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RESEARCH ARTICLE

The relative timing between eye and hand in rapid sequential pointing is affected by time pressure, but not by advance knowledge

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Abstract The present study examined the effect of timing constraints and advance knowledge on eye–hand coordination strategy in a sequential pointing task. Participants were required to point at two successively appearing targets on a screen while the inter-stimulus interval (ISI) and the trial order were manipulated, such that timing constraints were high (ISI = 300 ms) or low (ISI = 450 ms) and advance knowledge of the target location was present (fixed order) or absent (random order). Analysis of eye and finger onset and completion times per segment of the sequence indicated that oculo-manual behaviour was in general characterized by eye movements preceding the finger, as well as 'gaze anchoring' (i.e. eye fixation of the first target until completion of the finger movement towards that target). Advance knowledge of future target locations lead to shorter latency times of eye and hand, and smaller eye–hand lead times, which in combination resulted in shorter total movement times. There was, however, no effect of advance knowledge on the duration of gaze anchoring. In contrast, gaze anchoring did change as a function of the interval between successive stimuli and was shorter with a 300 ms ISI versus 450 ms ISI. Further correlation analysis provided some indication that shorter residual latency is associated with shorter pointing duration, without affecting accuracy. These results are consistent with a neural mechanism governing the coupling of eye and arm movements, which has been suggested to reside in the superior colliculus. The temporal coordination resulting from this coupling is a function of the time pressure on the visuo-manual system resulting from the appearance of external stimuli.

Keywords Gaze anchoring · Saccade · Oculomotor control · Manual control · Reaching · Pointing

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Introduction

Research into tasks involving coordinated eye and hand movements, such as reaching for an object or visuo-manual tracking, has demonstrated that the oculomotor and manual system operate in an interdependent relationship that provides the opportunity for reciprocal facilitation. For example, gaze shifts towards a target or smooth pursuit eye movements are facilitated when accompanied by similar movement of the arm (i.e. pointing at or manually tracking the target), resulting in shorter saccadic latency at onset (Epelboim et al. 1997; Lünenburger et al. 2000) and increased maximum velocity and gain of smooth pursuit (Gauthier et al. 1988; Steinbach 1969; Vercher et al. 1995). In a similar vein, efference copy from movement of the

eyes has been shown to provide essential information relating to direction and amplitude, which enables arm movement to be initiated in the absence of foveal feedback. It is, however, less clear how this interdependent relationship manifests in tasks requiring a succession of goal-directed eye and hand actions.

Clearly, there is an advantage of having interdependence between two effectors that can provide information to each other, while at the same time having different dynamic properties. A dependent coupling in which both effectors respond to a common central command would not permit one system to adapt without affecting the other (Scarchilli and Vercher 1999). It is perhaps not surprising, then, that there have been numerous studies showing that the spatial and temporal coordination of eye and hand is altered in response to changing task demands (Epelboim et al. 1995; Ma-Wyatt et al. 2010; Pelz et al. 2001). One such demand is the time available to complete a sequence of movements. During relatively slow sequences [e.g. making tea; see Land and Hayhoe (2001) for review], gaze typically lands on the target on average 560 ms prior to any hand movement, thus providing sufficient time to process and combine retinal and extra-retinal information for movement planning (Land et al. 1999). However, in more temporally demanding sequence tasks such as typing a text message on a mobile phone or picking up and moving objects on a fast-moving production line, the visuo-motor system would be challenged by feedback delays (up to 165 ms for visual processing; e.g. Young and Zelaznik 1992) in the sensory system if it were to simply operate closed-loop, in which each subsequent effector movement was made only after prior information had been processed.

Recognizing such limitations, Wilmut et al. (2006) proposed that expert control of sequential rapid pointing tasks accommodates feedback-processing delays by shifting reliance away from online processing of foveal visual feedback. For the first target in a sequence, gaze fixation prior to manual action in rapid pointing is short (e.g. 20–76 ms in Wilmut et al. 2006) or even absent (e.g. Abrams et al. 1990; Binsted et al. 2001), thus indicating that the hand movement is planned and initiated on the basis of peripheral visual information, in conjunction with feedforward information from ocular motor command (Desmurget and Grafton 2000; Prablanc et al. 1979a, b). Then, contrary to single-target aiming tasks, where foveal visual feedback plays an important role in the latter phase of the movement as the hand approaches the target (for a review, see Elliott et al. 2010), in sequential aiming or object manipulation tasks, gaze is often found to shift to the next point of interest before the preceding hand movement has been completed (e.g. Helsen et al. 2004; Johansson et al. 2001). It is reasoned that the final part of the aiming movement is guided by information from foveal vision and

ocular proprioceptive that is stored in a temporary 'buffer', i.e., spatial information held in memory. Since this early gaze shift also implies that saccadic efference towards the next target cannot be utilized directly to generate a subsequent hand movement, Wilmut et al. 2006 maintain that efference information must be buffered as well. This would mean that, except for the initiation of the sequence, the information (foveal, ocular proprioception and efference commands) that supports the pointing movement must be stored in memory and hence not used in real time (online).

It is notable that using a similar double-step pointing paradigm others have found that the eyes remain fixated on the target of interest for the entire duration of the pointing movement (Lünenburger et al. 2000; Neggers and Bekkering 2000, 2001). According to Neggers and Bekkering, this 'gaze anchoring strategy', characterized by the inhibition of a saccadic shift during an ongoing hand movement, facilitates online control using foveal vision of the hand as it approaches the target (Elliott et al. 2010). However, rather than being in direct opposition, it is possible that 'gaze anchoring' (Neggers and Bekkering 2000, 2001) and 'buffering' (Wilmut et al. 2006) reflect two modes of the visuo-motor system, which operate under different task constraints. A comparison of the experimental methods indicates that the time lag between the two visual stimuli in the study of Neggers and Bekkering (2000) was significantly longer compared (i.e. 585–607 ms) with that in Wilmut et al. (2006), i.e., 200 ms. In addition, the second step in the former study involved only a gaze shift (in absence of a pointing movement to the second target) and thus could have prioritized accuracy on the first target rather than speed of the entire sequence. In Wilmut et al., the task was to point as rapidly as possible at two successive targets, which implies that speed (and time) was the first objective.

The primary aim of the current study was to investigate the effect of external timing constraints on eye–hand coordination strategy in a sequential aiming task. To this end, eye and hand movements were examined in a double-step pointing protocol in which the inter-stimulus interval was either 300 or 450 ms. Participants were required to point at both targets in succession, thus emphasizing the need for accurate information to control the aiming movement to the second target (see Wilmut et al. 2006). Extending upon the work of Wilmut et al. (2006) and Neggers and Bekkering (2000, 2001), it is anticipated that a shorter ISI will lead to shorter gaze anchoring times and potentially to an early gaze shift, prior to completion of the pointing. The latter type of behaviour would be indicative of a shift towards a feedforward control strategy requiring buffering of sensory afferent (visual and proprioceptive) and efferent oculomotor information. A secondary aim was to determine whether and how eye–hand coordination in this task is modified by advance knowledge (i.e. a

comparison between trials presented in fixed and random order) regarding the spatial location of the targets within the sequence. This was deemed relevant because memorized target information generated over repeated trials may reduce the need for foveal visual information and/or favour the use of efferent feedforward information as it becomes more efficient and specific to the target sequence. A greater reliance on memorized information is expected to be reflected in a shortening of duration of gaze anchoring or early breaking of ocular fixation prior to completion of the pointing movement.

Methods

Experimental set-up

Twelve healthy, right-handed male adults with a mean age of 32.08 ± 7.86 volunteered to take part in the study. All participants had normal or corrected-to-normal vision and were without any oculomotor abnormalities. The experimental protocol was approved by the institutional Ethics Committee and in accordance with the Declaration of Helsinki. Before commencing with the experiment, participants were instructed on the procedure and gave informed consent.

Participants sat on a chair facing a 22-inch flat computer screen (iiyama, ProLite) at an average viewing distance of 342 ± 16 mm, with the head supported by a chinrest (see Fig. 1). The experimental stimuli were generated on a host PC ($1,024 \times 768$ pixels; 75 Hz refresh) using the COGENT toolbox implemented in MATLAB (Mathworks Inc.). To increase the visibility of the targets, the experiment was performed in low ambient light.

Eye movements were recorded at 200 Hz using a Chronos Eye Tracking Device (Chronos Vision, Berlin, Germany), which has a reported accuracy better than $0.1°$ in a range of measurement of $\pm40°$ (Clarke et al. 2002). A 3D motion capture system (Vicon, Oxford, UK) recorded finger movements (marker on the nail of right index finger) at 200 Hz. The residual values after 3D reconstruction of the finger marker position ranged between 0.1 and 0.8 mm. Three additional markers were placed on top of the screen to define the coordinates of the targets. A TTL signal from the parallel port of the host PC was generated in MATLAB and recorded via the AD card of the 3D motion capture system to enable temporal synchronization of eye and finger data.

Task and procedure

The double-step pointing task required participants to point at two targets appearing successively within a predetermined square grid. The grid consisted of 9 circular targets (diameter: 18.6 mm, visual angle: $3.1°$; 3 rows by 3 columns) separated by 95 mm (visual angle: $15.24° \pm 0.64°$) from each other in the horizontal and vertical directions (see Fig. 1). The targets were red with a black dot in the centre, except for the yellow home target (central target of the 9 square grid). A trial started when the participant fixated and touched the home target. After it was ensured that the participant was ready, the experimenter started the sequence by pressing a key on the host PC. On this key press, the home target disappeared, which was followed 300 or 450 ms later by the appearance of a red target located above, below, left or right (i.e. locations 8, 2, 6 or 4). A second target appeared after a further 300 or 450 ms and was located in either a horizontal or vertical direction; diagonal movements were never involved, and the first target remained visible. Participants were instructed to touch the targets as fast and as accurately as possible in the correct order.

Each participant performed eight blocks of ten trials ($N = 80$ trials) in which the inter-stimulus interval (ISI: 300 ms or 450 ms) and the order (fixed or random) was varied. In the two blocks where trials were received in fixed order, one movement sequence was repeated ten times. For the 300 ms ISI, the sequence was home-up-right, whereas for the 450 ms ISI, it was home-left-down (see Fig. 1). The different movement sequences for each ISI were chosen to avoid repetition and learning. In the remaining six blocks of trials received in random order (three per timing condition), the same movement sequences (i.e. home-up-right and home-left-down) were repeated five times, interleaved with 25 trials in which sequences of 2, 4 or 6 targets appeared at combinations of various other locations (e.g. home-right-up, home-left-up-right-right). Participants started with either the two fixed-order blocks followed by six random-order blocks, or vice versa, and this order was counterbalanced across participants. In each block of random-order trials, ISI was grouped (ISI300 or ISI450).

Prior to each block of trials, an eye movement calibration was carried out in which participants fixated all nine targets in a given order (1–9). The resulting visual angle between the eye and targets was taken as the reference for subsequent calculation of the point of gaze throughout a sequence.

Data analysis

Trials in which the participants did not fixate or point at the targets in the correct order were excluded from the analysis ($N = 19$, 7.9%). In addition, while the gap paradigm, i.e., when the initial fixation point disappears some time before target onset (300 or 450 ms later, in the current study), was used to facilitate disengagement of visual attention in preparation of the first saccade (Krauzlis and Miles 1996),

Fig. 1 Schematic sagittal view of the experimental set-up and frontal view of the screen with all potential target locations indicated; timeline of a trial procedure with the target locations in the ISI300 and ISI450 conditions
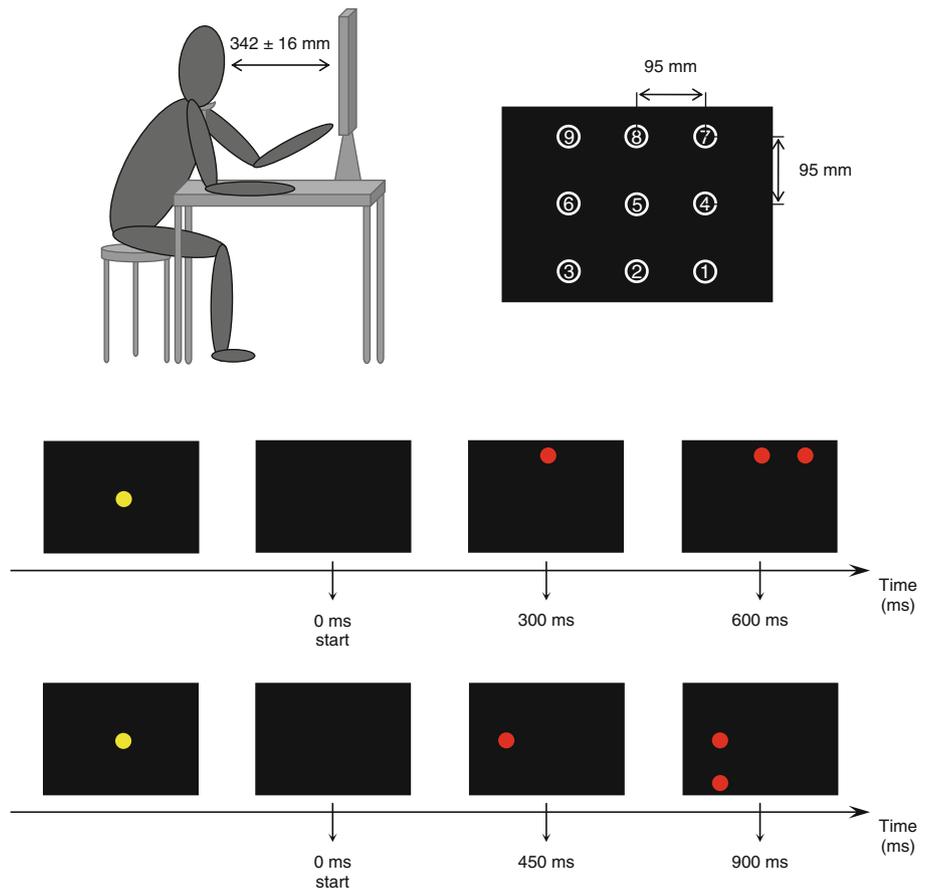
saccadic onset was checked for abnormal anticipatory responses. This procedure led to the elimination of 3 (1.25%) trials of the fixed-order conditions where the initial gaze shift occurred earlier than 80 ms after disappearance of the home target. For the random-order conditions, the cut-off point was 80 ms after onset of the first target, but none of the participants exhibited abnormal saccadic anticipation in these conditions. The 80-ms criterion was chosen based on previous studies showing no evidence of visually guided saccades at latencies less than 80 ms in gap conditions (Fischer et al. 1997; Gezeck et al. 1997). Finger movement was checked for cases where onset occurred earlier than 100 ms after disappearance of the home target or onset of the first target in the fixed-order and random-order conditions, respectively (see Carlton 1992), but no abnormal anticipation was found.

Three-dimensional finger position data were filtered with a second-order Butterworth filter, set with a 10-Hz cut-off frequency. Finger and eye position data were then differentiated with a two-point central difference algorithm. Timing and accuracy of finger and eye movements for each segment were then extracted using semi-automated, custom-written routines implemented in MATLAB. Finger movement onset and offset were derived from

velocity data in the primary movement direction of each particular segment (e.g. horizontal for a movement between target positions 5 and 6, i.e., home-left, and vertical for a movement between target positions 5 and 8, i.e., home-up). Finger initiation was defined as the moment when finger velocity exceeded 10% of peak velocity, whereas movement offset was defined as the moment after peak velocity when finger velocity dropped below this threshold (Lacquaniti and Soechting 1982; Yan et al. 1998). Saccadic onset and offset were determined for the left eye only. Saccadic onset was defined as the time when eye acceleration exceeded $750°/s^2$; saccadic offset was calculated as the time when eye deceleration dropped below this threshold (De Brouwer et al. 2002). When multiple saccades were used to shift gaze between two targets, onset was defined relative to the first saccade, whereas offset was defined relative to final saccade. Saccades with amplitudes smaller than 1° were not included in the analysis.

Timing variables for eye and finger movements were derived for each segment separately; suffixes 1 and 2 are used to refer to the first and second segment, respectively (see Table 1; Fig. 3). Saccadic and finger *latency* were defined as the time between presentation of the target and

Table 1 Breakdown and explanation of the temporal dependent variables

Dependent variable	Description
Latency[a]	Time from appearance of a target to movement onset to that target
Movement time[a]	Time from movement onset to completion of that segment
Lead time	Time from eye movement onset to finger movement onset to the same target
Foveation time	Time from eye movement completion to finger onset to the same target
Dwell time[a]	Time from completion of the first segment to onset of the second segment
Residual latency	Time from finger movement completion to the first target to eye onset to the second target
Total response time[a]	Total duration of the movement sequence, from onset to the first target to completion of the movement to the second target

The complete movement sequence is subdivided into two segments, from onset to completion of the movement to the first and second target, respectively

[a] Dependent variables calculated for both the eye and finger

onset of the saccade and the finger movement, respectively. *Movement time* of the eyes and the finger was defined as the time between onset and offset of the respective movement segment, and *dwell time* was the period between completion of the eye or finger movement towards the first target and onset towards the second target, indicating the period when the eyes or the finger were fixating or touching a target. Eye–hand *lead time* was defined as the time between saccadic onset and finger onset for each target. In order to determine whether the eyes fixated the target before onset of the finger movement, we calculated *foveation time*, the time between completion of the eye movement towards the target and finger onset to the same target. Note that negative foveation times indicate that the finger movement started before the eye landed on the target. The time between completion of the finger movement to the first target and onset of the saccade to the second target is referred to as *residual latency*. Positive residual latency indicates that a saccadic shift is postponed until the first finger movement has been completed and thus suggests 'gaze anchoring', whereas negative residual latency indicates that the eyes move ahead of the finger and leave the target before completion of the finger movement and thus suggests 'information buffering'.

Finally, we assessed the overall accuracy and duration of the eye and finger movement. *Absolute eye error* in the horizontal and vertical axes was defined as the resultant visual angle of the point of gaze at completion of each

segment relative to the calibrated visual angle for the respective target. *Absolute finger error* was defined as the Euclidean distance between the finger and target at completion of each segment. The 2D position of the targets was calculated using reference markers attached to the screen, which were located at a known distance relative to the targets. The standard deviation of absolute eye and finger error was defined as *variable eye and finger error*, respectively. *Total response time* for the eyes and finger was the time between the appearance of the first target and the completion of the second eye and finger movement.

Statistical analysis was performed using separate three-way repeated measures analysis of variance (ANOVA); target [1, 2] × ISI [300 ms, 450 ms] × trial order [fixed, random]. Because only a single value could be derived for residual latency, dwell time and total response time, these variables were analysed using a two-way repeated measures ANOVA; ISI [300, 450 ms] × trial order [fixed, random]. These analyses were conducted using mean data calculated from all five trials for the random-order conditions (random ISI300, random ISI450). For the fixed-order condition (fixed ISI300, fixed ISI450), means from trials 6–10 were entered into the analyses, which maintained an equal number of trials per combination of independent variables. Trials 1–5 were given as practice to establish advance knowledge of the sequence and hence were not included in the analyses. Main and interaction effects were further examined with Tukey's HSD post hoc tests, and alpha level was set at 0.05.

Results

Representative movement traces of eye and finger for a fixed-order and random-order trial (ISI 300 ms) are shown in Fig. 2. As will be described in more detail below, there was a typical temporal coordination whereby the eye movement (thick solid trace) precedes the movement of the hand (thin broken trace), but the saccade towards the second target (lower panels) is postponed until the finger has reached its goal (upper panels). In addition, it can be seen that latency to the onset of the first target (i.e. vertical movement; upper panels) is considerably reduced in the fixed-order compared with the random-order trial.

Global performance

Total eye and finger response times increased with ISI duration $[F(1,11) = 17.88, P = 0.001; F(1,11) = 7.28, P = 0.021;$ see Fig. 3]. In addition, response time of both the eyes and the finger were significantly shorter in the fixed-order compared with random-order condition $[F(1,11) = 14.11, P = 0.003; F(1,11) = 18.63, P = 0.001]$.
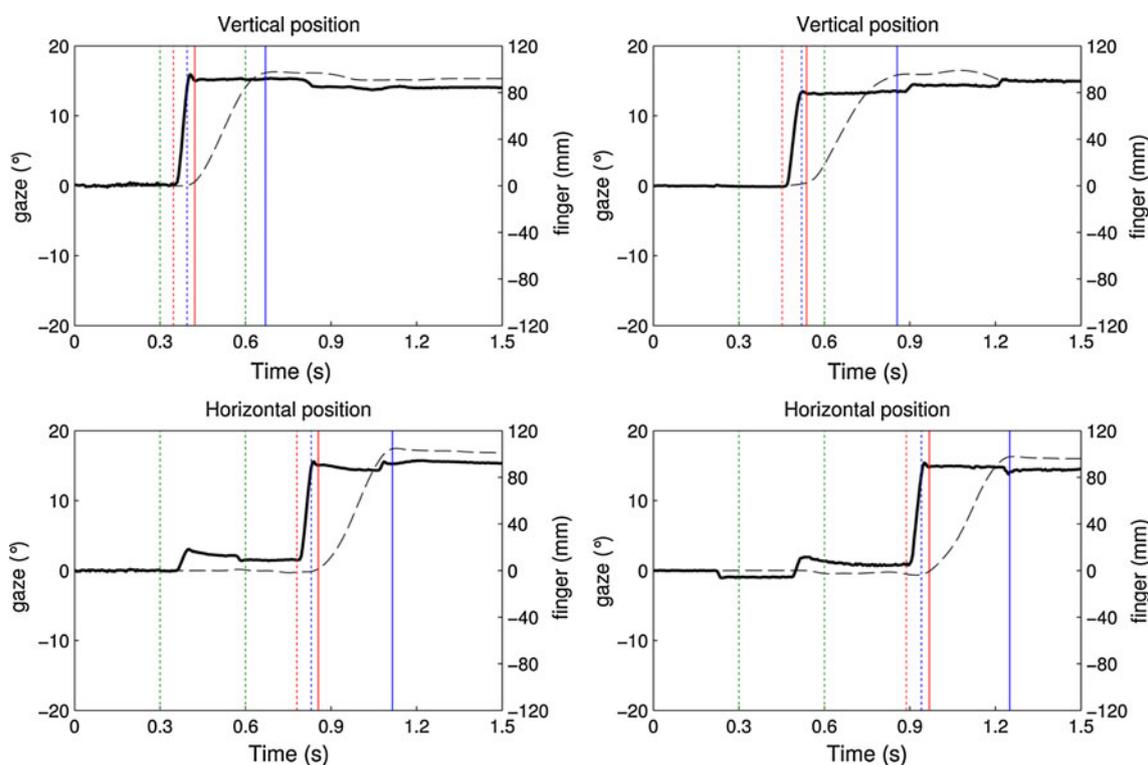
Fig. 2 Vertical and horizontal position trace of the eye (*bold*) and the finger (*dashed*) in a typical fixed-order trial with ISI 300 ms (*left panels*) and random-order trial with ISI 300 ms (*right panels*), involving a sequential movement to target 8 (*upward*) and target 7 (*right*). The *vertical lines* indicate the appearance of the first and the second target (*dashed green*), onset of the eye and finger movement (*dashed red* and *blue*, respectively), and end of eye and finger movement (*solid red* and *blue*, respectively)

Analysis of movement time of the eyes towards each target (see Table 2; Fig. 3) revealed an effect of target [$F(1,11) = 7.09$, $P = 0.022$] and trial order [$F(1,11) = 17.05$, $P = 0.002$], accompanied by an interaction between these two factors [$F(1,11) = 6.92$, $P = 0.023$]. Post hoc examination showed that in fixed-order trials only, movement time of the first segment was longer compared with movement time of the second segment. Movement time of the first segment was also longer in fixed-order than random-order trials. This was due to early anticipatory gaze shifts emerging after disappearance of the home target and prior to appearance of the first target. The primary saccade then undershot the target and was often followed by a corrective saccade, leading to a lengthening of duration of this saccadic episode.

Movement time of the finger was reduced on average by 28 ms in the shorter compared with longer ISI [$F(1,11) = 7.53$, $P = 0.019$] and also tended to be longer for the first target (segment 1) than the second target (segment 2) [$F(1,11) = 4.43$, $P = 0.059$] (see Table 2; Fig. 3). Movement time of the finger did not change as a function of trial order, and there were no interactions between independent variables.

Absolute eye error varied between 1.5° and 3.6°, which is within the expected range for this kind of task. Indeed, because absolute error was measured relative to the centre of the target (diameter = 3.1°), the largest eye errors were at most 2.05° off the outer edge of the target and thus would have placed at least part of the target on the fovea (assuming 1° of visual angle is equivalent to 0.3 mm on the retina, and fovea has diameter between 1 and 1.5 mm). There was, however, an effect of target [$F(1,11) = 20.26$, $P = 0.001$], and a significant interaction between target and ISI [$F(1,11) = 9.743$, $P = 0.010$]. Post hoc examination showed larger absolute eye errors for the second target compared with the first target in the ISI450 trials, whereas there was no difference between targets in the ISI300 trials. There was no effect of trial order or other interaction effects. For variable eye error, there was a main effect of trial order [$F(1,11) = 6.29$, $P = 0.029$]. Precision was higher in the fixed-order than random-order trials. In addition, variability of gaze in relation to the first target was smaller than for the second target [$F(1,11) = 8.97$, $P = 0.012$].

Absolute finger error ranged from 11.2 to 14.8 mm, which again is relatively small given a target radius of 9.3 mm. Both absolute and variable errors changed as a function of ISI [absolute: $F(1,11) = 17.75$, $P = 0.001$; variable: $F(1,11) = 10.02$, $P = 0.009$], such that accuracy was significantly higher and less variable with shorter ISI

Fig. 3 Timeline indicating the movement of the eyes and the finger (initiation: *open circle*; completion: *filled circle*). **a** ISI300—fixed order; **b** ISI300—random order; **c** ISI450—fixed order; **d** ISI450—random order. *Vertical dashed lines* T1 and T2 represent the appearance of the first and second target, respectively. The duration of 'gaze anchoring' is indicated by the *red shaded area*. Other dependent variables are highlighted in **b** (*Lat_e* latency eyes to onset of first target, *Lat_f* latency finger to onset of first target, *Lead* eye–hand lead time for first segment, *Fov* foveation time for second target, which is negative here)
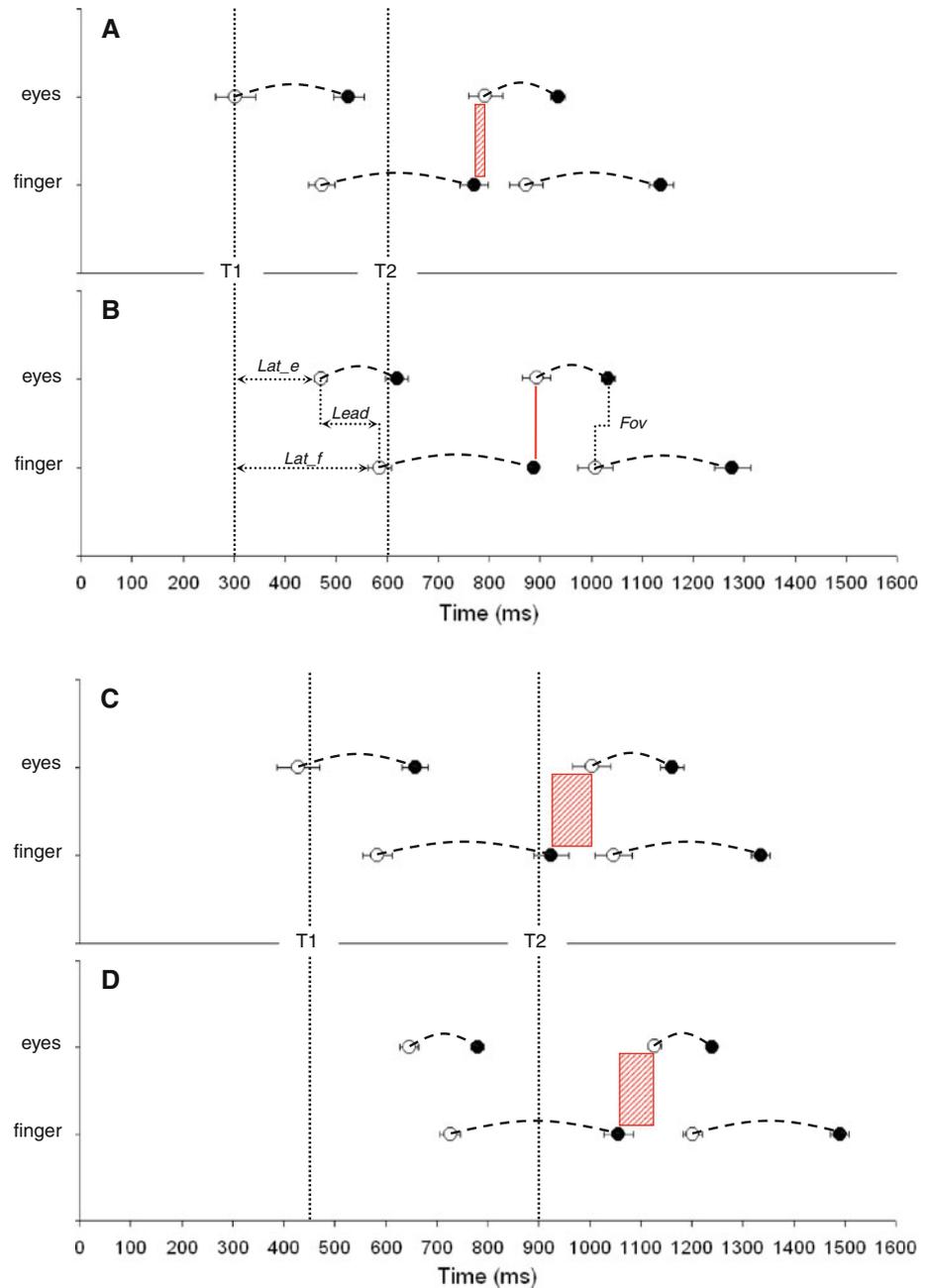
(mean absolute error: 11.6 mm; mean variable error: 2.7 mm) than with longer ISI (mean absolute error: 13.6 mm; mean variable error: 4.1 mm). Still, taking into account the fact that the marker was positioned at the centre of the finger nail, error of this magnitude would have resulted in the finger being placed on the target in both conditions. No other main or interaction effects were found.

Latency of eye and hand (see Table 2; Fig. 3)

Saccadic latency towards the second target was longer than towards the first target [$F(1,11) = 16.70$; $P < 0.001$], but was superseded by a significant target by trial order interaction [$F(1,11) = 11.84$; $P = 0.006$]. The lengthening of saccadic latency between target 1 and target 2 was greater in fixed-order trials compared with random-order trials. In addition, latency to both targets was shorter in fixed-order compared with random-order trials, and in the former was sometimes less than 0 ms for the first target. Trial order also interacted with ISI [$F(1,11) = 21.84$, $P < 0.001$], such that while latency to the first target did not differ with ISI duration, latency to the second target in the ISI450 condition was on average 78 ± 15 ms shorter than in the ISI300 condition.

Table 2 Mean (SE) of eye and finger accuracy (absolute and variable error), latency, movement time, lead time, and foveation time for the first (target 1) and second (target 2) movement segment across conditions

	Fixed ISI300		Random ISI300		Fixed ISI450		Random ISI450	
	Target 1	Target 2	Target 1	Target 2	Target 1	Target 2	Target 1	Target 2
Absolute error eye (°)	2.3 (0.3)	2.3 (0.3)	2.8 (0.6)	3.5 (0.6)	1.5 (0.3)	3.4 (0.4)	2.4 (0.4)	3.6 (0.5)
Absolute error finger (mm)	11.2 (0.5)	10.9 (0.6)	12.1 (1.1)	12.0 (0.8)	13.2 (0.6)	14.0 (0.7)	12.5 (0.9)	14.8 (1.1)
Variable error eye (°)	0.7 (0.2)	0.9 (0.2)	1.3 (0.2)	1.8 (0.4)	0.7 (0.2)	1.1 (0.2)	1.2 (0.3)	1.2 (0.2)
Variable error finger (mm)	2.3 (0.2)	2.4 (0.4)	3.4 (0.4)	2.7 (0.4)	3.3 (0.3)	4.3 (0.7)	3.7 (0.5)	4.9 (1.1)
Latency eye (ms)	3 (39)	193 (34)	170 (13)	292 (28)	−22 (42)	105 (37)	196 (18)	225 (14)
Latency finger (ms)	172 (26)	273 (33)	286 (23)	408 (35)	134 (29)	146 (37)	277 (20)	301 (19)
Movement time eye (ms)	222 (30)	142 (14)	150 (22)	141 (13)	230 (26)	158 (23)	134 (12)	113 (6)
Movement time finger (ms)	299 (28)	264 (24)	302 (10)	268 (35)	340 (35)	288 (19)	330 (29)	288 (18)
Lead time (ms)	165 (42)	76 (20)	113 (23)	112 (16)	150 (25)	36 (16)	79 (20)	73 (14)
Foveation time (ms)	−57 (42)	−66 (9)	−37 (36)	−29 (14)	−80 (24)	−121 (19)	−55 (22)	−40 (16)

For latency of finger onset, there was a significant effect of trial order $[F_{(1,11)} = 33.30, P < 0.001]$, indicating shorter latency for fixed-order trials compared with random-order trials. A significant effect of ISI duration $[F_{(1,11)} = 42.26, P < 0.001]$ and a target by ISI duration interaction $[F_{(1,11)} = 34.632, P < 0.001]$ showed that latency of finger onset to the second target was shorter with a 450 versus 300 ms ISI. Latency to target 1 was similar for the two ISI conditions.

Lead time and foveation time (see Table 2; Fig. 3)

Positive lead times (group mean = 101 ± 15 ms) were observed and indicate that, in general, the eyes preceded the finger movement. However, there was an interaction between trial order and target $[F_{(1,11)} = 32.60; P < 0.001]$. In random-order trials, lead time of the first and second segments of the movement sequence were comparable (96 ± 18 ms and 93 ± 13 ms, respectively), whereas in fixed-order trials, lead time was longer for the first than for the second target. This was a result of saccadic anticipation, which involved a larger reduction in latency of the eyes compared with the finger for the first target. Furthermore, ISI duration had a significant effect on lead time $[F_{(1,11)} = 6.45, P = 0.027]$, with a shorter ISI resulting in a longer lead time.

Despite the fact that eye movement preceded finger movement, the mean target foveation times were negative, which indicates that the finger movement was usually initiated before the eyes foveated the first or second target. Foveation time was shorter for the fixed-order trials (mean: −81 ± 16 ms) than for the random-order trials (mean: −40 ± 14 ms) $[F_{(1,11)} = 13.97, P = 0.003]$. The earlier onset of finger movement relative to the arrival of the eyes

on the target in fixed-order trials was the result of an increase in the movement time of the eye, combined with an eye–finger lead time that remained relatively constant (for target 1) or decreased (for target 2).

Dwell time of eye and hand (see Table 3; Fig. 3)

Trial order did not affect dwell time of the eyes or the finger, but for both effectors, dwell time was increased in the longer compared with shorter ISI $[F_{(1,11)} = 14.10, P < 0.003; F_{(1,11)} = 6.16, P = 0.03]$.

Residual latency (see Table 3; Fig. 3)

The group mean residual latency was positive for all trial types (mean: 48 ± 24 ms) and thus in agreement with a gaze anchoring strategy. However, it is notable that residual latency was relatively short, which suggests that the eye movement to the second target was partially planned during the ongoing finger movement. Two exceptions to this anchoring strategy were observed, and in these participants (1 and 7), residual latency was negative in 77 and 90% of all trials, respectively. ANOVA indicated that the residual latency increased with ISI duration $[F_{(1,11)} = 26.50;$

Table 3 Mean (SE) of eye and finger dwell time and residual latency across conditions

	Fixed ISI300	Random ISI300	Fixed ISI450	Random ISI450
Dwell time eye (ms)	268 (22)	273 (12)	346 (36)	347 (16)
Dwell time hand (ms)	102 (17)	121 (30)	123 (30)	145 (18)
Residual latency (ms)	26 (24)	8 (30)	87 (32)	71 (23)

$P < 0.001$], but there was no significant difference between fixed-order and random-order trials, or higher-order interactions.

To clarify whether a longer residual latency was associated with more accurate and/or overall slower performance, correlations were calculated with total finger error and total response time of the finger, for each condition separately. There was no significant relationship between residual latency and finger accuracy. However, residual latency was significantly correlated with total finger response time in the faster (ISI300) random-trial order condition ($r = 0.635$; $P = 0.03$), and there was a trend towards a significant correlation in the fixed-order trial conditions (ISI300: $r = 0.541$, $P = 0.069$; ISI450: $r = 0.530$, $P = 0.076$). Together, these results provide some indication that shorter residual latency is associated with shorter pointing duration, without affecting accuracy.

Discussion

To clarify the nature and determinants of eye–hand coordination during rapid sequential pointing, the current study examined whether there was an effect of inter-stimulus interval and prior knowledge of target coordinates on measures of timing and performance. In a double-step task, we found that a saccade always preceded the finger movement, but the finger movement was initiated before target foveation, i.e., in the absence of foveal visual feedback or ocular proprioception of the target location. This confirms earlier findings, suggesting that the initial part of pointing movements are planned on the basis of peripheral retinal coordinates and efference commands to the ocular system (Desmurget and Grafton 2000; Prablanc et al. 1979a, b). However, gaze was found to remain 'anchored' to the first target and thus the eyes did not move ahead to the second target before completion of the first finger movement.

Wilmut et al. (2006) suggest that the visuo-motor system has the capacity to overcome delays in processing online feedback in sequential pointing by operating almost exclusively in a feedforward mode. This was based on the finding that eye movements to the second target in a double-step task occurred prior to the arrival of the finger at the first target, thus necessitating temporary storage of both ocular proprioception and efference commands. Contradictory findings indicating gaze 'anchoring' (Neggers and Bekkering 2000; Neggers and Bekkering 2001) have been explained by the absence of need to make a finger movement to a second target. However, the results of the current study suggest a more complementary account. Using a protocol similar to Wilmut et al. (2006), but with longer-duration inter-stimulus intervals (i.e. 250 ms vs. 300 and

450 ms), we found that participants postponed a gaze shift until the finger movement to the same target had been completed. The duration of gaze anchoring (i.e. the time that gaze remained locked to the target after completion of the first finger movement; also referred to here as residual latency) ranged from 8 to 84 ms and increased as a function of inter-stimulus interval (ISI300 = 17 ms, ISI450 = 79 ms). Notably, though, the duration of gaze anchoring found here was relatively short compared with the times reported by Neggers and Bekkering (214–231 ms), who also used considerably longer-duration inter-stimulus intervals (585–607 ms). It would seem, then, that the duration of the inter-stimulus interval is a crucial determinant of the relative timing between eyes and the hand in sequential pointing. According to this perspective, the estimated threshold inducing a transfer from an 'anchoring' strategy to a 'buffering' strategy is in the region of 300 ms.[1]

Prior knowledge of the target coordinates gained from receiving trials in fixed order was found to facilitate anticipatory eye and finger movements, resulting in an overall shorter response time. In addition, eye–finger lead at the start of the sequence was increased in fixed-order compared with random-order trials. This increase in lead time was a result of an asymmetrical reduction in latency of the primary saccade compared with the finger. The implication is that expectancy gained from fixed-order trials primarily affected the oculomotor system, thereby supporting the notion that coupling of eye and hand is not the result of a common central command (Scarchilli and Vercher 1999); such a dependent coupling would lead to constant eye–finger lead times.

Expectation gained via repetition of a specific visuo-motor pattern was not found to impact upon the relationship between timing of eye and finger movements after onset to the first target. Instead, advance knowledge available in fixed-order trials resulted in a reduction in total response time by facilitating the planning and initiation of the eye and finger movement towards the first target (i.e. reduced latency) and by reducing eye–finger lead times relative to the second target. The latter effect also meant that foveation time became more negative and that the eye and finger began to move more in synchrony. A change in the relationship between timing of eye and finger movements after onset to the first target was evident, however, in conditions with shorter ISI duration (300 ms). Here, where both the oculomotor and the manual systems seem to be operating close to maximum capacity, residual latency (i.e.

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[1] It should be acknowledged, however, that this threshold is likely to be individual specific and also influenced by other factors such as expertise. This may be illustrated by the finding that in 2 out of 12 participants the residual latency was negative in a considerable amount of trials (77 and 90%), while in all other participants the prevalence of negative residual latency ranged between 0 and 34%.

the time period during which the two action phases are linked together) was reduced and contributed to an overall reduction in total response time in this rapid sequential movement task,.

The finding that residual latency was unaffected by trial order suggests that the phase during which the two actions of the sequence are directly linked is rather robust to advance knowledge. However, as noted earlier, the duration of gaze anchoring was influenced by the inter-stimulus interval and thus the time pressure on perceptual-motor system. In addition, Rand and Stelmach (2010) recently showed that residual latency was mediated by accuracy demands on the reaching movement such that gaze anchoring was not present when pointing to large targets. The implication is that gaze anchoring is not a prerequisite in sequential aiming tasks. Interestingly, the effects for residual latency were somewhat mirrored in the timing between appearance of the second target and onset of the finger movement towards the first target. For instance, in the random-order ISI300 trials, which had the shortest residual latencies (Fig. 3b), the emergence of the second target roughly coincided with the initiation of the first finger movement. As the interval between these two events gradually increased across the fixed-order ISI300 (Fig. 3a), random-order ISI450 (Fig. 3d) and fixed-order ISI450 (Fig. 3c) conditions, residual latency became longer. These findings are in accordance with the notion that movement of the arm acts as a gaze inhibitor and that the inhibition becomes stronger, the longer the movement is performed in the absence of a distracting, second target. In other words, the early appearance of the second target in the shorter ISI conditions seems to prevent attention from being directed to control of the first finger movement and thereby facilitates a shift in attention towards the second target. This shift or sharing of attentional focus is deemed imperative to prepare a subsequent saccade (Rizzolatti et al. 1987) and, contrary to previous findings (Deubel and Schneider 1996), was not influenced in the present study by advance knowledge of successive targets in a double-step pointing task.

At a neural level, it has been suggested that timing between eyes and upper limb in pointing tasks relies on signal interchange and probably resides in the superior colliculus where signals of the oculomotor and manual control systems converge (Reyes-Puerta et al. 2010; Stuphorn et al. 2000; Werner et al. 1997). Indeed, neuronal activity of the superior colliculus, an area classically linked with gaze fixation (Munoz and Wurtz 1993a, b), is known to be partly modulated by the arm movements involved in reaching (Reyes-Puerta et al. 2010; Stuphorn et al. 1999; Stuphorn et al. 2000; Werner et al. 1997). In this way, arm movement and the correlated 'reach neurons' can facilitate or inhibit gaze shifts by providing excitatory or inhibitory

input to saccadic build-up neurons (Lünenburger et al. 2000). The maintenance of gaze fixation until shortly after completion of the ongoing finger movement (i.e. gaze anchoring) would be consistent with gaze inhibition from reach neurons.

In summary, the present findings suggest that in rapid sequential pointing tasks, the nature of eye–hand coordination is a function of the time pressure resulting from the appearance of the external visual stimuli. When the interval between successive stimuli is short (300 ms vs. 450 ms), and when a subsequent stimulus appears early in the finger movement, the duration of gaze anchoring is decreased. While advance knowledge of the target coordinates gained through fixed repetition of a specific movement configuration allows individuals to anticipate the visual stimuli and reduce the overall response time, it does not affect the temporal coordination between eye movements and pointing. These findings are consistent with the neural coupling of eye and arm movements in the superior colliculus, which appears to act as a locus for signal interchange between the two systems.

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