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Reach endpoint formation during the visuomotor planning of free arm pointing

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Abstract

Volitional motor control generally involves deciding 'where to go' and 'how to go there'. Understanding how these two constituent pieces of motor decision coordinate is an important issue in neuroscience. Although the two processes could be intertwined, they are generally thought to occur in series, whereby visuomotor planning begins with the knowledge of a final hand position to attain. However, daily activities are often compatible with an infinity of final hand positions. The purpose of the present study was to test whether the reach endpoint ('where') is an input of arm motor planning ('how') in such ecological settings. To this end, we considered a free pointing task, namely arm pointing to a long horizontal line, and investigated the formation of the reach endpoint through eye–hand coordination. Although eye movement always preceded hand movement, our results showed that the saccade initiation was delayed by ~ 120 ms on average when the line was being pointed to as compared with a single target dot; the hand reaction time was identical in the two conditions. When the latency of saccade initiation was relatively brief, subjects often performed double, or even triple, saccades before hand movement onset. The number of saccades triggered was found to significantly increase as a function of the primary saccade latency and accuracy. These results suggest that knowledge about the reach endpoint built up gradually along with the arm motor planning process, and that the oculomotor system delayed the primary reach-related saccade in order to gain more information about the final hand position.

Introduction

Volitional motor control usually involves both deciding the goal of an action ('where to go', i.e. a target) and selecting between movements to achieve it ('how to go there', i.e. a trajectory) (Haggard, 2008). Understanding how these constituent pieces of decision-making and motor control coordinate is an important issue in neuroscience (Wolpert & Landy, 2012). The two processes are often thought to occur in series, because the task traditionally consists of reaching to one or a couple of target(s) (Desmurget *et al.*, 1998; Cisek & Kalaska, 2010). During reaching to localised spatial targets or to objects with specific grasping landmarks (Johansson *et al.*, 2001), the central nervous system is left with the degrees-of-freedom problem of selecting one among the many possible movements complying with the identified or selected goal. However, in daily life, goals are not always distinct. Imagine that you attend a cocktail party and that plenty of identical glasses are lined up on a table. Which one would you pick up? Your decision would imply different final hand positions, requiring different body movements. In other words, there are numerous task-equivalent targets. Your brain might handle this problem by first targeting one of the glasses before planning a grasp movement. However, the choice of the targeted glass could depend on the associated limb motion. The purpose of this study was to characterise the visuomotor planning process in such ecological situations.

To this end, we investigated eye–hand coordination during arm pointing toward a long, uniform, horizontal line. The originality of this experimental paradigm is to free the final hand position along one dimension, thereby emphasising both eye and arm motor decision processes. The purpose of the task is nevertheless to bring the hand to some spatial location, i.e. a self-chosen target. For this reason, the terms 'target' and 'reach endpoint' will be used interchangeably without ambiguity throughout this article, even though, strictly speaking, the line constitutes a 'target' in itself. Two extreme hypotheses can be drawn about whether the reach endpoint is a premise or an outcome of the arm motor planning process, as illustrated in Fig. 1.

On the one hand (hypothesis H0), target and movement selection may be serial processes whereby the reach endpoint is decided before the arm trajectory towards this self-chosen target is planned. In this case, three alternatives may characterise this initial decision step occurring before arm motor planning. First, no saccade at all

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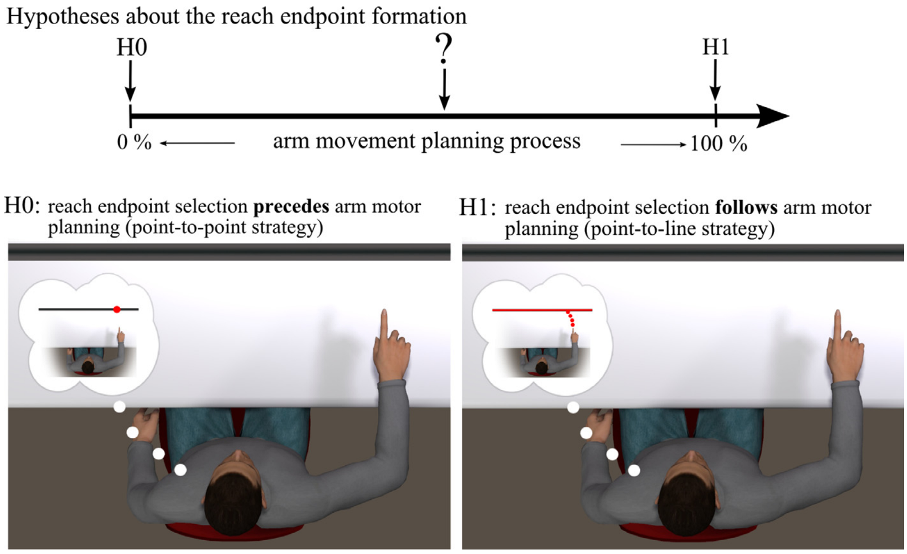


FIG. 1. Illustration of the two extreme hypotheses for reach endpoint formation. In H0 (left), the reach endpoint (i.e. final hand position, in red) is an input of arm movement planning. In H1 (right), the reach endpoint is obtained at the end of the arm motor planning process and derives from the chosen hand path (in red). Alternative hypotheses may exist in between these two extremes.

could be triggered if the subject simply points to the location on the line indicated by the subject's current gaze orientation. Second, one accurate saccade could be triggered as early as in the baseline condition for which a single target dot is displayed if the reach endpoint selection is based on some immediate choice or prior information. Third, several saccades could be triggered if a visual search occurs to compare candidate endpoints and different motor plans, at the price of increasing hand reaction time (RT). On the other hand (hypothesis H1), the reach endpoint may be a by-product of arm motor planning towards the line taken as a whole. In this case, one could predict the occurrence of a delayed saccade, triggered only once the arm motor planning process is completed or, at best, as soon as the upcoming final hand position is accurately known within this process. In particular, the latency and accuracy of saccade initiation could reflect the mechanisms underlying the reach endpoint formation during free arm pointing.

Materials and methods

Participants

Healthy right-handed subjects [17 participants; 10 males; age 27.6 ± 6.6 years (mean ± standard deviation throughout the article), range 21–42 years] volunteered to participate in the experiment. All of them had normal or corrected-to-normal vision. Written informed consent was obtained from each participant in the study, which was approved by the local ethical committee ASL-3 ('Azienda Sanitaria Locale' local health unit), Genoa, and was in accordance with the Helsinki Declaration.

Apparatus

Arm and head motion were recorded by means of a motion capture system (Vicon, Oxford, UK). Ten cameras were used to record the movement at 100 Hz of six retro-reflective markers (diameter, 15 mm), placed at well-defined anatomical locations on the right arm and head (acromial process, humeral lateral condyle, ulnar styloid process, apex of the index finger, and left/right auditory meatus). The eye movements were recorded with electro-oculography (EOG) by using appropriate electrodes and a high-level amplifier to record and amplify the signal (DIGITIMER D360, AC condition). EOG was well suited for our experiment, because only horizontal saccades were involved in the task and because we were primarily interested in the timing (acquisition frequency of 1000 Hz) and the number of saccades, which can be accurately and reliably detected from EOG measurements. Spatial orientation of gaze after the first saccade could nevertheless be estimated by means of a calibration procedure (see below). Note that only the amplitude of a saccade provided reliable information about the eye movement; the absolute value of the EOG signal was not related to an absolute eye-in-head position, owing to the properties of the AC amplifier. For three subjects, surface electromyography (EMG) activity of relevant muscles involved in the task (i.e. anterior/posterior deltoids, triceps, and biceps) was recorded with a wireless system (Aurion, Milan, Italy; acquisition frequency of 1000 Hz). Hand movement onset time was determined with an electronic device (i.e. the release of a pressure button). All analogical signals (EOG, EMG, and button) were synchronised with the 3D kinematic data of the motion capture system.

The stimuli were generated with a MATLAB (Mathworks, Natick, MA, USA) program by the use of PSYCHTOOLBOX (Brainard, 1997; Pelli, 1997). A videoprojector was used to display the stimuli on a large vertical screen (~ 2 × 2 m). The room was dark, and the background of the screen was black once the videoprojector was turned on. The different stimuli were as follows: a single dot (a disc, 20 mm in diameter, referred to as the DOT condition) and a line (i.e. a full-screen-width horizontal line, 20 mm in thickness, referred to as the LINE condition).

Experimental protocol

Participants sat on a chair in front of a large para-frontal screen on which all stimuli were subsequently projected. The screen coordinates were denoted by (x, y), with x being the horizontal axis and y the vertical axis. A calibration phase was first carried out in order to adjust the workspace to the individual characteristics before the real experiment could be started, as explained below.

Workspace calibration

In previous articles about the optimal control for arm movements (Berret *et al.*, 2011a,b), we showed that the final hand position depended on the initial arm position of a subject when reaching to a line, and that relatively large inter-subject variability could be present. Therefore, the experimental setup was adjusted for each subject. First, we ensured that the arm movements were comfortable and performed approximately in a transverse plane. To this end, the heights of the two reference points specifying the subject's starting positions (referred to as Left and Right in the following) and the height of the stimulus displayed on the screen (y_{stim}) were adjusted prior to the experiment (Fig. 3A). The distance between the initial hand position and the screen was 28.6 ± 3.4 cm for Left and 29.3 ± 3.8 cm for Right. We used two starting postures so as to test the robustness of our results and to avoid predictive behaviors. To calibrate the width and location of the workspace on the screen, the subject's nominal reach endpoints during pointing to the line were recorded. To do this, a horizontal line was displayed to the subject, who was then asked to point to it with the right (dominant) arm, alternatively starting from the Left or the Right positions (five trials each). Average reach endpoints were subsequently computed and used to define the two extremities of the workspace (i.e. left and right mean positions on the screen, denoted respectively by $\bar{x}_L$ and $\bar{x}_R$). The center of the workspace, located at coordinate $x_c = (\bar{x}_R + \bar{x}_L)/2$, was then used as the reference fixation point and was displayed to the subject as a green, cross-shaped marker. This calibration phase was important to allow comparison of the visuomotor processes underlying the planning of pointing movements in DOT and LINE with similar initial and final arm postures.

EOG calibration

In order to link EOG measurements to screen coordinates, we divided the workspace into 10 equidistant intervals around the green cross, each interval boundary being notified by a spotlight target. Before the experiment started, subjects were asked to perform a sequence of saccadic eye movements between the green cross and each spotlight target (five on the left of x_c and five on the right; Fig. 2A). A second and identical calibration was performed at the end of the experiment to detect any possible global drift of the EOG signal. With this calibration procedure, the EOG amplitude could be mapped onto the corresponding x-coordinate of the screen (expressed in mm) and vice versa via linear regressions ($R = 0.98 \pm 0.02$, $P < 0.001$ across participants; Fig. 2B). To do this, a mapping from screen coordinates (in pixels) to motion capture system coordinates (in mm) was obtained by asking subjects to put their fingertip marker at three predetermined locations forming a reference frame on the screen. This calibration procedure was crucial to quantify the reliability of the spatial analysis of saccades. The high R-values observed at the beginning and at the end of the experiment for each subject indicated that the relationship between the EOG magnitude of a saccade and the x-coordinate on the screen was strongly linear and that no significant global drift of the EOG signal was observed between the beginning and the end of the experiment. It is worth noting that only the amplitude of saccades was calibrated and reliable, not the instantaneous raw EOG values, owing to the amplifier characteristics. Spatial accuracy (i.e. mean residual error) as inferred during the calibration process was 2.4 ± 1.1 cm across subjects, which corresponded to 4 ± 2% of the workspace width. Additionally, the results obtained in DOT could be used to further account for the spatial accuracy during the experiment, as in this case a target dot was displayed to the subject. Indeed, the gaze direction as inferred from the amplitude of saccades could be compared with the known target position of the dot; we obtained a spatial accuracy of 2.4 ± 1.9 cm across subjects during the task. Saccade endpoints could be converted into degrees via the law of cosines. The head was at a distance of 0.59 ± 0.05 m from the screen. The law of cosines was used because the center of the workspace was not directly (orthogonally) in front of the subject's head, which resulted in a slight asymmetry between the Left and Right conditions (see Results).

Experimental paradigm

At the beginning of each trial, subjects were instructed to position the arm in the Left or Right configuration. A single trial consisted of the following sequence of events, as illustrated in Fig. 3B: (i) subjects looked at a green cross located at the center of the workspace on the screen; (ii) the green cross disappeared after 1.5 s, and this was immediately followed by the appearance of the target stimulus (either DOT or LINE); (iii) subjects executed an arm pointing movement until they stopped on the target (still displayed); (iv) the target disappeared after 1.5 s, and this was immediately followed by the re-appearance of the green cross; and (v) the subjects performed a saccade back to the green cross, without moving the arm. Note that we did not restrict the head motion. The last back-to-center saccade was recorded to compare the actual position of the eye with the actual position of the hand after movement execution. Subjects were asked to make a fast and uncorrected arm movement, without dedicating particular attention to final accuracy. For the Left condition, the horizontal coordinate of the target in DOT could be either $\bar{x}_L$ (i.e. the mean reach endpoint when the line was being pointing to, as obtained during the calibration phase; 12 trials) or x (i.e. a random coordinate within the workspace; 18 trials). Twelve trials were recorded in LINE. The same number of trials were recorded for the Right condition, the only difference being the use of $\bar{x}_R$ instead of $\bar{x}_L$ (i.e. 12 trials for $\bar{x}_R$, 18 for a random x, and 12 for the horizontal line). The 84 trials were presented in a random order to prevent subjects from being able to predict the next type of stimulus (dot or line) and its location (in the case of a dot).

Data analysis

Detection of saccades

Saccades were detected from EOG signals with standard procedures (Baloh *et al.*, 1975; Collewijn *et al.*, 1988; Pettersson *et al.*, 2013). EOG signals were low-pass filtered with zero-phase lag at 30 Hz (Prablanc & Martin, 1992). The procedure to extract saccades was based on the derivative of the EOG signals together with a set of rules. At first, we detected abrupt changes in the EOG signals. Local extremes of the EOG derivative (EOG′) were extracted, and those greater than a given threshold were selected for further analysis (the threshold was two standard deviations of the baseline of the EOG′ signals). These candidate saccades were then subjected to further verifications before being identified as a real saccade: (i) reaching a minimal amplitude according to the precision of our system that was determined during the calibration phase (for the smallest saccades); (ii) lasting for a minimal duration (30 ms) (otherwise it was considered to be an artefact or a false positive) (Pettersson *et al.*, 2013); and (iii) verifying a minimal inter-saccade time (10 ms) corresponding to a refractory period. The onset and final time of the saccades were obtained by descending (for a positive saccade) or ascending (for a negative saccade) along the

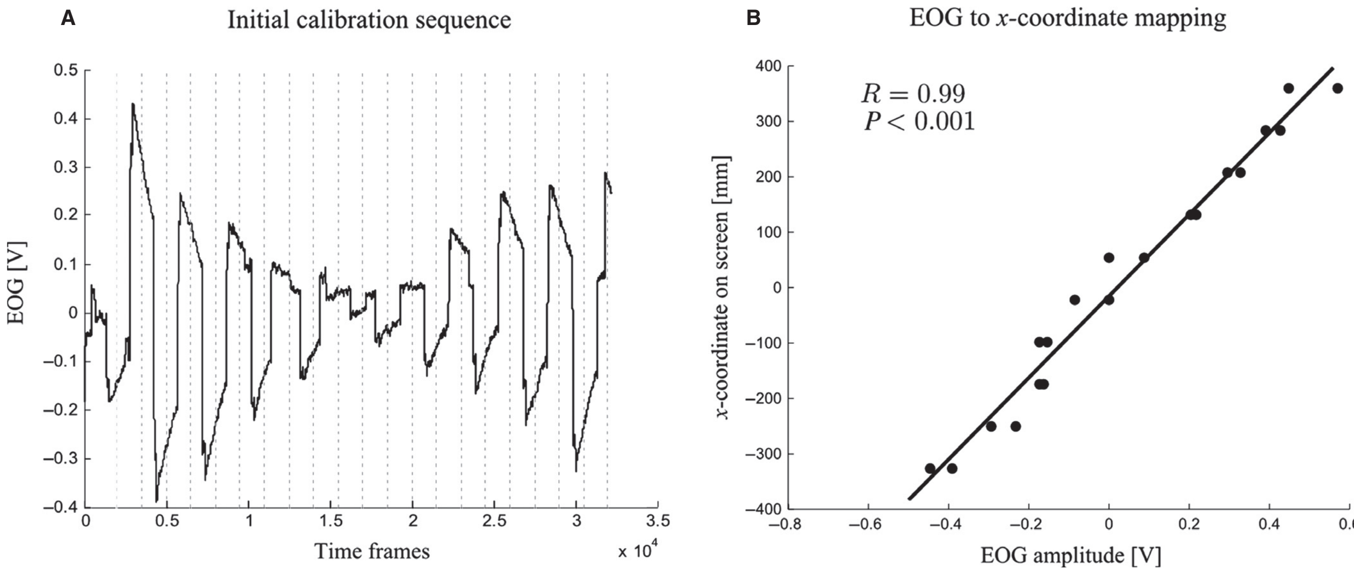


FIG. 2. Calibration procedure to map the EOG saccade amplitude to the *x*-coordinate of the screen. (A) Raw EOG signal for the sequence of 20 saccades for a representative subject: 10 back-and-forth saccades for the left side of the workspace, followed by 10 back-and-forth saccades for the right side. A similar sequence was also recorded at the end of the experiment to detect any possible drift of the EOG signal. (B) Linear regression that mathematically defines the mapping between EOG amplitude and horizontal screen position. The 20 dots correspond to 10 out-center saccades measured at the beginning of the task and 10 similar saccades measured at the end of the experiment. The out-center saccades were not used to form this affine mapping because, during the actual trials, subjects were always starting from the center of the workspace.

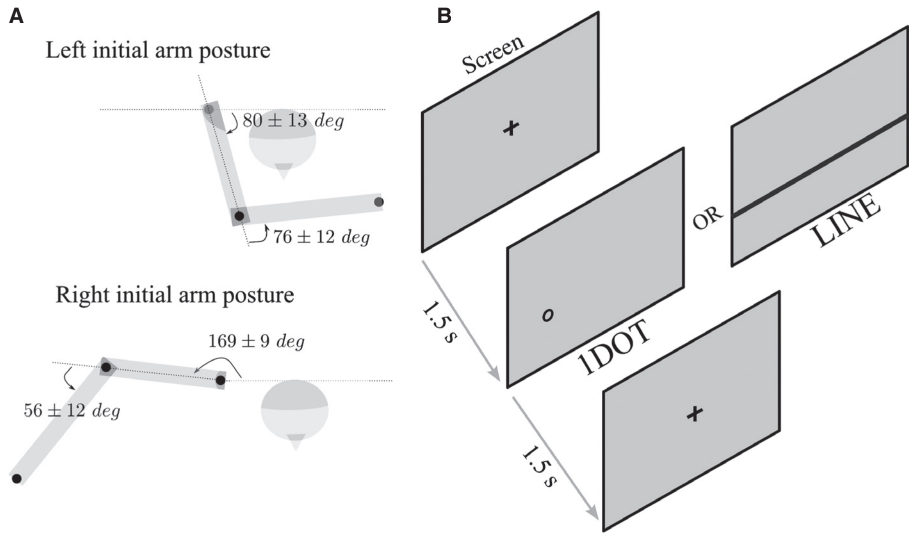


FIG. 3. Illustration of the task. (A) The two initial arm postures. Average joint angles (and standard deviations) are reported across subjects (computed in a transverse plane). (B) Visual stimuli for a single trial. Initially, a central cross is displayed. After 1.5 s, the cross is replaced by the target to reach to (of type either DOT or LINE). After 1.5 s, the arm movement is finished and the central cross is displayed again.

EOG′ signal until the slope was reversed (that is, a change of sign was detected). For all of the trials, a visual inspection was performed *a posteriori* to detect any obvious error in this automatic treatment. When an error was observed, that particular trial was removed from further analyses (< 3% of the trials).

Saccade parameters

Once saccades were identified reliably, they were counted and a number of parameters were computed for each saccade: amplitude, peak velocity (PV), mean velocity (MV), and duration. As we were primarily interested in the arm motor planning period, we only focused on saccades triggered before the hand movement onset. We also considered saccades occurring before any voluntary feedback control of the arm could happen. More precisely, saccades were sought in the time window from the stimulus presentation (t = 0) to the hand movement onset (defining the hand RT and denoted by RT_{hand}), and to extend our analysis, the same procedure was repeated with a delay of 100 ms added after RT_{hand} (i.e. RT_{hand} + 100 ms), which is the order of magnitude for the latency of visuokinesthetic feedback loops (Prablanc & Martin, 1992). Hence, we restricted our analysis to saccades triggered during the hand movement planning process or at least before any sensory feedback about the ongoing hand movement could invoke corrective saccades.

Specific temporal and spatial parameters were also analysed throughout this study. Defining the eye RT (RT_{eye}) as the time between stimulus appearance and the beginning of the first saccade, the primary saccade latency (PSL) index was defined as the ratio RT_{eye}/RT_{hand}. Normalisation of the eye RT was important, because we were only interested in the arm motor planning process, which we assumed to be performed at hand movement onset. This normalisation allowed us to evaluate the latency of saccade initiation with respect to the duration of the arm motor planning process. Another important parameter to examine was the primary saccade accuracy (PSA) index, defined as the ratio between the first saccade amplitude and the 'theoretical' amplitude that would be required to attain the actual reach endpoint within a single saccade (with no head motion). From our results, the accuracy of this index relying on EOG measurements could be estimated as ~ 10%.

Arm movement parameters

Kinematic hand movement parameters were computed with standard methods (e.g. Berret *et al.*, 2011b). Briefly, finger movement onset was defined as the instant at which the linear tangential velocity of the index fingertip exceeded 5% of its peak, and the end of movement as the point at which the same velocity dropped below the 5% threshold (here, we could also use the button pressure release time, and both methods turned out to coincide well). Other parameters were computed: movement duration (MD), PV, MV, index of finger path curvature [IPC = maximum path deviation (Dev)/linear distance], defined as the ratio of Dev from a straight line connecting the initial and final finger positions (linear distance), and curvilinear distance of the finger defined by the integral over time from 0 to MD of the norm of the finger velocity vector. The reach endpoint location was defined as the fingertip marker coordinates at the end of the motion.

Statistical analysis

Statistical analysis was performed to assess the significance of the results. Stimulus and Starting Position were considered as the main sources of variability. In order to evaluate how they affected eye and hand movements, repeated measures ANOVAS with Stimulus (two levels: DOT and LINE) and Starting Position (two levels: Left and Right) as within-subject factors were performed on the dependent parameters. *Post hoc* analyses were conducted with Newman–Keuls tests. Besides ANOVAS, paired *t*-test and correlation analysis were performed when relevant. The significance level was set to 0.05.

Results

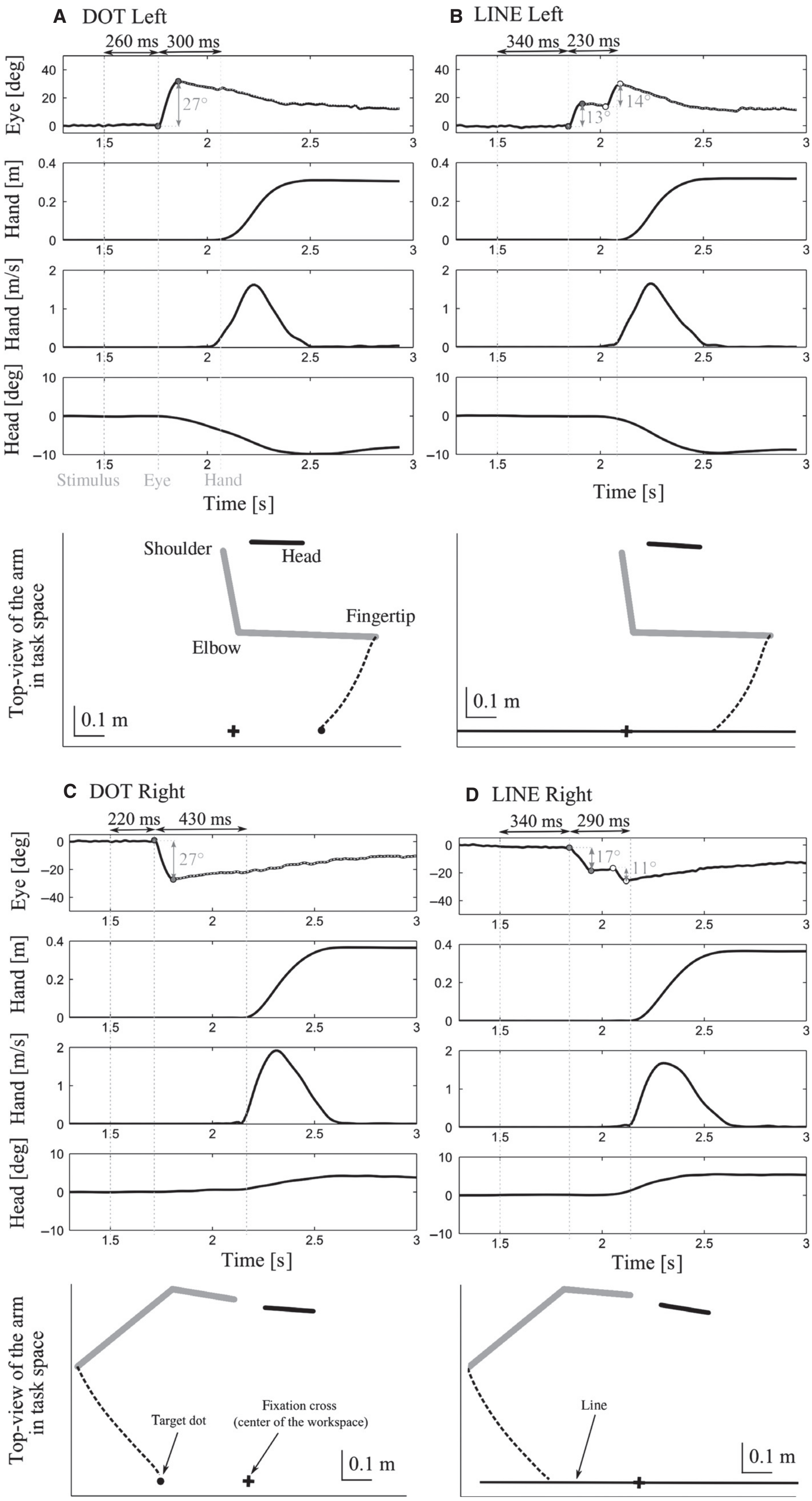
In the following, we mainly compare the two conditions DOT and LINE. In DOT, we restricted our analysis to the trials in which the targets were located at $\bar{x}_L$ or $\bar{x}_R$ for the Left and Right conditions, respectively (see Materials and methods).

Eye–hand coordination patterns differed qualitatively between DOT and LINE

Typical patterns of eye–head–hand coordination for some representative trials of a subject are shown in Fig. 4. A visual examination shows that, when the subject was reaching to the line, the reach endpoint did not correspond to the center of the workspace (location of the cross), although it could have been possible. This final point was self-chosen, in contrast to DOT, in which the reach endpoint was imposed on the subject. The head of the subject moved slightly during the task, owing to the eccentricity of the reach endpoints. However, head rotations did not exceed 10° on average, and, more importantly for this study, the head rotation was very small before the hand movement onset (ranging from 0° to 3°). For the depicted subject, two distinct oculomotor strategies were observed (compare Fig. 4A and C with Fig. 4B and D). In DOT, one saccade was triggered, and seemed to be sufficient for the subject to gaze at the upcoming reach endpoint. In LINE, a series of two saccades was observed wherever the subject's arm was initially positioned on the left or on the right side of the workspace. Note that the saccades always ended before or when the hand started to move in these samples. An increase in the primary saccade latency in LINE as compared with DOT was also clearly visible on these traces. Whereas differences were obvious at the eye level, neither the time-course of hand displacements nor the top view of the hand paths revealed any obvious difference between DOT and LINE in those trials. We present hereafter a more quantitative analysis of these main observations.

Main characteristics of hand trajectories in DOT and LINE

The main parameters of hand kinematics are shown in Table 1. Hand MD depended on both the initial arm posture and the type of stimulus, as indicated by a repeated measures ANOVA ($F_{1,16} = 11.3$, $P < 0.01$). A *post hoc* analysis showed that only DOT Left was not significantly different from LINE Left. Similar observations were made for MV and PV, with usually faster movements in LINE than in DOT. In DOT, the reach endpoints were located at $x = 29.8 \pm 6.7$ cm and $x = -30.7 \pm 7.3$ cm for the Left and Right conditions, respectively (Table 2; $x = 0$ is the center of the workspace in screen coordinates). This was in good agreement with the imposed target coordinates defined during the calibration procedure, which were $x = \pm 30.1 \pm 7.0$ cm across subjects. Accuracy (unsigned constant error) of the pointing was 4 ± 3 mm and 10 ± 12 mm and precision (variable error) was 4 ± 1 mm and 6 ± 1 mm for Left and Right, respectively. For the line, no endpoint was specified in advance, and the choice of the reach endpoint was left to the subject. Hence, because no reference point was present along the *x*-axis in LINE, no horizontal constant error could be computed in this case. The results nevertheless showed that subjects pointed, on average, to preferential locations of the line whose coordinates were $x = 23.6 \pm 8.7$ cm and $x = -22.4 \pm 8.4$ cm for Left and Right, respectively, and that were significantly different from those in DOT (paired *t*-tests, $P < 0.001$). As expected, the variable error increased significantly in LINE as compared with DOT (35 ± 18 mm and 46 ± 25 mm for Left and Right in LINE, $F_{1,16} = 69.44$, $P < 0.01$). This decrease in precision during line pointing agreed with previous findings (Berret *et al.*, 2011b). Note that it was still important for the subjects to control vertical accuracy even in LINE. Vertical accuracy was 7 ± 5 mm/14 ± 7 mm in DOT Left/Right and 8 ± 5 mm/13 ± 7 mm in LINE Left/Right. There was no significant difference between LINE and DOT ($F_{1,16} = 0.001$, $P = 0.98$), even though this constant error was significantly larger in the Right condition ($F_{1,16} = 21.6$, $P < 0.001$). Overall, hand paths were slightly longer in LINE than in DOT, owing to the different reach endpoints, which appeared to be closer to the center of the workspace in the former condition ($F_{1,16} = 28.42$, $P < 0.01$). However, the IPC and the velocity profiles were comparable (slightly curved and bell-shaped; not significantly different), indicating that there was no obvious on-line correction or reach endpoint modification during motor execution.



Hand RTs, but not eye RTs, were identical in DOT and LINE

Hand RT did not vary significantly across conditions ($F_{1,16}$ = 2.05, P = 0.17), and was ~ 0.59 s (Table 3). As subjects were not put under time pressure, these RTs agreed with previous studies (e.g. Gorbet & Sergio, 2009). In the baseline condition (DOT), eye RT was ~ 0.24 s (Table 3), which also agreed with values reported in

FIG. 4. Illustration of the eye–head–hand coordination for a representative subject and trials. (A) In DOT Left, the usual strategy involved one primary ocular saccade triggered before hand movement onset, here 260 ms after stimulus presentation, followed by hand movement onset 360 ms later. Up to RT_{eye}, no head movement was measured. However, the head rotated slightly in all conditions before hand movement onset (RT_{hand}). The eye-in-head position was inferred from EOG measurements and converted into degrees. Note that only the amplitude of a saccade was a reliable measure here. A drift caused by the AC amplifier is visible after the saccade (plotted in dotted lines), but this part of the signal does not correspond to an actual eye movement. (B) In LINE Left, a double saccade strategy is depicted. The first ocular saccade was triggered 230 ms before hand movement onset and 340 ms after stimulus presentation. The stick diagrams at the bottom show that the arm movements were similar in both conditions (e.g. same hand path and reach endpoint). (C and D) Similar observations for the Right condition.

the literature (e.g. Carpenter, 1981). In LINE, at least one saccade was observed before hand movement onset in most trials, even though the line did not provide the subject with any specific salient reach endpoint to look at. Interestingly, the average RT_{eye} values increased significantly as compared with DOT (0.36 ± 0.06 s and 0.41 ± 0.05 s for Left and Right, respectively; $F_{1,16} = 252.7$, $P < 0.001$). Given that RT_{hand} remained approximately constant, the average PSL index was also larger in LINE than in DOT (Table 3; $F_{1,16} = 225.5$, $P < 0.001$). Hence, whereas the first saccade happened relatively early with respect to the hand movement onset in DOT for all subjects, it occurred much later in LINE (but still before hand movement onset). When available, hand RT was also inferred from EMG recordings, in order to take into account electromechanical delays and limb inertia (Fig. 5). As expected, RT_{hand} EMG was smaller than RT_{hand} for the three subjects tested (a delay of 0.13 s on average). Interestingly, however, RT_{eye} was still smaller than RT_{hand} EMG in all conditions. This result was very obvious in DOT (~ 0.29 s on average) and was still present in LINE (~ 0.16 s on average), even though the first saccade was significantly postponed in LINE.

TABLE 1. Hand kinematic parameters

	DOT left	LINE left	DOT right	LINE right
MD (s)	0.89 ± 0.17	0.89 ± 0.17	0.99 ± 0.19	0.93 ± 0.16
MV (m/s)	0.41 ± 0.10	0.45 ± 0.11	0.45 ± 0.11	0.53 ± 0.12
PV (m/s)	1.15 ± 0.30	1.22 ± 0.31	1.20 ± 0.30	1.38 ± 0.36
CD (cm)	35.1 ± 5.5	38.4 ± 7.1	43.4 ± 6.2	48.2 ± 7.0
IPC	0.09 ± 0.02	0.09 ± 0.02	0.10 ± 0.04	0.08 ± 0.03

Average values across all subjects (and standard deviations) of MD, MV, PV, curvilinear distance of the finger (CD), and IPC.

TABLE 2. Comparison of endpoint positions along the *x*-axis in the screen coordinates

	Target position	Reach endpoint	Eye endpoint (first saccade)
DOT left (mm)	301 ± 70	298 ± 67	306 ± 73
DOT left (°)	27 ± 7	26 ± 6	29 ± 8
LINE left (mm)		236 ± 87	134 ± 55
LINE left (°)		21 ± 8	14 ± 6
DOT right (mm)	−301 ± 70	−307 ± 73	−290 ± 64
DOT right (°)	−23 ± 5	−23 ± 5	−19 ± 3
LINE right (mm)		−224 ± 84	−157 ± 53
LINE right (°)		−18 ± 6	−11 ± 3

Average values (across participants) are reported (± standard deviation). First column – theoretical target position defined by the stimulus. Second column – hand reach endpoint as inferred from the motion capture system. Third column – eye endpoint after the first saccade as inferred from the EOG recordings.

Primary saccades were smaller and slower in LINE than in DOT

The PSA was found to be reliable across subjects, as revealed by DOT, in which the actual reach endpoint was not significantly different from the one inferred from EOG measurements (Table 2; $P > 0.15$, paired *t*-tests). This corresponded to primary saccades of magnitude 29 ± 8° and 19 ± 3° for Left and Right, respectively. In contrast, the primary saccade amplitudes were estimated to be only 14 ± 6° and 11 ± 3° in LINE across subjects, revealing that the primary saccade measured in LINE had, on average, approximately half the magnitude of the one measured in DOT. In LINE, the actual reach endpoint differed significantly from the one inferred from the primary saccade amplitude ($P < 0.001$, paired *t*-tests). Because the reach endpoints were also different between DOT and LINE, we further examined the PSA index. As expected, a between-subject analysis showed that the PSA index was close to 1 on average in DOT (1.03 ± 0.07 and 0.96 ± 0.11 for Left and Right, respectively), meaning that gaze orientation after the first saccade tended to match the expected (imposed) one quite accurately. In contrast, in LINE the mean PSA index was significantly lower than 1 (paired *t*-tests, $P < 0.001$; 0.65 ± 0.33 and 0.74 ± 0.26 for Left and Right, respectively), with larger inter-individual variability, suggesting that subjects could use different ocular strategies (see below). The other saccade parameters varied according to the classic main sequence (Bahill *et al.*, 1975). For instance, the average PV of the saccades was 458 ± 89°/s in DOT and 335 ± 85°/s in LINE, which agreed with standard values obtained for horizontal saccades of similar magnitudes (Collewijn *et al.*, 1988).

Multiple saccades were often observed before hand movement onset in LINE but not in DOT

So far, we have focused on the characteristics of the primary saccade. However, as noted above, additional saccades were often observed before hand movement onset, with strong differences between LINE and DOT, as shown in Table 4. The percentage of trials with no, one, two or three saccades was calculated in all conditions (including all trials of all subjects). In DOT, the target stimulus automatically triggered a saccade, so that at least one saccade was always observed in this condition. The most typical

TABLE 3. Hand and eye RTs

	DOT left	LINE left	DOT right	LINE right
RT_{hand} (ms)	580 ± 130	590 ± 70	570 ± 110	610 ± 100
RT_{eye} (ms)	240 ± 30	360 ± 55	240 ± 40	410 ± 50
RT_{eye}/RT_{hand} (%)	41 ± 9	61 ± 11	42 ± 8	67 ± 9

First two rows – absolute RT (mean and standard deviation across subjects). Last row – normalised eye RT defined as the ratio RT_{eye}/RT_{hand}.

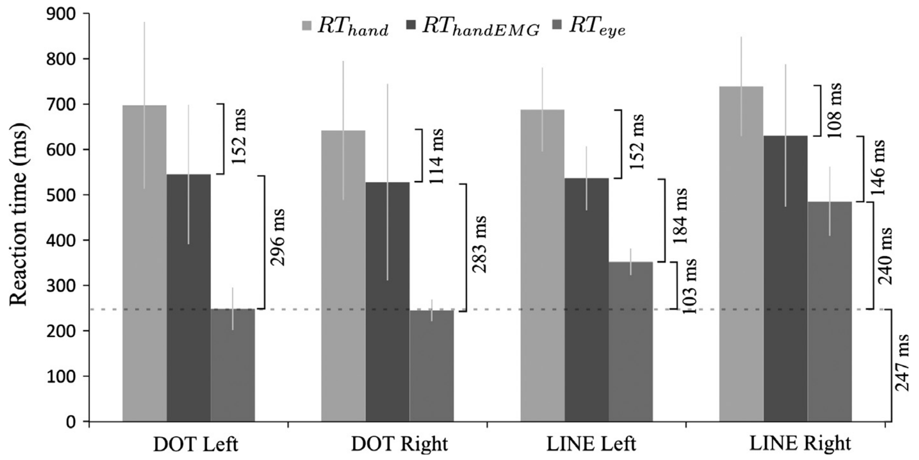


FIG. 5. Hand RT evaluated from kinematics (RT_{hand}) and EMG (RT_{hand}EMG) measurements for all conditions and comparison with eye RT (RT_{eye}). Results are shown for the three subjects tested and for the EMG signal with the smallest RT. Even when electromechanical delay and limb inertia are taken into account, it appears that eye movement still preceded hand movement by > 140 ms in LINE and by > 280 ms in DOT. The delay between the kinematic and muscle RTs was ~ 150 ms and 110 ms for the Left and Right conditions, respectively.

TABLE 4. Proportion of strategies involving no, one, two, three and four saccades triggered before hand movement onset (RT_{hand}) or before RT_{hand} + 100 ms (values in parentheses), for all conditions (counted for all trials and all subjects)

	No saccade	One saccade	Two saccades	Three saccades	Four saccades
DOT left (%)	0 (0)	91 (87)	8 (12)	1 (1)	0 (0)
LINE left (%)	6 (6)	45 (23)	41 (47)	8 (21)	0 (3)
DOT right (%)	0 (0)	95 (86)	5 (13)	0 (1)	0 (0)
LINE right (%)	6 (6)	65 (41)	27 (45)	2 (7)	0 (1)

strategy involved a unique saccade triggered before RT_{hand} (in > 90% of the trials). In LINE, 6% of the trials did not involve any detectable saccade. This was a possible strategy that was actually chosen by only one subject, who, most times, pointed close to the reference fixation point (i.e. the cross location). This strategy did not require any large change of gaze orientation or head rotation, but implied a rather long hand displacement and possibly expensive arm movement (see Berret *et al.*, 2011a,b). For the other 94% of the trials, at least one saccade was detected in LINE. More precisely, 50% of the trials involved a single saccade and > 40% of the trials showed a series of at least two saccades (i.e. multiple saccades). This difference between DOT and LINE was significant (*t*-test, $P < 0.001$). The number of trials involving two saccades increased dramatically (e.g. from 8 to 41% of the trials for Left); the remaining strategies consisted of performing three saccades before the hand started to move. When this analysis was extended to RT_{hand} + 100 ms (i.e. before sensorimotor feedback about the motion could be taken into account by the nervous system to trigger corrective saccades), our observation was still valid, but more saccades were detected in LINE (whereas it had no effect in DOT; Table 4). In this case, a majority of trials involved two or three saccades, and even some trials with four saccades were detected in LINE Left, meaning that the third or fourth saccade could be triggered during or just after hand movement onset. To sum up, single saccade strategies were mainly found for pointing to a target dot, whereas double, triple and even quadruple saccades were observed for pointing to the line.

The number of saccades increased as a function of PSL index and PSA index

We tested the link between the number of saccades and the latency or accuracy of the primary saccades. A between-subject analysis showed a correlation between the mean PSL index and the average number of saccades triggered before hand movement onset, as shown in Fig. 6. In LINE, the rule of thumb was as follows: the shorter the latency to first saccade, the greater the total number of saccades prior to hand movement onset. Note that this trend was also present in DOT, but that the correlation became strong and significant only in LINE. When counting the number of saccades until RT_{hand}, we found correlations of $R = -0.24$ and -0.31 ($P > 0.1$) in DOT, whereas these correlations jumped to $R = -0.79$ and -0.76 in LINE ($P < 0.001$), for Left and Right, respectively. For the latter correlations, we considered the total number of saccades. When we limited our analysis to saccades triggered in the same direction as the first saccade, we observed only slight changes in the above correlations, and the main effect remained ($R = -0.24$ and -0.26 in DOT, $P > 0.1$, and $R = -0.79$ and -0.63 in LINE, $P < 0.001$, for Left and Right, respectively). This is because almost all of the multiple saccade strategies involved a succession of saccades all directed towards the upcoming reach endpoint, and intermediate saccades therefore typically undershot rather than overshot the final endpoint. When the analysis was performed by counting the saccades until RT_{hand} + 100 ms, similar observations were made ($R = -0.19$ and -0.24 in DOT, $P > 0.1$, and $R = -0.77$ and -0.72 in LINE, $P < 0.001$, for Left and Right, respectively).

Figure 7A shows the distribution of the PSL index for all trials at a single-trial level (pooling the Left and Right conditions and all the subjects together). Trials were grouped with respect to the number of saccades triggered before RT_{hand} + 100 ms. One-way ANOVAS with two groups for DOT and four groups for LINE revealed a significant decrease in the PSL index when the number of saccades increased. In DOT, the PSL index varied from 0.44 ± 0.13 to 0.34 ± 0.14 ($F_{1,378} = 12.76$, $P < 0.001$) for single and double saccade strategies, respectively. In LINE, the PSL index changed from 0.77 ± 0.18 to 0.60 ± 0.13 to 0.50 ± 0.11 to 0.42 ± 0.07 for single, double, triple and quadruple saccade strategies, respectively ($F_{3,354} = 54.11$, $P < 0.001$). A *post hoc* analysis of the Scheffé type showed that the PSL indexes for one, two and three saccades were

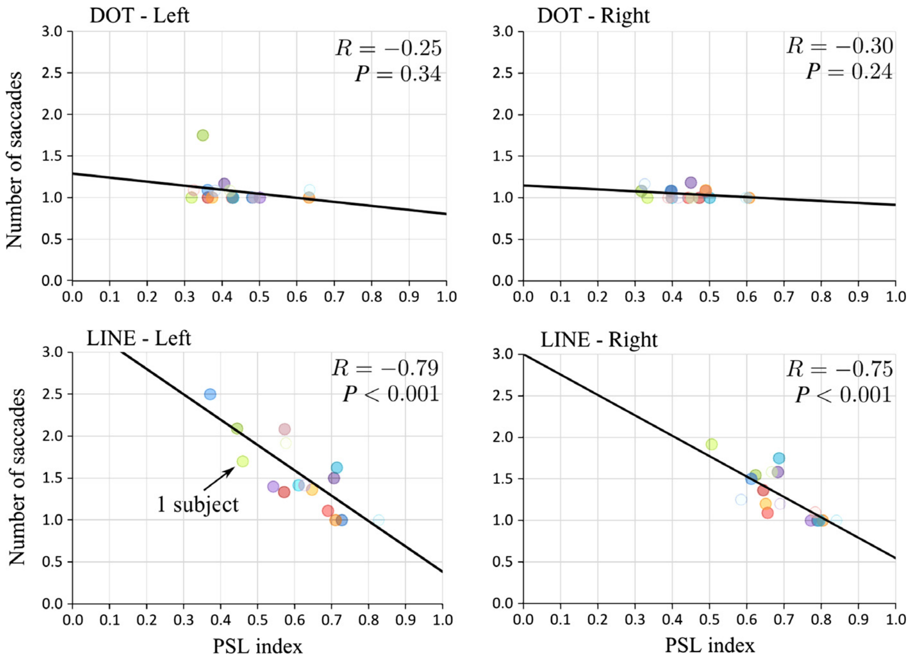


FIG. 6. Correlation between the PSL index and the average total number of saccades before hand movement onset. Each dot represents the average value for a given subject. Correlations are reported for the four conditions (DOT Left, DOT Right, LINE Left, and LINE Right). In DOT, correlations are relatively weak and non-significant. The link between the average PSL index and the average number of saccades is strong and significant in LINE.

significantly different from each other. To investigate the link between the PSA and the number of saccades, we performed a similar analysis for the PSA index. Figure 7B shows the distribution of the PSA index for all of the trials in DOT and LINE separately, depending on the number of saccades triggered within that trial. In DOT, the PSA index was relatively close to 1 on average, whatever the number of saccades (one saccade, 1.00 ± 0.15; two saccades, 0.92 ± 0.26). In particular, this proved that the second saccade sometimes observed in DOT corresponded to a rather small and corrective eye movement. Interestingly, however, the PSA index changed gradually in LINE from 1.00 ± 0.56 to 0.60 ± 0.39 to 0.39 ± 0.33 to 0.42 ± 0.12 for strategies involving one, two, three and four saccades, respectively. ANOVAS revealed that the number of saccades had a significant effect on the PSA index in DOT ($F_{1,378}$ = 5.01, P < 0.05), but that this effect was magnified in LINE ($F_{3,354}$ = 15.62, P < 0.001). A *post hoc* analysis revealed that the PSA indexes with one, two, three or even four saccades were significantly different from each other.

The final hand and eye positions coincided in all conditions

After hand movement completion, the gaze direction and the final hand position matched quite well in all cases. Figure 8 shows the horizontal eye endpoint as a function of the horizontal hand endpoint. High correlations were observed in both DOT and LINE, indicating tight coupling between the final gaze direction and the final hand position. The final eye positions were inferred from the back-to-center saccades that the subjects were asked to perform after the reach movement. A statistical analysis of the ratio between the final eye and hand endpoints showed that it was close to 1 in all conditions (1.09 ± 0.11 and 1.01 ± 0.11 in DOT, and 1.02 ± 0.13 and 1.06 ± 0.19 in LINE, for Left and Right, respectively). Overall, this analysis showed that the eye and the hand eventually pointed to the same location irrespective of the type of visual stimulus ($F_{1,16}$ = 0.04, P = 0.85). Therefore, even though complex eye kinematics could be observed prior to hand movement, the eye and hand endpoints coincided once the hand movement was performed.

Discussion

Despite the lack of predetermined final hand and eye positions during the present free pointing task, we found a classic eye–hand coordination sequence whereby eye movement onset typically preceded hand movement onset (Prablanc *et al.*, 1979; Desmurget *et al.*, 1998). However, the eye–hand coordination pattern was remarkably different. Whereas hand movement latency was unaffected by the type of stimulus, latency to first saccade significantly increased for pointing to a line as compared with a single target dot. In the former condition, multiple saccades were often observed prior to hand movement execution, and their number increased with both the brevity and the inaccuracy of the primary saccade.

This is not the first time that relatively late saccade initiation or multiple saccades have reported in the literature. For example, extended oculomotor procrastination (Carpenter, 1981, 2004) has already been observed in motor learning experiments involving visuomotor reversals (Gorbet & Sergio, 2009; Armstrong *et al.*, 2013). In parallel, multiple saccades have already been observed in developmental studies during saccadic eye movements towards peripheral targets. Whereas multiple saccades are quite common in young children (Salapatek *et al.*, 1980), they are rather rare and hard to elicit in adults (< 5% of the trials) (van Donkelaar *et al.*, 2007). The originality of the present results is the consistent observation of both phenomena in a simple ecological setting. In the following, we discuss these findings by contrasting the present free pointing task (pointing to a line) with the classic reflexive visuomotor mechanism (pointing to a single dot).

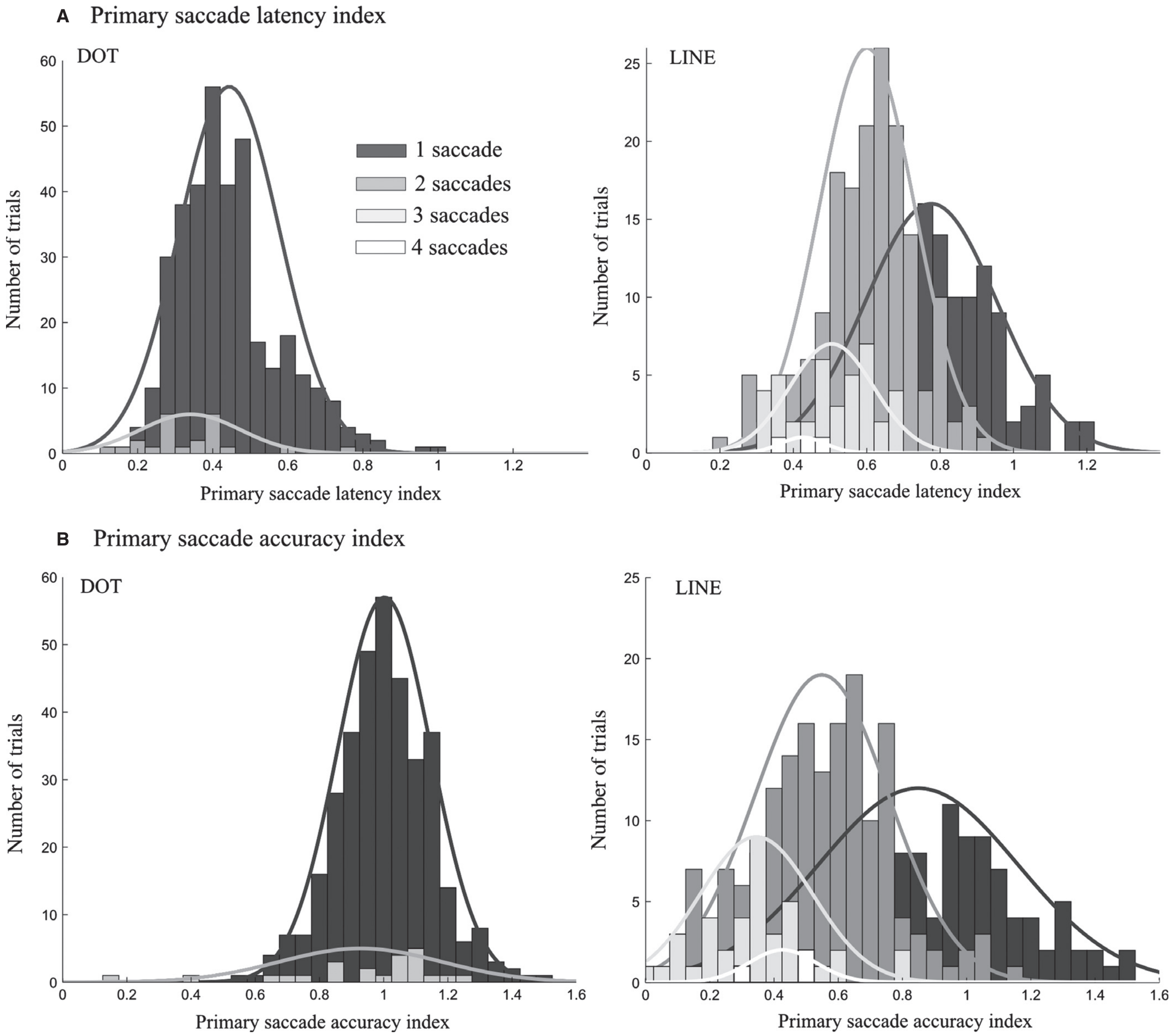


FIG. 7. PSL and PSA on a single-trial basis. (A) Histograms of the PSL index. (B) Histograms of the PSA index. All trials of all subjects were included in the analysis. DOT and LINE were plotted separately. Trials involving one, two, three and four saccades were distinguished to assess the latency and accuracy of the first saccade with respect to the actual hand RT and the actual reach endpoint, respectively. For each number of saccades, the distributions of the PSL and PSA indexes were fitted to Gaussian curves by use of a maximum likelihood estimation to facilitate visualisation. We considered all saccades until RT_{hand} + 100 ms. Overall, significant decreases in both the PSL index and the PSA index as a function of the number of saccades could be observed.

Reach endpoint formation within the arm movement planning process

In most cases, reaching to a line involved at least one saccade preceding hand movement onset (even when EMG signals were considered), which may seem to agree with the idea that behavior results from the choice of a reach endpoint followed by planning of an arm trajectory towards this self-chosen target (hypothesis H0). In this case, free-endpoint reaching would reduce to classic point-to-point reaching. This possibility is, however, ruled out by the observation that hand RT is unaffected by the type of visual stimulus, despite an increase in eye RT. A serial process from target selection to arm trajectory planning should have implied an increase in hand RT approximately similar to the one observed for the eye, as shown, for example, by Armstrong *et al.* (2013). The invariance of hand RT despite multiple saccades before hand movement onset is also incompatible with an overt or covert visual search prior to the hand motor response (Nothdurft *et al.*, 2009). This actually suggests that it is not harder for the central nervous system to plan a movement towards a line than towards a predetermined spotlight target for which a trajectory could be trivially associated. Therefore, a strategy of comparing candidate motor plans before action selection seems also unlikely to occur in the present task (e.g. Cisek & Kalaska, 2002). However, target selection and arm movement planning could still be processed in series, despite the invariance of hand RT, if a reach endpoint could be chosen exactly at stimulus onset. The subject could indeed select a reach endpoint as soon as the stimulus is displayed, based on some immediate choice or prior knowledge

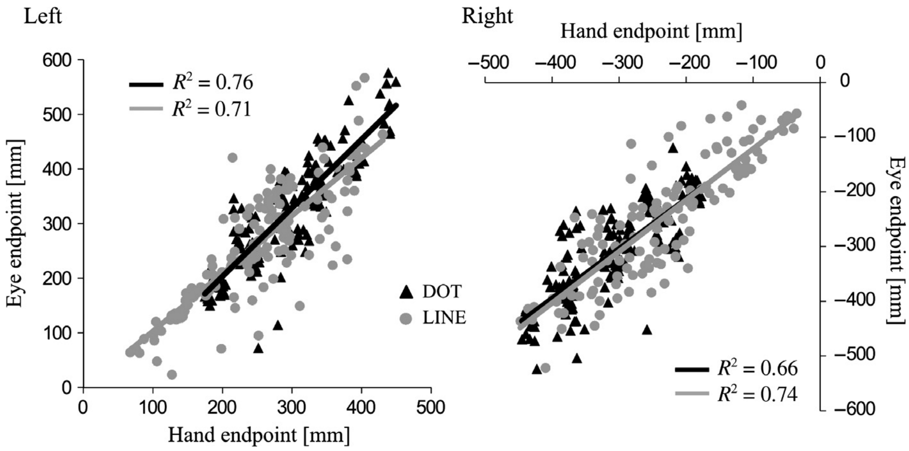


FIG. 8. Correlation analysis for hand and eye endpoints. Eye endpoints (inferred from the final back-to-center saccade) were correlated with the final hand positions. All trials of all subjects were pooled together, but the Left and Right conditions were distinguished. Values are reported in millimeters, and correspond to the final location along the *x*-axis of the screen of either the eye or the hand. There are relatively high correlations irrespective of the type of visual stimulus (DOT or LINE).

about the type of target (i.e. a straight line) and with respect to the initial state of the arm before planning an arm trajectory to it. This possibility, however, disagrees with the unusually long latency of the first saccade when a line is being pointed to, and with the correlation between the degree of ocular procrastination and the relative accuracy of the first oculomotor response [see also van Donkelaar *et al.* (2007)]. Indeed, previous observations showed rather good precision of gaze orientation towards an imagined target position (Guitton *et al.*, 1986).

Rather, invariance of hand RT and delayed saccade initiation may reflect motor planning towards the line taken as a whole, thus suggesting that reach endpoint selection results from the arm movement planning process (hypothesis H1). One explanation is that the initial retinal input could provide the necessary information for the brain to extrapolate the complete target (i.e. a horizontal line) and that this information could be transmitted to the hand motor system. The motor system could then elaborate the reach endpoint at some stage of the arm motor planning process, possibly on the basis of the knowledge of the intended hand trajectory. Previous studies have indeed shown how it is theoretically possible to handle both target indeterminacy and arm movement planning at once (Berret *et al.*, 2011b) by using optimal control and a subjective cost function expressed in terms of minimal energy consumption and maximal joint smoothness (Berret *et al.*, 2011a). In other words, the final hand position could be viewed as the endpoint of the arm trajectory, and not as a spatial constraint for trajectory planning. It is worth distinguishing motor planning from motor execution here, because, during execution, sensorimotor corrections are integrated within an optimal feedback control scheme (Todorov & Jordan, 2002). This is known to account partly for the variability of the reach endpoint during actual movement execution in LINE, owing to the minimal intervention principle and the size of the target (Nashed *et al.*, 2012). In the present work, we instead focused on reach endpoint formation within the planning process.

Are saccades driven by endogenous processes related to arm movement planning?

Ocular saccades were typically triggered after ~ 240 ms with a single dot, whereas saccade initiation occurred > 120 ms later, on average, with the line. The origin of endogenous saccades may be inferred from the presence of multiple saccade strategies before hand movement onset. Note that 'endogenous' refers here to volitional goal selection, in contrast to other 'endogenous' orienting behaviors that classically correspond to the response to an external visual cue predicting a target location [see Corbetta & Shulman (2002) for a review]. Several saccades were often triggered to anchor the gaze onto the upcoming reach endpoint, as though an 'error-correction' process occurred before arm movement execution. Nevertheless, because there was no prescribed target point on the line, such an iterative correction process cannot occur unless a reach endpoint is defined by the subject. Interestingly, these additional saccades did not delay hand RT, suggesting that they occur along with the arm motor planning process. The link between the latency and accuracy of the primary saccade and the number of saccades further supports a possible flow of information from the hand to the eye motor systems during this process. More precisely, this suggests that the number of saccades depends on the degree of completion of the arm motor planning process. We speculate that a single (but delayed) saccade is possible only when the arm motor planning process is completed (see H1, Fig. 1). Thus, saccade latency would reflect the neural computations associated with the selection of the hand trajectory and, as a by-product, the reach endpoint. Our results additionally indicate that knowledge about the reach endpoint accumulates through time. Thus, premature eye movement in the course of the arm motor planning process would lead to inaccurate saccades with respect to the actual reach endpoint that would, however, be complemented when novel information becomes available. In this context, the increase in the number of saccades with respect to the first saccade latency and accuracy would reflect the progressive refining of the reach plan for deciding what hand trajectory and thus what reach endpoint are the most appropriate for the task. The benefit of relatively premature saccades remains to be elucidated, but an explanation might be related to pointing accuracy (which was task-relevant in the vertical direction) or to subjects' risk aversion leading to a quick check of task feasibility prior to hand movement execution.

Possible neural substrate for the present free arm pointing task

The primate cortical networks involved in visually guided arm reaching have been extensively investigated in tasks involving one or multiple target dots, but not for a line. Thus, we may only speculate on the neural substrate involved in pointing to a line. The neural events associated with visually guided reaching always start with an image on the retina and end with impulses to the arm muscles; in between these, a reach plan is formed (Andersen & Cui, 2009). During reaching to a salient target dot, a fast oculomotor response using a visual map and direct pathways from the retina to the superior colliculus is elicited (Munoz *et al.*, 1991). Such a rapid visual response cannot occur during pointing to a line, owing to the target indeterminacy. However, the functions of the superior colliculus are not restricted to oculomotor control, but also contribute to the sensorimotor control of arm movements (Werner, 1993; Lünenburger *et al.*, 2001; Krauzlis *et al.*, 2004; Linzenbold & Himmelbach, 2012). Thus, reach-related saccades could be elicited by other brain areas linked to the arm motor system, which could broadcast to the superior colliculus information related to the upcoming reach endpoint.

Decision-making for the reach endpoint could involve the reward-related circuitry if one assumes that target indeterminacy is resolved during the arm movement planning process based on the cost of the associated limb trajectory (Berret *et al.*, 2011b; Wolpert & Landy, 2012). Here, the cost of an arm trajectory could represent an intrinsic affordance instead of an extrinsic motivation (e.g. food or money). Hence, the dopaminergic system originating in the substantia nigra and ventral tegmental area and projecting to the prefrontal cortex and basal ganglia (Haber, 2003) might play an important role in the formation of an optimal reach endpoint. The parietal reach region in the posterior parietal cortex could then be activated to shift the visual attention towards the predicted reach endpoint in eye-centered coordinates (Andersen *et al.*, 1997; Batista *et al.*, 1999; Buneo *et al.*, 2002; Scherberger & Andersen, 2007). Thus, in contrast to the fast dorsal route from the occipital visual cortex to the motor cortex that is activated during pointing to a salient spotlight (Caminiti *et al.*, 1999), the present free pointing could involve this broader putative circuitry that follows indirect pathways but may account for the observed oculomotor procrastination and multiple saccades.

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Abbreviations

EMG, electromyography; EOG, electro-oculography; IPC, index of finger path curvature; MD, movement duration; MV, mean velocity; PSA, primary saccade accuracy; PSL, primary saccade latency; PV, peak velocity; RT, reaction time.

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