Exp Brain Res (2004) 157: 468–471
DOI 10.1007/s00221-004-1860-y

RESEARCH ARTICLES

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Online control of the direction of rapid reaching movements

Received: 14 April 2003 / Accepted: 19 December 2003 / Published online: 9 March 2004

Abstract Online visual control of the direction of rapid reaching movements was assessed by evaluating how human subjects reacted to shifts in seen hand position near movement onsets. Participants (*N*=10) produced saccadic eye and rapid arm movements (mean duration = 328 ms) towards a peripheral visual target in complete darkness. During the saccade, visual feedback of hand position could be shifted by 1, 2, 3 or 4 cm perpendicularly to the main movement direction. The resulting discrepancies between visual and proprioceptive information about hand position were never consciously perceived by the subjects. Following the shifts, hand trajectories deviated from those produced in a control condition (without shift) in order to bring seen hand position closer to the target. Globally, the deviations corresponded to 45% of the shifts, regardless of their magnitude or movement duration. This finding highlights not only the efficiency of visual feedback processing in online motor control but also underlines the significant contribution of limb proprioception.

Keywords Reaching movement · Online control · Direction · Peripheral vision · Arm proprioception

Introduction

The contribution of visual feedback of hand position/displacement in the control of reaching movement direction has received support in several studies (for a review, see Paillard 1996). A frequently used paradigm consists in comparing terminal accuracy of goal-directed arm movements performed with different types of visual feedback (e.g. no feedback, feedback during either the first or last portion of the trajectory, feedback during entire trajectory). Using such a paradigm, a number of studies reported that directional accuracy of rapid arm movements was greater when the hand could only be seen early in the trajectory than when visual feedback was not available (Abhanini and Proteau 1999; Bard et al. 1985; Blouin et al. 1993b). Authors of these studies concluded that visual feedback of the moving limb can be processed online and rapidly to optimise directional accuracy.

However, a series of studies has cast doubts on the possibility that visual feedback of the hand is continuously processed to control rapid arm movements. Among these studies are those that reported similar accuracy for reaching movements performed with or without vision of the moving limb (e.g. Prablanc and Martin 1992; Vercher et al. 1994). The possibility that the benefit in directional accuracy when visual feedback of the moving limb is available could rely on enhanced feedforward processes rather than feedback processes has also been tested (Blouin et al. 1993a), but no definitive conclusions about online visual control of rapid arm movements could be reached. More recently, Bédard and Proteau (2001) have suggested that, for movements lasting between 240 and 310 ms, visual feedback of the trajectory can only be used offline to increase the directional accuracy of subsequent movements (facilitation of feedforward processes) and not online.

In the present experiment, we used a new experimental protocol to determine whether visual feedback of the hand trajectory could be processed to control online the direction of rapid arm movements. During the saccade towards the peripheral target, seen hand position was unconsciously shifted perpendicularly to the main movement direction, near reaching onset. If reaching movements were controlled purely by feedforward processes, no change in movement trajectory should be observed when the randomly introduced shift of visual feedback occurred. If visual feedback of the hand was processed online, the shifts should have resulted in predictable modifications of movement direction.

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A second goal of the experiment was to determine whether the importance given to hand visual feedback in movement control (in relation to proprioceptive feedback of the arm) increased with the magnitude of the visually detected deviation of hand trajectory compared to the desired trajectory. To explore this possibility, we assessed the effect of different magnitudes of the shifts in seen hand position on movement trajectories.

Methods

Ten right-handed subjects (males, 24–37 years old) performed the experiment, which was approved by the local Ethics Committee. In complete darkness, seated subjects held a pointer at chest level (see Fig. 1A). Nine light-emitting diodes (LEDs), mounted on the upper end of the pointer, were used to provide visual feedback of hand position (see Fig. 1B). One LED was directly above the pointer, hereafter referred to as the LED indicating true hand position; the other LEDs were positioned 1, 2, 3 and 4 cm both to the left and to the right of this LED. Signals from two potentiometers, located at the pointer base, were sampled at 500 Hz to obtain the pointer coordinates. A head-rest prevented head movements. The virtual images of two green LEDs, located above a semi-reflecting horizontal glass and appearing at chest level at 0° (straight-ahead) and 24° (to the right), were used as fixation point and target, respectively. Hand starting position was near the abdomen of the participant, 44 cm from the target plane. Horizontal eye movements were recorded at 500 Hz, by DC electro-oculography.

A trial started with subjects gazing at the fixation point for 1.5 s. The pointer LED indicating true hand position was also lit. At the extinction of the fixation point, the target appeared for 1 s. Subjects produced a saccadic eye movement towards the target and stretched out the arm to full extension in order to "pass through" the virtual target. Therefore, the task did not have an amplitude requirement: only movement direction had to be controlled. Participants were requested to synchronise eye and arm movement onsets and to produce rapid arm movements. At mid-flight of the saccade, the pointer-LED could be (1) continuously lit, still indicating true hand position (H0 condition), (2) switched off, whereas the LED positioned 1, 2, 3 or 4 cm on its left was lit (H-1, H-2, H-3 or H-4 condition, respectively), (3) switched off, whereas the LED positioned 1, 2, 3 or 4 cm on its right was lit (H+1, H+2, H+3 or H+4 condition, respectively).

In the fronto-parallel plane of the target, shifts of 1, 2, 3 and 4 cm represented 1.2°, 2.4°, 3.6° and 4.8° of visual angle, respectively. The nine experimental conditions were pseudo-randomly presented in one session (six trials per condition). The main measured parameter was the direction of the hand (rather than the direction of the illuminated LED).

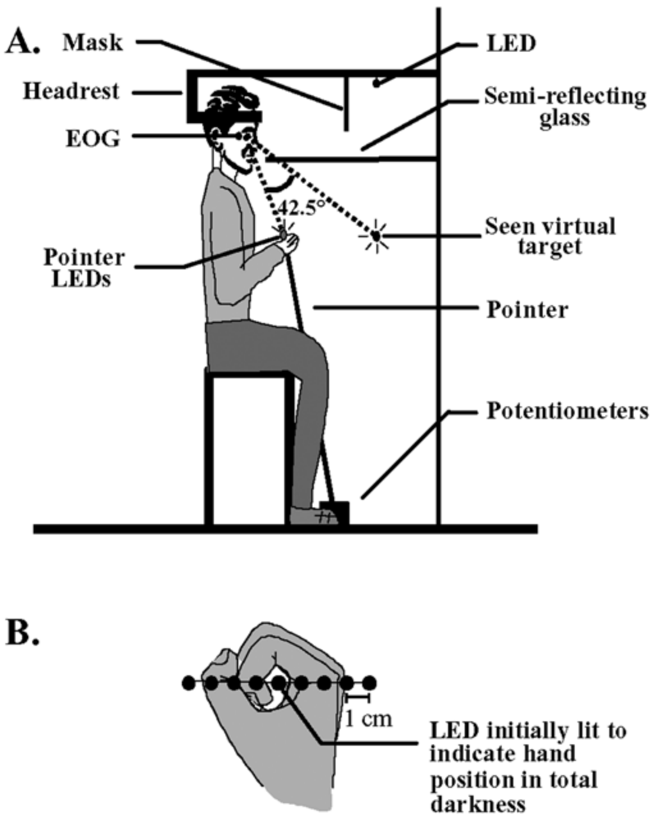

Fig. 1 **A** Side view of the apparatus. **B** Top view of the nine LEDs that were used to provide true or erroneous visual feedback on hand position in complete darkness. Only one LED was lit at the same time

Results

Subjects never reported seeing the shifts in the pointer LED. This is because the shifts occurred during the saccade towards the target, that is when the spatial perception of visual stimuli is highly reduced (Bridgeman et al. 1994). Subjects reached accurately the 24° target when the pointer LED continuously indicated true hand position (mean=23.3°). However when a shift in pointer-LED occurred, hand trajectories deviated in the opposite direction to the shift (see Fig. 2A). An ANOVA showed that hand direction at the target plane was significantly affected by shifts in pointer LED ($F_{(8,72)}=28.4$; $P<0.001$). Post hoc tests (Newman-Keuls; $P<0.05$ unless otherwise specified) showed that hand direction in H-2 (mean=24.4°), H-3 (mean=24.9°), H-4 (mean=26.0°), H+2 (mean=22.3°; $P=0.06$), H+3 (mean=22.3°) and H+4 (mean=21.2°) conditions differed from the H0 control condition. No significant change in hand direction was observed following the smallest shifts in pointer LED despite a tendency to do so (means of 23.9° and 22.7° in H-1 and H+1 conditions, respectively, compared to mean=23.3° in H0 condition). This was presumably due to the small trajectory deviations that were expected if the small shifts in seen hand position were taken into account. Shifting the pointer LED had no significant effect on the within-subject variability of hand direction at the target plane (mean=1.7°; $F_{(8,72)}=0.7$; $P>0.05$). To determine whether pointer LED shifts to both sides had similar effects on movement trajectories, we computed the absolute hand deviations obtained in each pointer LED shift condition with respect to hand direction in the H0 condition. The side to which pointer LED was shifted did not significantly affect hand deviations (absolute values) as an 2×4 ANOVA [Side (Left, Right) × Shift magnitude (1, 2, 3, 4)] did not show significant Side effect ($F_{(1,9)}=0.37$; $P>0.05$) or significant interaction ($F_{(3,27)}=1.14$; $P>0.05$).

Figure 3 plots the observed deviation in hand trajectory against the required deviations for the pointer LED to be on target. The data were well fitted by a linear regression

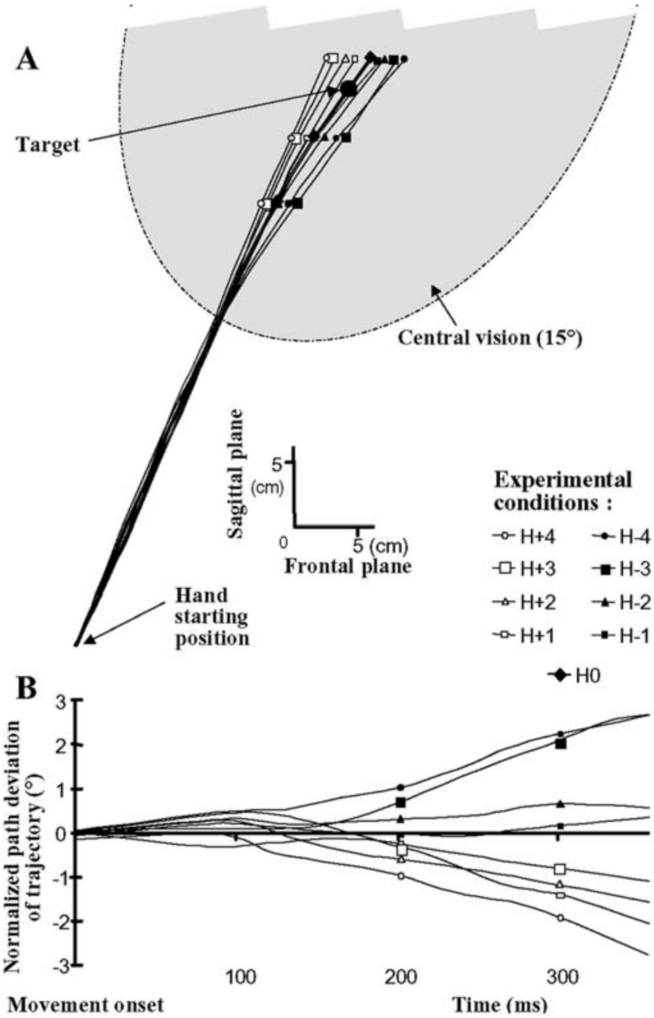

Fig. 2 **A** Top view of mean spatial paths obtained in each experimental condition for one subject. The *grey area* represents the zone covered by the central vision when the subjects were looking at the target. **B** Normalised hand deviations (with respect to control H0 condition) plotted as a function of movement time

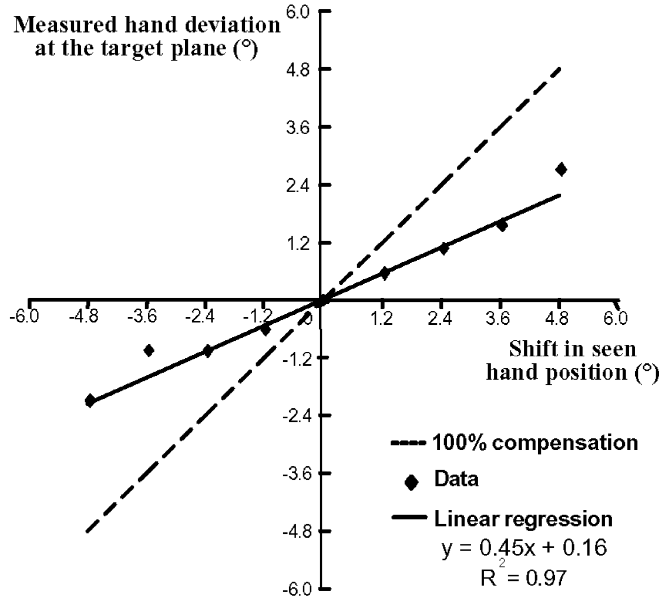

Fig. 3 Hand deviations on reaching target plane (compared to control condition H0) plotted against the magnitude of pointer LED shifts. The *solid line* represents the linear regression whereas the *dashed line* represents theoretical hand deviations if subjects had brought exactly the seen hand position onto the target

(R^2=0.97) with a slope of 0.45. This suggests that subjects modified movement trajectory such that 45% of the unconsciously perceived shift was taken into account, and this proportion did not depend on the magnitude of the pointer LED shift.

Movement duration (time elapsed between the first time hand velocity reached 5 cm/s and the moment the hand intersected the target plane) was not significantly affected by the shifts of visual feedback (mean=328 ms; $F_{(8,72)}$=0.89; P>0.05). Neither peak velocity (mean=219 cm/s; $F_{(8,72)}$=1.49; P>0.05) nor time-to-peak velocity (mean=204 ms; $F_{(8,72)}$=0.52; P>0.05) were significantly affected by the shifts of visual feedback. One reason why path deviations were smaller than the shifts of visual feedback (45%) could be because movements durations were too short to allow subjects to bring the pointer LED to the target. Because movement durations were highly variable (ranging between 178 and 630 ms), it was possible to test this hypothesis by plotting hand direction at the target plane against movement duration. However, R^2 values of the linear regression were very low, ranging between 0.15 and 0.37 for all conditions (mean=0.21). This suggests that hand visual feedback was similarly processed irrespectively of the speed of the movements (including those that were very fast).

The timing between the shift in pointer LED and movement onset was not affected by the experimental conditions ($F_{(7,63)}$=0.9; P>0.05). In most of the trials, the shift occurred before movement onset (mode=130 ms, using 4 ms bins) but the shift/movement onset latency was highly variable (SD=117 ms). To determine whether longer latencies were associated with greater trajectory deviations, hand deviation at the target plane was plotted against the corresponding latency shift/movement onset. R^2 values of the linear regression ranged between 0.16 and 0.42 (mean=0.25) across experimental conditions. Therefore similar hand deviations were observed irrespectively of the length of time during which subjects had access to the modified visual feedback of hand position during the reaction time and irrespectively of whether hand visual feedback was shifted before or after movement onset. This suggests that the deviations in movement trajectories observed in the present study were the result of an online control of the reaching movement. This is also supported by the fact that the initial hand direction was not affected by the shifts in the pointer-LED and the fact that path deviations appeared only near mid-trajectories (see Fig. 2B).

Discussion

Shifting seen hand position resulted in marked and predictable deviations of rapid arm movements. As the shifts were randomly introduced near movement onset, only online control of movement direction based on hand visual feedback could account for the observed deviations. These results do not support the suggestion of Bédard and Proteau (2001) that the increase in directional accuracy observed when visual feedback of rapid movements is allowed only derives from enhanced feedforward processes and does not involve online motor control. Differences between the present results and those reported by Bédard and Proteau (2001), who studied video-aiming movements, support the view that the control of manual- and video-aiming movements relies on distinct processes (Clower and Boussaoud 2000). The complex sensorimotor transformations required in video-aiming tasks (due to motions of the monitor-viewed cursor and of the hand occurring in different planes) could therefore explain why Bédard and Proteau (2001) found no significant online contribution of visual feedback of the fast (cursor) movement. Results from Lhuisset and Proteau (2002) however showed that visual feedback of the cursor can be processed online to control video-aiming movement direction when slower movements are performed (movement duration about 550 ms).

Shifting seen hand position has also been used to test the online control of the amplitude of rapid movements (Sarlegna et al. 2003). The effect appeared to be smaller than in the present study where subjects had only to control movement direction. First deviations of movement trajectory appeared when the hand's visual image entered in central vision. However, considering both the delays inherent in visual information processing and the time necessary to amend the arm motor commands, the change in movement direction likely resulted from visual feedback of the hand when it swept the peripheral retina. Taken together, these results support the suggestion that movement direction is controlled early in the trajectory by processing hand visual feedback from peripheral vision and that movement extent is under visual guidance towards the end of the reaching movement when the hand appears in central vision (Bard et al. 1985; Blouin et al. 1993b). The high speed of the movement in Sarlegna et al.'s study (2003; movements lasted about 450 ms for a 36 cm target) presumably prevented optimal control of movement amplitude by the low-speed sensitive central vision (see Paillard 1996).

Subjects changed movement trajectory such that about half of the unconsciously perceived shift in hand visual feedback was taken into account, regardless of shift magnitude. This suggests that the contribution of visual feedback did not depend on the magnitude of the visually detected errors in hand trajectory. The limited use of hand visual feedback neither came from the spatio-temporal constraints of the task. For instance, while subjects could produce trajectory deviations as large as 2.8° (as evidenced in H-4 condition), they only produced a 1.1° deviation when a 2.4° deviation was required to bring the pointer LED on the target (H-2 condition). Corrections following a change in the seen hand position were smaller than those that resulted in a shift in the target position (e.g. Prablanc and Martin 1992). This could be due to the fact that with respect to target position information (derived through vision), visual feedback of the hand during the movement can be thought of as being less essential in the online control of arm movement because the proprioceptive sense also informs the CNS about hand position (Sarlegna et al. 2003). These results suggest that online control of movement direction not only involved visual feedback but also proprioception of the limb. Visual and proprioceptive information were presumably integrated with respective weights of 45% and 55% during the (rapid) reaching movement to control direction, as suggested by the slope of the linear regression (see Fig. 3). However, the respective contributions of vision and proprioception in hand position/movement coding are probably task-specific as they vary with hand position relative to the body (Plooy et al. 1998; van Beers et al. 2002).

Acknowledgements This work received financial support from the CNRS (Program ROBEA) and the Université de la Méditerranée. We thank Alain Donneaud for technical assistance and Marcel Kaszap and Thelma Coyle for programming expertise. We also thank Luc Proteau and an anonymous reviewer for numerous comments made on an earlier version of this paper.

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