a stationary base that was affixed to the

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tabletop. The other free end was fitted with a small vertical shaft (length: 3 cm, radius: 1 cm), hereafter called “the stylus”, that could be easily gripped by the participant. The starting base consisted of a thin strip of Plexiglas glued to the tabletop that was parallel to the leading edge of the table and had a small indentation on one of its faces. The indentation was located directly in line with the lateral center of the computer screen and the participant’s midline. This indentation enabled the participants to easily position the stylus at the start of each trial. Each axle of the manipulandum was fitted with a 13-bit optical shaft encoder (U.S. Digital, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°) that enabled the displacement of the stylus to be tracked online and illustrated (hereafter called “the cursor”) using a 1:1 ratio on the computer screen. Moving the stylus away from the body in the frontal and sagittal planes resulted in an identical displacement of the cursor on the computer screen.

The cathode ray tube computer screen (Mitsubishi, Color Pro Diamond 37 inches, refresh rate 60 Hz, resolution 1024 x 768) was mounted face down on a ceiling-support positioned directly over the table; the computer screen was oriented parallel to the surface of the table. Its image was reflected on a semi-reflecting mirror placed directly beneath it and parallel to the tabletop, thereby making it visible to the participant.

The mirror was located at the midpoint between the computer screen and the tip of the stylus, which were 40 cm apart. This allowed free displacement of the manipulandum on the tabletop. In addition, the experimental setting enabled the participants to perceive the cursor as aligned with the tip of the stylus. A headrest was affixed on the side of the computer screen. It was aligned with the lateral center of the computer screen and standardized the perceived location of the target, the starting base and the stylus when appropriate (see procedures).

A piece of cardboard and a light source were placed underneath the semi-reflecting mirror. Different cardboard configurations were used for each of the three experimental conditions (see procedures and Figure 1). The light source consisted of a series of 60 white LEDs and was located beneath the cardboard, slightly in front of the stylus’ starting base. When the light source was turned on,

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the participants could see any information not blocked by the cardboard, whereas when it was turned off, the vision of anything located beneath the semi-reflecting mirror was occluded.

Procedures

The participants used their self-declared right dominant hand and were asked to try stopping the cursor on the target by performing a single straight and smooth movement (i.e., no stop and go). The cursor and targets (3.5 mm and 5 mm in diameter, respectively) were white on a black background. Although the participants could initiate their movement as they pleased (i.e., not as a reaction time task), they were required to complete their movement within a time frame ranging from 480 to 620 ms (550 ms +/- 12.5%). Participants whose movements were completed outside this time frame were reminded of the appropriate window. Having a restricted time frame to complete the movement reduces the possibility of speed-accuracy trade-offs between the different experimental conditions (Fitts 1954).

At the beginning of each trial, all participants could see the cursor they would be moving. Once the stylus/cursor was stabilized on the starting base for 500 ms, a target was presented on the screen. During data acquisition, movement initiation was detected when the cursor had been moved by 1 mm, whereas movement completion was detected when the cursor did not move by more than 2 mm in a time frame of 50 ms.

The participants were randomly assigned to one of three experimental groups (n = 14 per group). For all groups, the cursor remained visible until the initiation of the movement. In the Virtual group, only the cursor was visible prior to movement initiation, and a cardboard was used to occlude the vision of each participant's hand and arm (Figure 1). In the Hand group, the cardboard contained a window that permitted each participant to see only his/her hand, but not his/her arm. In the Upper limb group, the cardboard was positioned such that each participant could see his/her entire arm from the hand to the shoulder. Note that for the last two groups, vision of the hand and/or upper arm was permitted only prior to movement initiation.

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The participants completed two series of 36 trials each. In both series, the target was visible at all times once the stylus was stabilized on the starting base, and the light source remained activated until movement initiation. This set-up allowed either the hand or entire arm to be seen, as appropriate. The cursor remained visible throughout the entire movement execution (Cursor-visible condition) in the first series of trials, whereas the cursor was hidden once the movement was initiated (Target-only condition) in the other set of trials. The presentation order of the two series was randomized both within and between each group. Once the movement completion was detected, the cursor was concealed until the hand was back on the starting position.

Under both the Cursor-visible and the Target-only conditions, the participants aimed for three different targets, with 12 trials for each target. The first target was located 320 mm directly in front of the starting base (0° target). The other two targets were also located 320 mm from the starting base and 10° to either its left (-10° target) or its right (10° target). The presentation order of the targets was randomized, with the only restriction being that no target could be consecutively presented more than 2 times.

Data reduction

The tangential displacement data of the stylus over time were first smoothed using a second order recursive Butterworth filter with a cut-off frequency of 10 Hz. The filtered data were then numerically differentiated one time using a central finite technique to obtain the velocity profile of the aiming movement, a second time to obtain an acceleration profile, and a third time to obtain a jerk profile. Movement initiation was defined as the moment at which the tangential velocity of the cursor reached 10 mm/s[1], and movement completion was the moment when the cursor was not displaced by more than 2 mm within a time frame of 50 ms. For most trials, this procedure does not allow the participant to produce a secondary corrective impulse (< 1% in the present study; see also Veilleux and Proteau, 2011); trials

[1] The procedure used to detect movement initiation differed from that used during data collection. The procedure used during data acquisition enabled us to provide feedback quickly after movement completion. The procedure used during data reduction is commonly used in motor learning and control research. Data were analyzed using both procedures with no impact on the outcome of the ANOVA computed on movement time data.

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showing a secondary corrective impulse were removed from all analyses. These profiles were used to determine the moments and locations (in Cartesian coordinates) at which the peak acceleration, velocity, deceleration and endpoint of the movement's primary impulse (hereafter referred to as "movement endpoint") occurred.

The movement endpoint data were used to compute the angular error and the radial error of the manual aiming. The angular error was defined as the gap (in degrees) between the movement vector (joining the starting base and movement endpoint) and a reference vector (joining the starting base and the center of the target). A positive value indicates a movement ending to the right of the target, and a negative value indicates a movement ending to its left. The radial error was defined as the signed difference between the length of the movement vector and that of the reference vector (in mm). A positive value indicates hypermetric movements and a negative value indicates hypometric movements.

The kinematic profile data were used to compute the within-participant variability (direction and extent) of the location at which each kinematic landmark occurred. If movement execution reflects the outcome of response planning and execution processes and if those processes are assumed to be variable (Meyer et al. 1988; Schmidt et al. 1979; van Beers et al. 2004), then the within-participant variability over a series of trials in the Cartesian space of the position reached by the stylus at any given moment should increase as the movements unfold. A reduction in the rate of increase of the within-participant variability during movement execution coupled with a small aiming error would provide evidence of efficient online control processes (Khan et al. 2002; Lhuisset and Proteau 2002; Proteau 2005).

To facilitate an understanding of the data presented herein, the details of the relevant statistical analyses along with the original degrees of freedom are given at the beginning of each subsection within the results section. In all cases, the effects reported were determined to be significant after the application of the Greenhouse-Geisser correction (performed when Epsilon < 1). Any significant interactions were then separated into their constituent simple main effects. Significant main effects and simple main

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effects involving more than two means were broken down using Dunn's technique. All effects are reported for p <.05 (adjusted for the number of comparisons using Bonferroni's technique).

Results

Movement endpoint

The first aim of this study was to determine whether endpoint accuracy could be affected by a variety of experimental manipulations. An inspection of the angular and radial constant error revealed that approximately half of the participants were biased to the right of the targets and that the other half were biased to their left; similarly, half of the participants overshot the targets, whereas the other half undershot them. Thus, we opted to report the results of the angular and radial absolute constant error (i.e., |constant error|). The angular and radial |CE| as well as the movement time data were individually analyzed by ANOVA, contrasting 3 Groups (Virtual, Hand, and Upper limb) x 2 Feedback conditions (Target-only vs. Cursor-visible) using repeated measures for the last factor. The target factor was not included in these analyses because the results of a series of preliminary analyses did not reveal a significant difference that would have influenced the data interpretation (Figures 2 and 3).

The ANOVA computed on the angular and radial |CE| and on movement time only revealed a significant main effect of Visual feedback, (F [1, 39] = 177.63, 41.68, and 31.28, $p < .001$, respectively). The angular (Figure 2) and radial |CE| (Figure 3) were significantly smaller under the Cursor-visible than under the Target-only condition (1.0° vs. 5.2° and 6.5 mm vs. 29.1 mm, respectively). Movement time was significantly longer under the Target-only condition than under the Cursor-visible condition (558 ms vs. 541 ms, respectively). Neither the Group main effect nor any interaction involving it approached significance ($p > 0.29$ for all cases).

Variability of the movement trajectory

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The second aim was to determine whether, and how, the variability of the movement trajectory was affected by the static visual information available prior to the movement initiation and by the feedback source available during movement execution. Therefore, the within-participant direction and extent variability at peak tangential acceleration, velocity, and deceleration as well as at the movement endpoint were calculated. The direction and extent variability data were each analyzed by ANOVA, contrasting 3 Groups x 2 Feedback conditions x 4 Markers using repeated measures for the last two factors. Because the within-participant variability data are not normally distributed (standard deviation data are skewed), the raw data were submitted to a logarithmic transformation (log [10] + 1) before being submitted to the ANOVA.

With respect to the movement direction, the ANOVA revealed significant Group x Marker and Feedback x Marker interactions (F [6, 117] = 5.08, p = .001 and F [3, 117] = 18.93, p < .001, respectively). The breakdown of the Group x Marker interaction revealed that for all three groups, the direction variability significantly decreased from peak acceleration to peak deceleration (p < .001). There was a further significant decrease in direction variability between peak deceleration and movement endpoint for the Hand and Upper limb groups (p < .01), but not for the Virtual group (p = .22). Figure 4a also illustrates that the decrease in direction variability observed as one neared the target was generally steeper for the Hand and Upper limb groups, which did not differ significantly from one another, than for the Virtual group.

The breakdown of the Feedback x Marker interaction revealed that the direction variability significantly decreased between peak acceleration and peak deceleration (p < .01) with no further decrease between peak deceleration and movement endpoint (p = 1.0, Figure 4b). Under the Cursor-visible condition, direction variability decreased significantly from one marker to the next (p < .01) between peak acceleration and movement endpoint.

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With respect to the movement extent, the ANOVA revealed significant Group x Marker (Figure 5a) and Feedback x Marker interactions, (F [6, 117] = 5.14, $p < .01$ and F [3, 117] = 10.03, $p < .001$, respectively). The breakdown of the Group x Marker interaction revealed that for all three groups, the extent variability significantly increased from peak acceleration to peak deceleration ($p < .001$). This increase in variability was significantly steeper for the Virtual group than for the Hand and Upper limb groups, which did not differ significantly from one another. In addition, there was a significant decrease in extent variability between peak deceleration and movement endpoint for all three groups ($p < .01$), and this decrease was significantly steeper ($p < .01$) for the Upper limb and the Hand groups (3.2 and 4.1 mm, respectively) than for the Virtual group (2.4 mm).

The breakdown of the Feedback x Marker interaction revealed that, for both the Target-only and Cursor-visible conditions, the extent variability significantly increased ($p < .001$) between peak acceleration and peak deceleration (Figure 5b). Although extent variability did not significantly increase further under the Target-only condition, it significantly decreased ($p < .001$) between peak deceleration and movement endpoint under the Cursor-visible condition.

Correlation analyses

In addition to the steeper increase in variability noted between peak tangential acceleration and deceleration for the Virtual group when compared with the Hand and Upper limb groups, the steeper decrease in variability observed between peak tangential deceleration and movement endpoint for the latter two groups compared with the Virtual group represented another important finding. This observation suggested that the online control was more efficient when one could see his/her hand or entire upper limb prior to movement initiation than when the initial position of one's hand was defined by a cursor. One explanation is that the distance travelled at peak velocity determines whether the deceleration phase should be shortened or lengthened. If this premise is correct, a negative correlation between the position of the hand/cursor at peak velocity and the distance travelled between peak velocity and peak

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deceleration and/or between peak velocity and movement endpoint should be observed (Elliott et al. 1999). Similarly, if a modulation of the deceleration phase (shortening/lengthening of the movement) occurs mainly later in the movement, as suggested by the results of the preceding section, a negative correlation between the position of the hand/cursor at peak deceleration and the distance travelled between peak deceleration and movement endpoint should be observed. To test these hypotheses, we computed Pearson's correlation between the distance travelled by the stylus: (a) at peak velocity and that travelled by the stylus between peak velocity and peak deceleration, (b) at peak velocity and that travelled by the stylus between peak velocity movement endpoint, and (c) at peak deceleration and that travelled by the stylus between peak deceleration and movement endpoint. These data were submitted to Fisher's transformation (r to Z) and to an ANOVA contrasting 3 Groups x 2 Feedback conditions x 3 Comparisons with repeated measures for the last two factors (Figure 6).

The ANOVA revealed a significant Group main effect (F [6, 117] = 6.97, p = .003) and a significant Feedback x Comparison interaction (F [2, 78] = 46.19, p < .001). For the Group main effect, the negative correlations for the Hand and Upper limb groups were significantly larger than those for the Cursor group (p <.035). The breakdown of the Feedback x Comparison interaction demonstrated that the negative correlations under the Cursor-visible condition were significantly larger than those under the Target-only condition. This observation was true for both the comparisons between the location of the stylus at peak velocity and at peak deceleration and the distance travelled by the stylus between these markers and movement endpoint (p <.001). The larger negative correlations observed for the peak deceleration comparison suggests that the modulation was initiated close to the occurrence of this kinematic marker.

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Discussion

Goal-directed movements require one to define a movement vector that dictates the appropriate motor commands. The aim of the present study was to determine whether the vision of one's hand or of one's upper arm prior to movement initiation results in a more accurate/reliable coding of the origin of the vector than when this origin is defined by a cursor representing one's hand. Another aim was to determine whether the visual information used to define the origin of the movement vector influenced the efficacy of the online control processes that take place during movement execution.

The results revealed that the visual information available prior to movement initiation did not significantly influence the direction or extent endpoint accuracy, whereas the Cursor-visible condition yielded more accurate endpoint accuracy than the Target-only condition. This observation was not unexpected, particularly given it concurs with numerous observations obtained both early in practice and after extended practice (for a review, see Proteau 1992; see also Khan et al. 2003; Knill et al. 2011; Proteau 2005; Sarlegna and Blouin 2010). The finding that the Virtual, Hand, and Upper limb conditions led to equally accurate movements, however, is somewhat misleading. This aspect of the results indicates that, *on average*, the participants determine the direction and extent of the movement vector equally well regardless of the information available prior to movement initiation. The variability data revealed that this is not true on a trial-by-trial basis, however.

Specifically, seeing one's hand on the starting base rather than a cursor representing the hand reduced both (a) the direction trial-to-trial variability and (b) the increase in movement extent trial-to-trial variability that is normally observed as movements progress toward the target (Khan et al. 2002; Khan et al. 2006; Khan et al. 2003; Proteau 2005; Proteau and Isabelle 2002; Robin et al. 2005; Veilleux and Proteau 2010). It also resulted in a larger decrease of both direction and extent variability during the final portion of the movement (Figures 4 and 5). The results also revealed that being able to view one's entire arm provided no additional benefits compared with being able to view just one's hand on the starting

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base. These observations support our hypothesis (Veilleux and Proteau 2011) that the tight coupling of the visual and proprioceptive information concerning the origin of the movement vector improves the accuracy/reliability of the internal representation of one's hand on the starting base, with the vision of the arm configuration not adding significantly to this representation. This improved encoding results in more efficient online control of the aiming movement as revealed by both the greater decrease in movement variability and larger negative correlations observed between peak deceleration and movement endpoint.

Our findings support and add to those reported by Desmurget and colleagues in a series of earlier papers (Desmurget et al. 1997; Desmurget et al. 1995; Rossetti et al. 1994). Briefly, the participants aimed at visual targets with (condition Static) or without (condition Never) the vision of their hands prior to movement onset (Desmurget et al. 1995). The results showed a shortening of the movement's acceleration phase with a corresponding lengthening of its deceleration phase under the Static condition but not the Never condition. In addition, the movement endpoint variability under the Static condition was smaller than that under the Never condition. The authors concluded that the smaller endpoint variability under the Static condition resulted from time consuming online control processes that lengthened the deceleration phase of the movement. These results later led Desmurget and Grafton (2003) to conclude that by permitting participants to more accurately and reliably define their initial hand location, the Static condition then provided a more accurate/reliable input for the forward model responsible for the online control. Although attractive, this interpretation was weakened by the absence of spatial data showing a larger online reduction in spatial variability under the Static when compared with the Never condition. Our variability data and correlation analyses of different kinematic markers provide new evidence that seeing one's hand on the starting base results in more efficient online control.

In addition, under the normal vision condition used herein, the cursor was visible for all participants during movement execution, with only the static visual information available prior to movement onset being variable across conditions. Therefore, any difference in online control efficacy

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should be regarded as arising from either poorer or better encoding of the initial hand position. To the best of our knowledge, the present study is the first to show that the availability of visual feedback of the ongoing movement (a cursor in the present case) still ensures that seeing one's hand is more advantageous than seeing a cursor on the starting base.

This finding strongly suggests that a more reliable estimation of the initial hand position due to congruent inputs of vision and proprioception results in more accurate online control of the cursor/hand position at any one time. Because all participants add access to the same sources of sensory information to control their ongoing movement, it is unlikely that the differences observed between the Virtual and the other two conditions in the later portion of the movement reflect differences in a feedback process comparing the position of the cursor with that of the target. There are at least two not mutually exclusive interpretations of our findings. First, static visual information of the hand could have help recalibrate proprioception (the difference between the cursor indicating the location of the hand and the proprioceptive information used by the CNS for movement planning and control), which in turn, might have rendered proprioceptive feedback loops more efficient.[2] Second, our results might reflect differences in forward modeling between the Virtual and both the Hand and Upper limb conditions. Specifically, Desmurget and Grafton (2003) proposed that an efference copy of the motor commands is processed by the forward model to estimate the motor state. This estimate is then compared with the available afferent information to detect an error in the motor state estimate. If indeed an error is detected, the forward model is updated and a new estimate of the final state is generated (Desmurget and Grafton 2003). This new estimate is compared to the target location. If a discrepancy is detected, an error signal is generated and the appropriate modulation of the motor commands is triggered. In the present study, it could be that the

[2] It is unlikely that proprioception needed to be calibrated by vision because it drifted over time as it was first thought (Wann and Ibrahim, 1992), because more recent evidence indicated that proprioception does not quickly drift over time (Desmurget et al., 2000) and also that vision is not use to recalibrate proprioception (Smeets et al., 2006).

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efference copy sent to the forward model was more accurate/reliable when one could see his or hand prior to movement onset rather than a cursor representing it. This resulted in a more reliable estimate of the motor state, which increased the probability to detect an error in the motor state estimate. In turn, the updated forward model generated a more reliable final state estimate, which increased the probability to detect an error and trigger the appropriate modulation of the ongoing movement.

Absence of disparities between visual and proprioceptive information favors better encoding of the origin of the movement vector

Our hypothesis that the vision of one's hand would optimize performance was based on the research of Graziano et al. (2000). This study demonstrated that bimodal neurons in the primate posterior parietal cortex, which fire in reaction to both proprioceptive and visual stimuli relative to the location of the arm/hand in space, no longer fire when the vision of the faked arm is occluded and replaced by paper markers. Although speculative at this point, their data suggest that replacing a real hand by a cursor under our Virtual condition might have deprived the CNS of the information conveyed by these bimodal neurons. This interpretation is supported by (Jarvelainen et al. 2001), who reported an increase in cortical activation during the observation of live rather than filmed hand movements. Along the same lines, Perani et al. (2001) reported activation of the right inferior parietal cortex during observation of live right hand grasping movements, but not during the observation of movements shown as either 2D or 3D presentations. Because the right inferior parietal cortex is involved in movement planning in the presence of visual cues (Deiber et al. 1996) and is further involved in the visuomotor and spatial processing underlying the computation of an egocentric frame of reference (Vallar et al. 1999; Burgess et al. 1997), Perani et al. argued that this part of the brain provides the egocentric and allocentric coordinates necessary for high-order movement planning. The results given herein suggest that activation of the right inferior parietal cortex is reduced during movement planning under the Virtual condition compared with

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that under the two live conditions (Hand and Upper limb), which leads to more variability in online control processes.

Vision of the arm is not necessary to accurately define the initial hand location

In the present study, being able to see their entire upper limb prior to movement initiation did not allow participants to be more accurate/less variable than being able to see only their hand. These results not only concur with similar observations reported by van Beers et al. (1999) but also provide important additional data. In the study by van Beers et al. (1999), the participants had to match the position of their right index finger with that of their left index finger. The participants could see their entire right arm under one condition but could only see the tip of their right index finger under the other condition. The results did not reveal any significant difference in position matching variability between the two conditions, which concurs with our results. Our results supplement those of van Beers et al.(1999) by showing that the vision of the upper arm does not add significantly to the information provided by the vision of one's hand on the starting base even when target location can only be seen and not felt.

Dynamic vs. static visual information for defining initial hand location

There is one final point from this study that should be noted. As previously discussed, the enhanced representation of the vector's origin resulted in online control processes that were more efficient. Our data regarding the directional component of the task concur with previous studies that showed smaller variability at peak deceleration when the hand rather than a cursor was seen on the starting base (Veilleux and Proteau 2011; for similar observations see Bo et al. 2006). In contrast, our results regarding the extent component of the task differ from those of our previous work (Veilleux and Proteau 2011). Herein, the increased variability between peak acceleration and peak deceleration was significantly smaller for those conditions in which the hand rather than the cursor was visible on the starting base, but no such difference was observed in our earlier study. This discrepancy likely results

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from a procedural difference between the two studies. The participants in the present study could not see their hand or the cursor as it returned to the starting base, while this visual information was available in the previous study (Veilleux and Proteau 2011). Unpublished data from our laboratory indicates that participants in a virtual condition used the available information from trial *n* to better plan the extent component of their movement during trial *n+1*. One possible explanation is that dynamic, but not static, visual and proprioceptive information are congruent. Specifically, the movement of one's hand 2 cm to the right, which is initiated by a motor command sent by the individual for that displacement, is felt through proprioception and seen as the movement of the cursor 2 cm to the right. Together, these inputs create a stronger bond between proprioceptive and visual information. This interpretation is supported by data from a recent study by Mackrous and Proteau (2010), in which the participants performed out and back movements under a virtual condition very similar to the one used herein. They demonstrated that direction variability 100 ms after movement initiation (out movement) was significantly larger than direction variability 100 ms after movement reversal (back movement), suggesting that movement-planning processes were less variable when based on dynamic (back movement) rather than static (out movement) afferent information.

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Figure captions

Fig. 1 Illustrations of the Virtual, Hand and Upper limb conditions. Note that participants used their right dominant hand.

Fig. 2 Angular absolute constant error as a function of the Group and Feedback conditions and the Target. Note the similar effect of the Group and Feedback conditions for all target locations. The error bars represent the standard error of the mean.

Fig. 3 Radial absolute constant error as a function of the Group and Feedback conditions and the Target. Note the similar effect of the Group and Feedback conditions for all target locations. The error bars represent the standard error of the mean.

Fig. 4 The effects of Group and Feedback on the within-participant direction variability at the occurrence of key kinematic landmarks (peak acceleration, peak velocity, peak deceleration, and movement endpoint). Note the smaller variability later in the movement for the Hand and Upper limb groups than for the Virtual group. The error bars represent the standard error of the mean.

Fig. 5 The effects of Group and Feedback on the within-participant extent variability at the occurrence of key kinematic landmarks (peak acceleration, peak velocity, peak deceleration, and movement endpoint). Note the smaller variability for the Hand and Upper limb groups than for the Virtual group. The error bars represent the standard error of the mean.

Fig. 6 Coefficients of correlation (r) between kinematic landmarks as a function of the Group and Feedback conditions.

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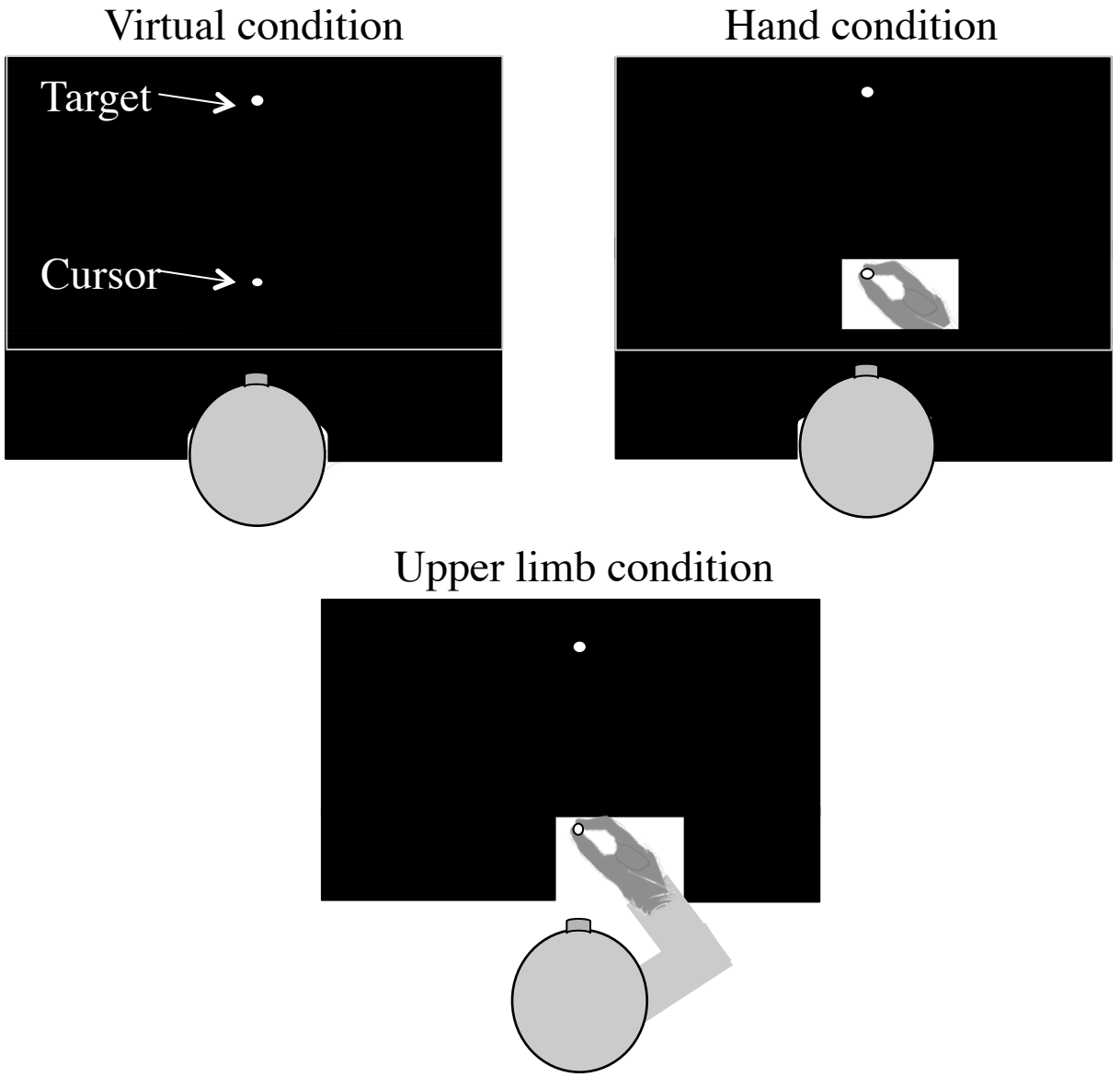

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Fig.1

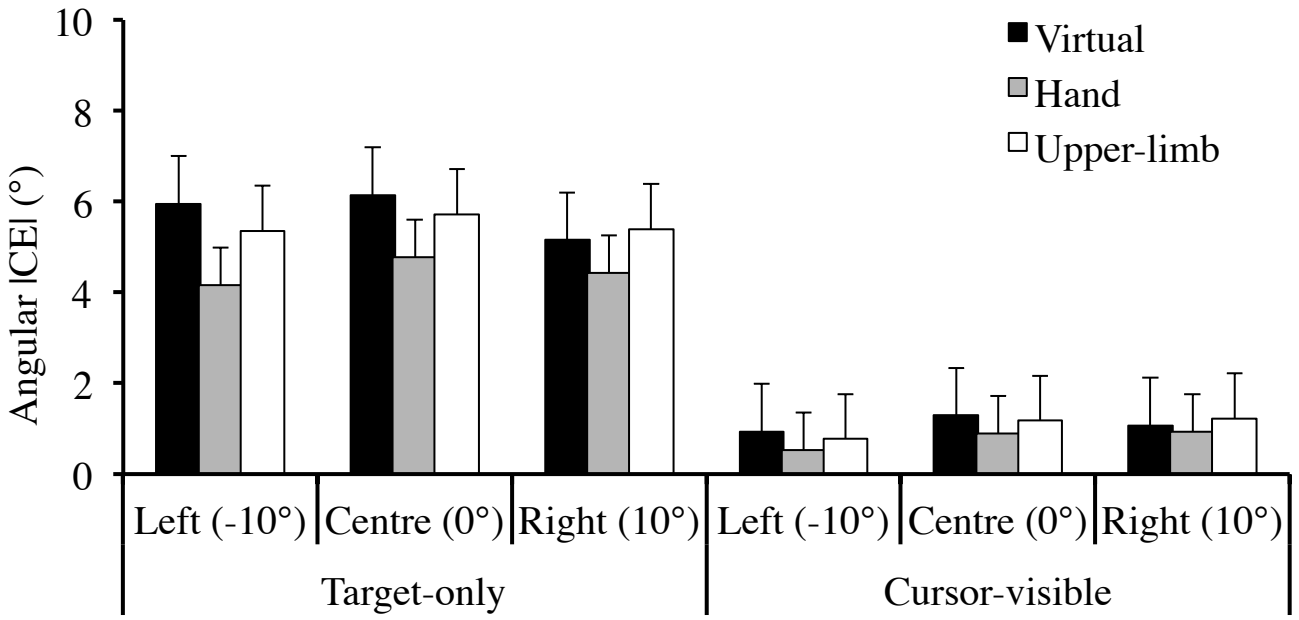

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Fig.2

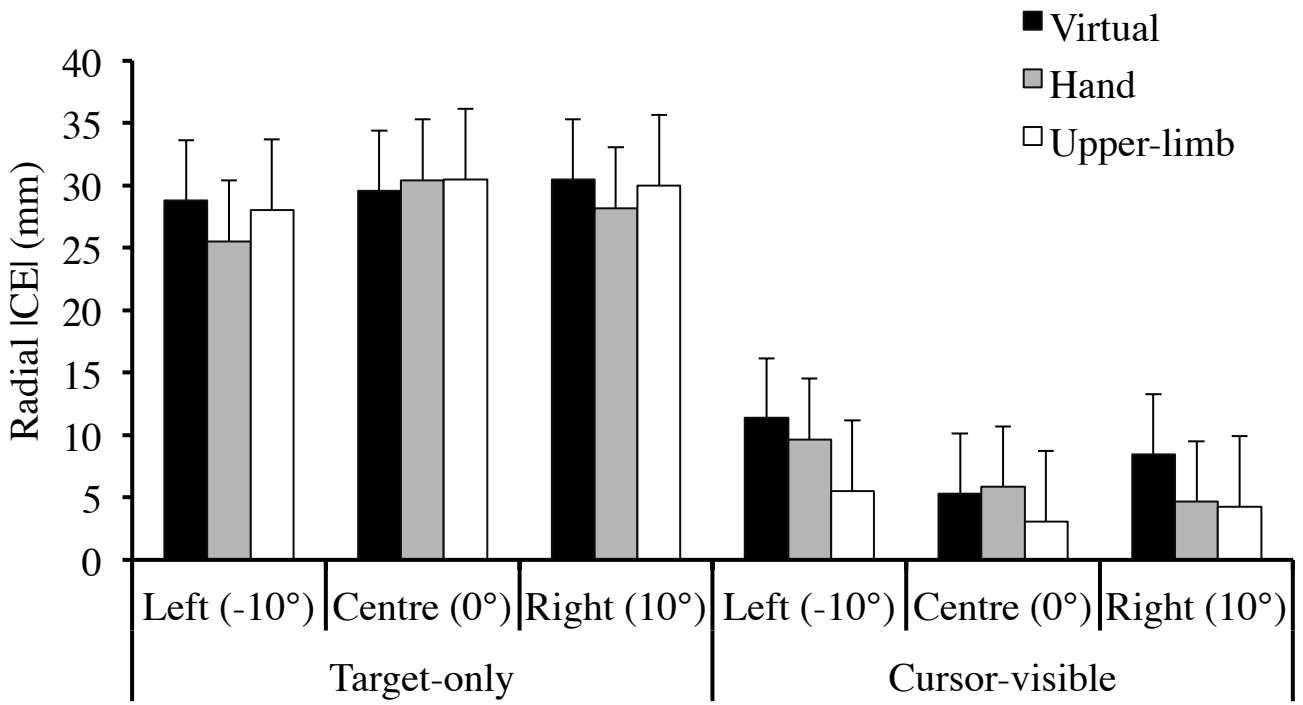

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Fig.3

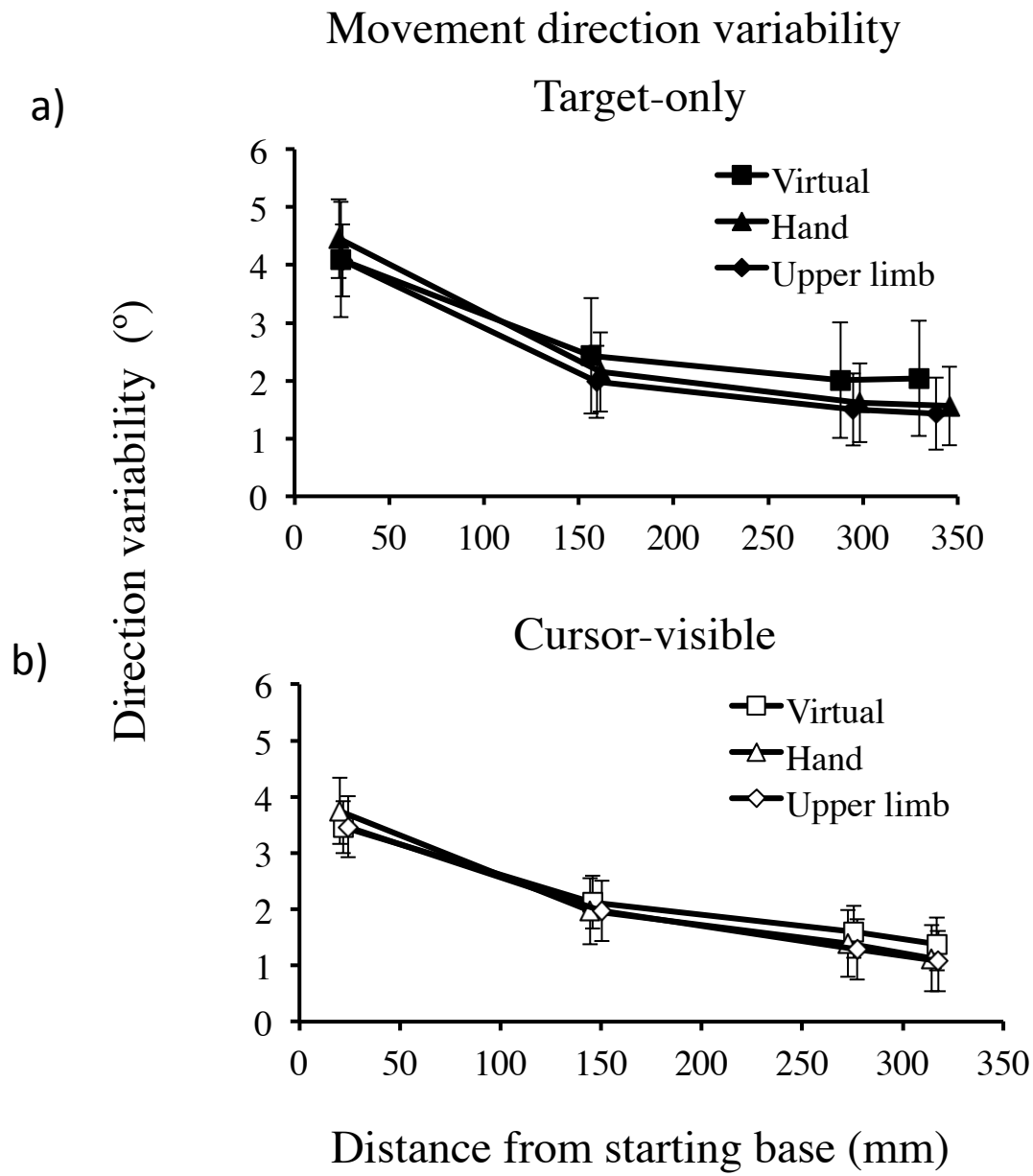

Fig.4

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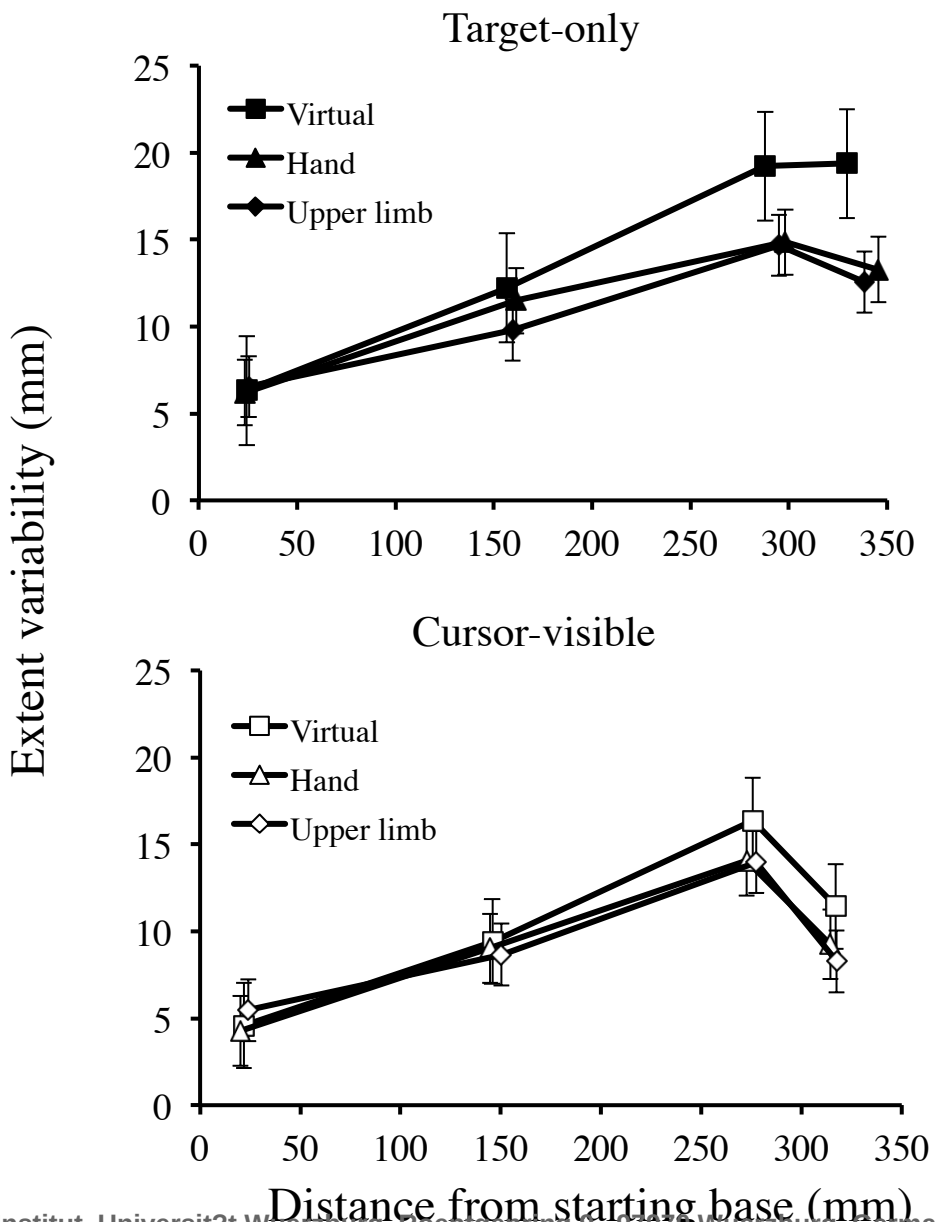

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Fig.5

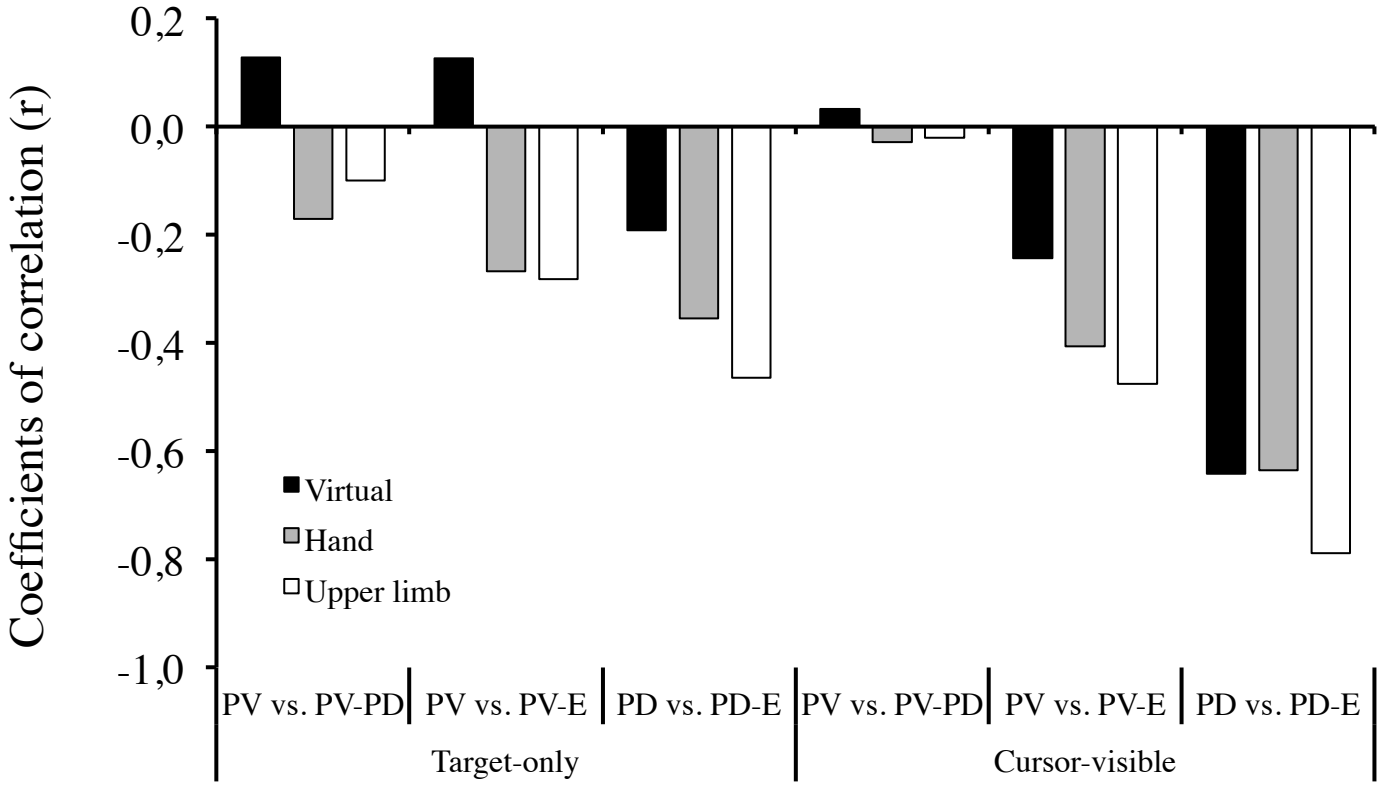

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Fig.6