Gaze Affects Pointing Toward Remembered Visual Targets After a Self-Initiated Step

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Admiraal, M. A., N.L.W. Keijsers, and C.C.A.M. Gielen. Gaze affects pointing toward remembered visual targets after a self-initiated step. J Neurophysiol 92: 2380–2393, 2004. First published June 9, 2004; 10.1152/jn.01046.2003. We have investigated pointing movements toward remembered targets after an intervening self-generated body movement. We tested to what extent visual information about the environment or finger position is used in updating target position relative to the body after a step and whether gaze plays a role in the accuracy of the pointing movement. Subjects were tested in three visual conditions: complete darkness (DARK), complete darkness with visual feedback of the finger (FINGER), and with vision of a well-defined environment and with feedback of the finger (FRAME). Pointing accuracy was rather poor in the FINGER and DARK conditions, which did not provide vision of the environment. Constant pointing errors were mainly in the direction of the step and ranged from about 10 to 20 cm. Differences between binocular fixation and target position were often related to the step size and direction. At the beginning of the trial, when the target was visible, fixation was on target. After target extinction, fixation moved away from the target relative to the subject. The variability in the pointing positions appeared to be related to the variable errors in fixation, and the co-variance increases during the delay period after the step, reaching a highly significant value at the time of pointing. The significant co-variance between fixation position and pointing is not the result of a mutual dependence on the step, since we corrected for any direct contributions of the step in both signals. We conclude that the co-variance between fixation and pointing position reflects 1) a common command signal for gaze and arm movements and 2) an effect of fixation on pointing accuracy at the time of pointing.

INTRODUCTION

Reaching for nearby objects requires only an arm movement, which brings the hand to the object. However, when an object is at a distance that exceeds the length of the arm, a movement of the whole body or a few steps may be needed to reach the object. In such a case, the internal representation of target position relative to the subject must be updated for the movement of the body to preserve a correct representation of the target position relative to the subject. If the pointing movement is made toward a remembered visual target and the body movement is made in total darkness, the task is even more complex, since the internal representation of object position relative to the body has to be updated for the body displacement without any visual feedback. Moreover, incorporating egomotion to make the proper hand movement requires that the subject adequately combines egocentric and allocentric information about target position and egomotion displacement.

The updating of a target position for a body movement has been addressed by several studies before. For example, Medendorp et al. (1999) investigated the accuracy of pointing movements to a remembered visual target after a step and the frames of reference that are involved in such a task. Their main conclusion was that subjects underestimate the size of the step, leading to systematic errors in reaching to the remembered targets. Based on the observed errors in reaching after a step, they concluded that the underestimation of the step was better described in Cartesian coordinates than in egocentric coordinates.

These results raise many questions regarding the underlying mechanisms for pointing. First of all, the study by Medendorp et al. (1999) did not measure eye movements. Since the accuracy of pointing depends on fixation (Henriques et al. 1998), it is not clear whether errors were due to errors in fixation to the remembered target during the delay period between stimulus presentation and pointing or whether pointing errors are due to errors in the updating of target position relative to the subject during and after the step. Moreover, a firm conclusion regarding the use of egocentric versus world coordinates requires that subjects are tested in conditions with various feedback conditions. We will elaborate on these questions in more detail below.

The issue of accuracy of fixation during egomotion has been studied from a different perspective by many studies on gaze control. Most of these studies investigated the role of the visual and vestibular system on gaze in subjects while they were rotated or translated passively (see e.g., Harris et al. 2000; Paige et al. 1998). Only a few studies have investigated gaze control in subjects who made active movements. During active body motion, visual, vestibular, proprioceptive information, and possibly, corollary discharges are available to assist the control of gaze for target fixation.

In a recent study, Medendorp et al. (2002) measured the quality of gaze control in subjects during head translations in complete darkness while subjects were instructed to fixate a visual or remembered visual target. In the latter condition, the gain of the required changes in gaze—necessary to fixate the target—decreased, especially for near targets (e.g., 20 cm in front of the subject). This indicates that fixation position does not always match the real position of the remembered target during active movements in the dark.

These results on gaze control are relevant in the context of reaching to remembered visual targets, since several studies (e.g., Henriques et al. 1998; Van Donkelaar and Staub 2000)

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have shown that the accuracy of reaching to a remembered target depends on gaze direction. In addition, Flanders et al. (1999) have indicated a relationship between reaching and head orientation during egomotion. These authors measured head orientation (not eye movements!) during a reach that included a step and reported that the reaching errors were related to the variability in the orientation of the head. Based on these findings, Flanders and colleagues suggested that the orientation of the head might serve as a reference for the control of arm movements. In a recent study on binocular fixation during reaching toward remembered visual targets without a step, we have shown that binocular fixation, resulting from both the head orientation in space and the eye orientation in the head, affects the accuracy of reaching movements (Admiraal et al. 2003).

With this information in mind, we can define several hypotheses regarding the control of pointing and gaze to remembered visual targets and their interaction. A common input signal (i.e., visual information about target position) might provide input both to the oculomotor system to direct gaze to the remembered target and to the motor system to bring the hand to the remembered target. Any errors in this common input signal should cause a co-variance in gaze and pointing accuracy. An alternative hypothesis, that gaze would affect the accuracy of pointing, would also cause a co-variance between position of gaze and pointing. However, we can distinguish between these two hypotheses, since gaze can change in the delay period. If gaze changes during the delay period after offset of the visual target (i.e., when the common input does not change any more), the co-variance between gaze and pointing due to a common input should decrease after target offset. However, if gaze affects pointing, changes in gaze in the delay period should give rise to a gradual increase of co-variance in the period from target onset until the pointing movement. A third alternative could be that the stored target position is incorrectly updated during the step. In that case, errors in stored target position relative to the body might increase in the delay period and will affect both gaze and pointing. We can discriminate between the hypothesis of a co-variance between gaze and pointing due to the step and the hypothesis, that gaze affects pointing, by subtracting any co-variance of gaze and pointing signal with the step signal from gaze and pointing. Any co-variance that is left after correcting for any co-variance by the step has to be due to an effect of gaze on pointing or the other way around.

Previous studies have shown that visual information of the environment may affect the perception of self-motion (Harris et al. 2000; Panerai et al. 2002; Philbeck 2000) and that vision of the environment, along with information from the vestibular system, helps the CNS to accurately direct gaze. Furthermore, visual feedback of the finger was shown to influence reaching accuracy (McIntyre et al. 1998). To investigate the various relevant frames of reference that are involved in pointing to a remembered visual target after a step, we have tested subjects in three visual feedback conditions: 1) DARK, without any visual feedback at any time; 2) FINGER, with visual feedback of the finger position during reaching; and 3) FRAME, with a visible environment and with visual feedback about finger position during the step and the pointing movement. In the DARK condition, subjects have to store the target position relative to the subject, and they have to incorporate the step using proprioceptive information, vestibular information, or efference copies to update the remembered target position relative to the subject after the step. In the FRAME condition, subjects may be less dependent on updating of target position relative to the subject by using proprioceptive or vestibular information or efference copies, since they can remember the target position relative to the external visual environment. Therefore we expect that pointing errors will be much smaller in the FRAME condition than in the DARK condition if errors in pointing after the step are due to underestimation of the step, as suggested by Medendorp et al. (1999). Since an illuminated environment might provide enough light to make the finger visible to the subject, the FRAME condition might differ from the DARK condition in two aspects: the visible environment and the visible finger. To investigate the effect of vision of the finger, we included the FINGER condition. Since visual information is more accurate than proprioceptive information (Van Beers et al. 2002), differences in pointing accuracy in the DARK and FINGER condition reflect an effect of visual information of finger position on pointing accuracy.

In summary, the aim of this study was to investigate the updating of a remembered target position for egomotion. Since previous studies have suggested that errors in pointing after a step are due to underestimation of the step size, the first aim of this study was to investigate how the constant and variable errors of pointing depend on the size of a step in conditions of variable visual feedback. Second, there is evidence that deviations of binocular fixation from the target position affect the accuracy of pointing (see e.g., Henriques et al. 1998). Therefore the second aim of this study was to measure gaze during and after the step and to explore whether and how the variable error in pointing co-varies with the change of gaze in time. Since gaze changes in time, we tested whether the co-variance between fixation and pointing, if any, is strongest in the delay period near target offset or near pointing.

**Methods**

Six subjects (aged 21–49 yr) participated in this study. All subjects had normal or corrected to normal vision, and none of the subjects had any known history of neurological, sensory, or motor disorders. All subjects were right handed, except for subject MA. All subjects performed the pointing movements with the right arm. Two subjects (MA and SG) were familiar with the aim of this study. Their results were not different from those of the other subjects. The experimental protocol was approved by the Medical Ethical Committee of the University of Nijmegen, and all subjects gave informed consent before the experiment.

**Experimental paradigm**

All experiments were performed in a completely dark room, and subjects were tested in three visual feedback conditions: pointing to a remembered visual target in complete darkness (DARK), pointing with visual feedback of finger position by means of a red light emitting diode (LED) on the tip of the index finger which was visible at all times (FINGER), and pointing with a finger led and in the presence of an illuminated cubic frame of 90 × 90 × 90 cm$^3$ (FRAME). This frame formed a well-defined visual environment by means of illuminated optic fibers along its edges (see Admiraal et al. 2003). In this study, we shortened the length of the lower optic fiber at the right side of the cubic frame to avoid collision of the subject with the frame during the step. For symmetry, we also shortened the lower optic fiber at the left side of the cubic frame.
Three targets were used in the experiments, which were located within the cubic frame (see Fig. 1). One (central) target was positioned 15 cm above, 15 cm to the right, and 50 cm in front of the center of the cube’s back plane. The other two targets (targets 2 and 3) were positioned 25 cm to the left and 25 cm behind the central target, respectively. The most distant target lay about 20 cm in front of the back plane of the cubic frame. The number of targets had to be restricted to three to keep the duration of the experiment under 45 min. The 45-min period is roughly the limit to comfortably wear the search coils, which were used to measure eye movements.

Before each trial, subjects positioned their feet in a L-shaped obstacle, which was attached to the floor. This certified a unique and reproducible starting position of the subject for each trial. The subject’s hand was relaxed, with the arm pointing downward along the body. Each trial started with the onset of one of the three target LEDs, which were used to measure eye movements.

Immediately after disappearance of the target, the frame with targets was canted away, denying any visual or tactile feedback during pointing. The frame with targets was rotated downward along a horizontal axis by \( \sim 135^\circ \), bringing it behind the back-plane of the cubic frame and making the targets invisible to the subject even when the luminous cubic frame was on. Subjects were instructed to make a leftward step of about 50 cm immediately after target offset, which would bring the subject’s cyclopean eye at a distance of about 25 cm in front of the position halfway between targets 1 and 2. Since different subjects made steps of different sizes (range, \( \sim 10 \) cm), we positioned the L-shape obstacle for each subject individually, such that each subject would end at the intended position after stepping their average step size.

Usually subjects started to make a step about 500 ms after target offset, which provided enough time to remove the targets and prevented any chance of hitting the frame during the step. Two seconds after target disappearance, an auditory signal cued the subject to start the movement by placing the index finger at the remembered target position. Subjects were instructed to simply lift the arm and to keep the tip of the index finger at the pointing position for at least one-half of a second. Then subjects returned to the starting position to prepare for the next trial.

Each feedback condition was tested in two blocks with 20 trials each. All three targets appeared in a quasi-randomized order in each block, which resulted in \( \geq 13 \) trials per target. Blocks with different visual feedback conditions were presented in randomized order. A block of 20 trials typically lasted about 3 min, and after each block, the room lights were switched on for about 1 min to avoid dark adaptation. Before the experiment, one block of test trials was run to familiarize the subject with the procedure.

**Experimental setup**

The position of various segments of the subject’s body and the position of the targets were measured with an OPTOTRAK 3020 system (Northern Digital), which measures the three-dimensional position of infrared-light-emitting-diodes (IREDs) with a resolution better than 0.2 mm within a range of about 1.5 m\(^3\) (see Admiraal et al. 2003). The positions of IREDs were measured with a sampling frequency of 100 Hz.

IREDs were placed on the subject’s shoulder (acromion) and elbow (epicondylus lateralis). The position of the tip of the index finger was measured by means of an IRED attached on a thimble on the index finger. This thimble also contained a visible red LED that provided the subject with visual feedback of finger position in the FINGER and FRAME conditions. During the experiment, the subjects wore a helmet with six IREDs, which were configured such that the positions of at least three of them were visible for the OPTOTRAK system at all possible head orientations. This was necessary to calculate three-dimensional head location and orientation at all times.

At the beginning of the experiment, we asked subjects to orient their head such that all IREDs on the helmet were visible to the OPTOTRAK camera. We then held an IRED at both of the subject’s closed eyes and measured the position of the two eyes relative to the IREDs on the helmet. With this calibration, we could derive the position of the eyes in space at any time during the experiment from the orientation and location of the helmet in space, even when the subject was facing away from the OPTOTRAK system. We made sure that the orientation of the helmet on the subject’s head did not change throughout the experiment.

Binocular eye orientation was measured using the scleral search coil technique (Collewijn et al. 1975) in a large magnetic field system (Remnel Laboratories). This system consists of a cubic frame of welded aluminum of \( 3 \times 3 \times 3 \) m\(^3\), which produced three orthogonal magnetic fields at frequencies of 48, 60, and 80 kHz. Subjects were tested as close as possible to the center of the large magnetic field system.

During each trial, subjects performed a step, and therefore, their position relative to the large magnetic field varied. To correct for
changes in the eye-coil signals due to small inhomogeneities of the magnetic field within the range of the step, we performed two calibrations of the eye coil signals: one at the location where subjects stood before the step, and one approximately at the location where they arrived after the step. During the calibration procedures, subjects fixated a series of red leds attached to a board at a distance of 75 cm in front of the subject, which resulted in a calibration range from about $-40^\circ$ to $+40^\circ$ in both elevation and azimuth (for the full calibration procedure; see Adriaal et al. 2003). For each eye, the two-dimen- sional calibration errors—defined as twice the SD of the data relative to the calibration fit—were typically about 0.5° in azimuth and $1^\circ$ in elevation on average; resolution was $<0.04^\circ$. The errors in three- dimensional fixation position within the target range tested here were on average about 0.6° and $1.1^\circ$ in azimuth and elevation, respectively, and 3 cm in radial distance from the cyclopean eye. Coil signals were sampled at 500 Hz. In off-line analyses, the coil signals were re- sampled at 100 Hz (same sample frequency as the OPTOTRAK system) by cubic spline interpolation.

**Data analysis**

We define pointing position as the position of the red on the tip of the index finger at the end of the pointing movement toward the target. We distinguish between two types of pointing errors: the constant error, which is the distance between the led position of a target and the average of all pointing positions toward that target, and the variable error, which reflects the distribution of the pointing positions toward a target relative to the average pointing position to that target. The distribution of the pointing positions for target $i$ is described by the three-dimensional co-variance matrix $S_i$:

$$S_i = \frac{1}{n - 1} \sum_{j=1}^{n} (\mathbf{p}_i - \bar{\mathbf{p}})(\mathbf{p}_i - \bar{\mathbf{p}})^T$$

where $n$ is the number of trials to target $i$ and $\mathbf{p}_i[r] = p_i^r[r] - \bar{\mathbf{p}}^r$ is the deviation of the finger position in trial $j$ to target $i$ relative to the mean pointing position $\bar{\mathbf{p}}^r$ to target $i$. The three orthogonal eigenvectors of the co-variance matrix $S_i$ describe the main axes of the orientations of the variable error. The corresponding eigenvalues of the matrix give the size of the variable error in the directions of the eigenvectors. These eigen- values of the co-variance matrix $S_i$ can be scaled to compute the limits that contain 95% of the data (see McIntyre et al. 1997). If one or two pointing positions deviated $>3$ SD from the ellipsoid fitted to the pointing positions, we left out these pointing positions and derived the co-variance matrix again. Due to this rejection procedure, $<3\%$ of the data were not incorporated in further analyses.

We tested whether variability in the pointing position was corre- lated to variability in the step. When the co-variance between pointing position and the step was significant, we tested to what extent the variability in pointing positions could be explained by the variability in the step size, by fitting a linear regression, minimizing the quadratic error $\sum_i (\varepsilon_i)^2$ in

$$\mathbf{p}_i = \tau \cdot \mathbf{s}_i + \varepsilon_i$$

where $\mathbf{\sigma}_i = \mathbf{s}_i - \mathbf{s}^{-1}$ is the deviation of the step in trial $j$ relative to the mean step $\bar{s}$ for pointing to target $i$. Since, by the above definitions, $\mathbf{\sigma}_i$ and $\mathbf{\sigma}_j$ have mean values equal to zero, $\varepsilon_i$ represents Gaussian noise with mean value zero. The weight $\tau$ corresponds to the slope of the linear regression. In the analysis to investigate any relation between gaze and pointing except for a mutual correlation by step size, the step’s contribution $\tau \cdot \mathbf{\sigma}_j$ was subtracted from the pointing position data $\mathbf{p}_i$. By doing so we corrected the pointing positions for any direct effect of the step’s variability. The same was done to correct gaze for the influence of the step’s variability, when gaze showed a significant co-variance with the step. A $\chi^2$ test showed that second- or higher-order terms did not result in a significantly better description (taken into account the number of degrees of freedom and the uncertainty of the higher order fit parameters; see RESULTS).

Although subjects were rather consistent in the timing of their stepping, slight differences in onset, duration, and extent of the step were observed. For each trial, the velocity profile was fit by a normal distribution centered around the time of peak velocity as a bell-shaped approximation of the velocity profile. The onset and offset of the step were derived from this fit, as the moments in time, when the velocity exceeded a threshold of $e^{-(t/3.75^2)}$ times the peak velocity, which corresponds to positions at 3.75 SD of the normal distribution.

For an accurate estimate of the average trajectory of the binocular fixation position during the step, the gaze position data during the steps were resampled onto 300 samples between onset and offset of the step, using cubic spline interpolation. The average trajectory of fixation position in time is then derived from all time-resampled trajectories.

To calculate the co-variance between pointing position and fixation position, we focused on the interval from the end of the step until the time when the index finger had reached the pointing position. To derive the average behavior of the fixation position during intervals that were different in length for different trials, we stretched the fixation data in each such interval onto 300 samples, as explained above. The co-variance between fixation position and pointing position was derived between the resampled fixation data and the corre- sponding pointing position for that trial for each sample $i$ (with $i$ between 1 and 300). This procedure revealed the changes in the co-variance between fixation and pointing during the delay period when the subject has completed the step until the index finger has reached the pointing position.

**RESULTS**

**Pointing results**

In this study, we investigated pointing movements toward remembered visual targets after an intervening self-initiated step. This task requires memorizing the target position and updating of target position relative to the subject after the step. We will first focus on the errors in pointing and fixation after a step and their relation to the size and direction of the step. Then we will discuss the relation between pointing position and fixation during and after the step.

Figure 2 shows a top view of the main results for subject JV for pointing after a step for three different feedback conditions (DARK, FINGER, and FRAME, in Fig. 2, A, B, and C, respectively). All pointing positions lie to the left and slightly in front of the targets, relative to the subject. The constant pointing errors in Fig. 2 are on average about 10, 11, and 7 cm for the DARK, FINGER and FRAME condition, respectively (range, 6–13 cm). The results for this subject are typical for all subjects: For all subjects and all conditions, constant pointing errors ranged from 2 to 18 cm. Averaged over all subjects, the constant errors were not significantly different in the DARK and FINGER condition: $10 \pm 3.5$ (SD) and $10 \pm 3.4$ cm, respectively ($t = 0.6$, $P > 0.10$). In the presence of the illuminated frame (FRAME condition), the average constant error was significantly smaller than in the DARK and FINGER condition ($7 \pm 3.1$ cm; $t = 2.7$; $P < 0.05$ for both).

The variability of the pointing responses—as indicated by the ellipsoids—is large for pointing after stepping in complete darkness (DARK and FINGER conditions, Fig. 2, A and B) compared with that in the FRAME condition (Fig. 2C). Aver- aged over all subjects, the variable errors in the FRAME condition—measured as the volume of the 95% confidence ellipse—were more than twice as small as the variable errors in
the DARK and FINGER condition. These differences were significant ($P < 0.01$). Variable errors were not significantly different in the DARK and FINGER condition ($P > 0.10$).

During the step to the left, the subject in Fig. 2 (JV) tended to step slightly backward by about 5 cm. Some subjects systematically stepped slightly backward, whereas others stepped slightly forward. The size of the forward/backward component of the step was on average about 10% or less of the size of the sideward component (maximum 5.7 cm). The variability in step size appeared to be highly useful in our analyses to determine the relation between step size, fixation position, and pointing position. If subjects incorporate the step perfectly in the pointing movement to the remembered target, pointing position would be on the target, irrespective of variability in the step. However, for pointing after a step in a dark environment (DARK and FINGER conditions), the variability in pointing appeared often to be significantly correlated with the variability of the step ($P < 0.05$), in the forward or sideward direction or in both. Figure 3 shows an example of regressions for subject JV in the FINGER condition (same data as shown in Fig. 2), for targets 1, 2, and 3 (left, middle, and right, respectively) in sideward and forward direction separately (top and bottom, respectively). This figure shows that, for this subject, the pointing variability revealed a significant co-variance in the sideward or forward direction for each target: Targets 1 and 3 show a significant co-variance for the forward direction, whereas target 2 shows a significant co-variance for the sideward direction ($P < 0.05$).

The co-variance between step-size and pointing position was positive for almost all subjects in all conditions. A Wilcoxon

![FIG. 2. Top view of the pointing positions for subject JV in the complete darkness with visual feedback of the finger (FINGER) condition (B), complete darkness (DARK) condition (A), and FRAME condition (C). Target positions are indicated with large, black symbols: a triangle (target 1), a dot (target 2), and a square (target 3). Pointing positions are indicated with the small open symbols corresponding to the target symbol. Ellipses show the 95% confidence distribution of the pointing positions. A drawing of a fictive subject indicates the position of the subject before the step (dashed lines) and after the step (solid lines).](image)

![FIG. 3. Example of the relation between the variability in pointing and the variability of the step for subject JV (same data as in Fig. 2) in the FINGER condition, for targets 1 (left), 2 (middle), and 3 (right). Regression plots are shown for the variability in the step and pointing for sideward direction (top) and forward direction (bottom) separately. A regression fit is only displayed when the relation between pointing and the step is significant ($P < 0.05$).](image)
signed-rank test showed that the co-variance across subjects was significantly larger than zero \((P < 0.05)\) for each condition. We did not use an ANOVA to test the significance of the co-variance, because that would require a normal distribution of data, which was not the case. The Wilcoxon signed-rank test is a parameter-free test, and therefore more suitable for these data. However, the co-variance, although significantly positive across all subjects and conditions, was not always significant because of the scatter in the data (e.g., Fig. 3). A rank-sum test (Krauth 1988) revealed that more subjects showed a significant co-variance for targets 1 and 2 than for target 3 \((P < 0.05, \text{ see also Table 1})\). Averaged over all cases, where the co-variance was significant, the mean co-variance was \(0.69 \pm 0.18, 0.60 \pm 0.23, \text{ and } 0.64 \pm 0.25\) for the FINGER, DARK, and FRAME conditions, respectively. These values were not significantly different for the three conditions.

When a significant correlation was present, the slope of the linear regression of variability in pointing as a function of the variability in step was usually larger than 0.4 and not significantly different for the forward and sideward direction or for different targets. The average slope for all subjects and all targets was \(0.60 \pm 0.23\) (range, 0.32–1.19) in the DARK condition and \(0.69 \pm 0.18\) (range, 0.40–0.95) in the FINGER condition. In the FRAME condition, the subjects accounted almost exactly for the step size in pointing. As a consequence, the co-variance between the variability of pointing and step variability was low \((<0.4)\) and usually not significant in the FRAME condition \((P > 0.1)\).

The goodness of fit of the significant linear regression showed that about 23% of the sideward pointing variability was explained by the variability in the step, whereas in the forward direction, the variability in the step explained about 35% of the pointing variability. This indicates that about 65% of the variability is not explained by the step. This remaining variability has to be attributed to noise or to other inputs such as possibly the variability in gaze.

We used a \(\chi^2\) test to evaluate whether a second-order fit of pointing variability as a function of step variability gave a significantly better fit compared with the linear regression. This test showed that including a second- or higher-order term did not result in a significantly better description (taken into account the number of degrees of freedom and the uncertainty of the higher order fit parameters). Thus a linear regression was sufficient.

### Gaze during the step

Several studies have reported that gaze direction might affect pointing accuracy (Admiraal et al. 2003; Henriques et al. 1998; Medendorp and Crawford 2002). Therefore we investigated

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### Table 1. Number of subjects that showed a significant co-variance between the variability of pointing and stepping

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### Gaze during the step

Several studies have reported that gaze direction might affect pointing accuracy (Admiraal et al. 2003; Henriques et al. 1998; Medendorp and Crawford 2002). Therefore we investigated
The difference between the direction and distance of measured and ideal fixation are very similar for all targets. The difference is close to zero just before target offset (t = 1 s) and increases until the time of the auditory cue to start pointing. The error for distance decreases for all targets for the FINGER and FRAME condition, but less so for the DARK condition. Errors in direction increase until the time of the auditory cue to start pointing, and remain more or less constant until pointing has been completed.

**Comparison of fixation and pointing**

For a good comparison of the fixation position of the eyes and the pointing position, Fig. 6 shows a top view of the fixation positions directly after the step (top) and at the time of pointing (bottom) along with the corresponding pointing distributions (represented by ellipses) for the same subject as shown in Fig. 2.

Fixation at the end of the step is too far behind and to the left of the target when viewed from the subject. For subject JV, the deviation of fixation position from the target position at the end of the step is about the same in the DARK and FINGER conditions: averaged over all subjects, the directional errors relative to the cyclopean eye are 10° ± 11° and 12° ± 8° to the left for the DARK and FINGER conditions, respectively. On the other hand, fixation errors in distance relative to the cyclopean eye are larger in the FRAME condition than in the DARK and FINGER conditions: on average (over all subjects) 31 cm ± 17 cm in the FRAME condition and 13 cm ± 11 cm and 5 cm ± 15 cm in the DARK and FINGER conditions, respectively.

Figure 6, A–C, clearly shows that the distributions of the pointing positions (indicated by ellipsoids) do not correspond to the distributions of fixation positions at the end of the step. However, in the period between the end of the step and the pointing movement, gaze moves in the direction of the pointing position (compare data in top and bottom panels for corresponding conditions). Comparison of Fig. 6, A and D, shows that, in the DARK condition, fixation position remains more or less at the same location taken at the end of the step and is not affected by the pointing movement. However, in the conditions where subjects have feedback of their finger position during...
pointing (FINGER and FRAME conditions), fixation position at the time of pointing is clearly different from fixation position at the end of the step. In the FINGER condition, fixation positions at the time of pointing lie close to the distribution of pointing positions (see Fig. 6E), which is easily understood, since the tip of the finger is visible in this condition. In the FRAME condition (Fig. 6F), fixation returns only partly toward the pointing position.

The mean constant errors for pointing and fixation for all subjects are shown in Fig. 7. The top two panels in this figure show the constant errors in fixation position at two moments in time during the trial: top and middle panels show fixation errors directly at the end of the step and at the end of the pointing movement, respectively. The bottom panels display the constant errors in pointing.

At the end of the step, errors in binocular fixation position are relatively large and mainly in radial direction relative to the subject’s cyclopean eye (Fig. 7, A–C). Mean distance errors are (averaged over all subjects) 10 ± 4.5 and 13 ± 4 cm in the DARK and FINGER conditions, respectively, and somewhat larger in the FRAME condition (21 ± 5.5 cm). In all feedback conditions, directional fixation errors at the end of the step are largest for target 1 (mean over all subjects, 9 ± 2°) and smaller for targets 2 and 3 (mean, 5 ± 2°). At the time of pointing, the distribution of the fixation errors in the DARK and FINGER conditions clearly depends on the target position: for the most distant target (target 3), fixation distance is underestimated by 4 ± 2 and 5 ± 2.5 cm (averaged over all subjects) for the DARK and FINGER conditions, respectively, whereas the fixation distance toward the two proximal targets (targets 1 and 2) is overestimated by 7 ± 3 cm for target 1 and 14 ± 3.5 cm for target 2 (see Fig. 7, D and E). In the FRAME condition, fixation errors are significantly smaller during pointing than at the end of the step (P < 0.05). However, gaze direction is always too far to the left and fixation distance is too large for all targets (average over all subjects, 17 ± 2, 13 ± 2, and 6 cm while pointing to targets 1, 2, and 3, respectively, compared with 24 ± 5, 27 ± 6, and 10 ± 3 cm at the end of the step).

For an easy comparison between fixation and pointing, the bottom panels in Fig. 7 show the constant pointing errors for the three feedback conditions for all subjects. The figure shows that pointing errors are on average much smaller than errors in fixation during pointing. In particular, the higher accuracy in pointing in the FRAME condition is not accompanied by a higher accuracy in fixation.

Relation between pointing and fixation

To remove the effect of the step on the relation between pointing position and fixation position, we corrected the fixa-
tion position directly after the step for the influence of the variability of the step by fitting a linear relation, as we did for the pointing position. Similar to the pointing positions, fixation variability sometimes correlates significantly to the variability in the step (Table 2). However, this is less often the case than for the co-variance between the variability of pointing position and step variability (compare data in Tables 1 and 2).

Similarly, as for pointing position, the variability in step size affects the fixation position directly after the step by different amounts for the three targets: target 2 often shows a significant co-variance of fixation and step in most subjects, most often in the DARK and FINGER conditions. In the FRAME condition, a significant effect of the variability of the step on fixation variability is found for two subjects only and for each of them for a different target (targets 2 and 3; see Table 2). In all conditions the co-variance is positive, and for those that were significant, the average linear regression has a slope of about 0.80.

To test whether there is a correlation between pointing positions and fixation other than due to a mutual dependence on the step, we first corrected fixation position and pointing position for the variability related to the step, when the co-variance between step variability and pointing or fixation variability was significant. When the co-variance was not significant, no correction was made.

<table>
<thead>
<tr>
<th>Target</th>
<th>DARK</th>
<th>FINGER</th>
<th>FRAME</th>
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<tbody>
<tr>
<td>Target 1</td>
<td>2</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Target 2</td>
<td>4</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Target 3</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

Subjects are counted if the co-variance was significant either in forward direction, in sideward direction, or in both. In each condition, six subjects participated.
In the following, we will consider the co-variance between pointing position and fixation position for distance and direction separately, in the time interval between the end of the step until the end of the pointing movement. The pointing position is defined as the position of the fingertip at the end of pointing and therefore does not change in time (see METHODS). Changes in the co-variance during the time interval are therefore the result of changes in fixation. The duration of the time interval varies for different trials, with an average duration of 900 ± 350 ms. To compare fixation and pointing during intervals of different length, we divided the time interval between step offset and the end of the pointing movement for each trial in 300 equidistant time intervals (see METHODS), and we interpolated the corresponding gaze-in-time data to match the new time scale.

For each of the resulting 300 samples, we calculated the co-variance between fixation position and pointing position. Figure 8 shows the resulting co-variance as a function of time for the DARK, FINGER, and FRAME conditions (left, middle, and right, respectively). The co-variance between fixation and pointing for distance (R) and direction (φ) are displayed separately in the top and bottom panels, respectively. The horizontal axes correspond to the time interval between the end of the step and the time when the index finger reached the pointing position. The minimum value of the correlation coefficient that indicates a significant relation between fixation and pointing (P < 0.05) is marked by a horizontal gray bar. The number of correct trials differed slightly between subjects and conditions. The minimum value of the correlation coefficient that indicates significance is therefore also slightly different. In each condition, the width of the horizontal bar indicates the range of minimum values for the subjects displayed in the panel.

In the FINGER condition, only two subjects showed a significant co-variance between the radial distance of pointing and fixation at the time just after completion of the step. By the time the finger has reached the pointing position, a significant co-variance was found for four subjects (Fig. 8B). Two subjects never showed a significant co-variance between radial distance of fixation and pointing in the FINGER condition. In the DARK and FRAME conditions, the average co-variance in radial distance per subject was slightly (but not significantly) lower than in the FINGER condition. For two subjects, the co-variance did never reach significance. These subjects were not the same as the subjects that did not show a significant co-variance in the FINGER condition.

The largest co-variance was found for the directional components of fixation position and pointing position (Fig. 8, D–F). The bottom panels clearly show a highly significant (P < 0.01) co-variance directly after completion of the step. This co-variance tends to increase to larger values by the time of pointing. The co-variance for the directional component found in the FINGER condition (Fig. 8D) is significantly higher (P < 0.05) than in the other conditions (Fig. 8, E and F), which may not be very surprising, since in this condition, subjects tend to redirect gaze toward the (visible) index finger. In the frame condition, in which feedback of the index finger is also available, subjects do not show such a clear change of gaze toward the index finger (e.g., Fig. 6).

**DISCUSSION**

In this study, we have investigated the performance of binocular fixation and pointing toward remembered visual targets in three-dimensional space after a self-initiated step. The presence or absence of visual feedback of the environment appeared to have a large effect on the constant and variable errors of pointing. Similarly, fixation position differed quite considerably from the target position after the step depending on the visual feedback condition. These errors in pointing and gaze are compatible with the notion that subjects underestimate the size of the step, as suggested earlier by Medendorp et al. (1999). Moreover, when the variability in pointing and fixation was corrected for any mutual correlation to the variability in the step, the remaining variability in the final position for the pointing movement is to a large extent related to the variability of fixation. The co-variance between the latter two signals...
increases in the delay period after the step, but is larger for direction, than for distance.

We will first discuss the effects of the step on the accuracy of pointing and fixation during the step. After that, we will discuss the relation between fixation and pointing after a step and its implication in terms of frames of reference.

**Influence of the step on pointing**

Several studies have shown that subjects make considerable constant pointing errors toward remembered visual targets without a step (e.g., Admiraal et al. 2003; McIntyre et al. 1997; Soechting and Flanders 1989) and after a step (Daghestani et al. 1999; Flanders et al. 1999; Medendorp et al. 1999). Our results show that the size of the constant pointing errors after a step depends on the amount of visual feedback: visual feedback of the index finger alone (FINGER condition) does not significantly decrease the constant pointing relative to that in the DARK condition, but vision of the environment (FRAME condition) does. A comparison of the constant errors for pointing without and with a step shows that the errors are considerably larger for pointing movements after a step (compare errors in Figs. 2 and 7 in this study with those in Fig. 3 of Admiraal et al. 2003). In agreement with previous authors (Daghestani et al. 1999; Flanders et al. 1999; Medendorp et al. 1999), we found that constant pointing errors were mainly in the direction of the step. If subjects would incorporate the step size perfectly, pointing would be on target irrespective of step size. However, if subjects incorporate the step only for about 80% of the true step size in the pointing response, as suggested by Medendorp et al. (1999), subjects will make systematic errors. The constant errors that we found in this study are about 10–20% of the step size, which corresponds quite well to the estimate of accounting for about 80% of the true step size by Medendorp and colleagues.

**Gaze during the step**

The fixation position after the step shows a large constant error in radial direction relative to the subject (see Fig. 7). This radial component of the constant error in fixation is due to a drift of gaze in radial direction after target offset, which has been described before for subjects who did not make a step while fixating at a remembered visual target (Admiraal et al. 2003). However, in this study, which included a step, the fixation position after the step also has a large sideward component. In the following, we will discuss possible explanations for these sideward fixation errors. A first explanation may be that the radial drift in gaze during the step introduces a sideward error at the end of the step. This is shown schematically in Fig. 9. For equal time intervals during the step, we have plotted the vector of a constant radial drift component relative to the subject’s position. We have assumed a bell-shaped velocity profile for the step, and for each of the two targets in Fig. 9, the simulated drift velocity was chosen such that simulated fixation ends at the same distance behind the target as the measured trajectory of fixation. Obviously, the trajectory of fixation depends on the target position relative to the subject before and after the step, and so will the final fixation position at the end of the step.

In Fig. 9 we also included two of the typical trajectories for fixation during the step from Fig. 4. For the target on the right (target 1), the simulated trajectory seems to end closely to the end of the measured trajectory. The curvature of the measured trajectory, however, is very different from that of the simulated trajectory. The simulated trajectory for the leftward target (target 2) clearly shows a much larger excursion than the measured trajectory, and its endpoint lies too far to the left of the measured position.

The scheme in Fig. 9 with a constant drift velocity in radial direction is obviously oversimplified. Presumably, the drift velocity of gaze is not constant and may not start immediately at the onset of the step. Moreover, gaze may not drift indefinitely, but may continue until a particular distance at about 80 cm from the subject (“dark vergence,” see e.g., Heuer and Owens 1989). Incorporating each of these aspects will reduce the amount of drift and thereby will reduce the drift component in the direction of the step. However, neither of these modifications can provide a good fit to the measured drift trajectories for all targets. This can be shown by the trajectories in Fig. 9: the first part of the measured trajectory for target 1 requires the simulated gaze drift to be largest at the beginning of the step, whereas the measured trajectory of target 2 is best described with a gaze drift that is largest halfway through the step. These results are typical for all subjects and show that a radial drift in gaze alone cannot explain the constant error in fixation position at the end of the step.

Another explanation for the constant error in fixation position in sideward direction could be an inadequate translational vestibuloocular reflex (tVOR) in the dark. Previous studies have studied the tVOR in subjects while making active movements in hip and trunk or during walking and running (Crane and Demer 1997; Medendorp et al. 2002). In these studies, the
adequacy of the tVOR was evaluated in terms of its “sensitivity,” defined as the ratio between the velocity of the gaze response and translational eye velocity. For a perfect tVOR for head movements perpendicular to the target direction, the sensitivity is equal to the inverse of target distance (see Medendorp et al. 2002). The sensitivity of the tVOR in the dark was found to be too small to keep fixation at the (world-fixed) remembered target position. However, when the target was visible, any errors between ideal and measured gaze were almost negligible (Crane and Demer 1997; Gielen et al. 2004; Medendorp et al. 2002). This may explain why the constant errors in the direction of the step are much smaller in the FRAME condition, which allows for more visual feedback to stabilize gaze.

Crane and Demer (1997) compared the stability of fixation on a visible target during self-initiated head translations and during walking and running. They found that the ocular response to natural head movements such as the sway during walking and running was adequate to stabilize fixation. During the—more artificial—self-initiated translations resulting from active movements in hip and trunk, the VOR gain corresponded closely to the rotational component of the movement, but did not correctly take into account the translation of the head. When the target was extinguished (remembered target), the SD of fixation position in horizontal direction is at most about 2° during walking and running. For the active head translations, the variability of fixation in horizontal direction had a SD of about 4°.

Can the results of Crane and Demer (1997) and Medendorp et al. (2002) explain the present results? If we consider the step—which typically had a duration of about 1 s—as one-half of a periodic back-and-forth movement of 0.5 Hz—as studied by Crane and Demer (1997) and Medendorp et al. (2002)—we predict that the sideward gaze error due to insufficient sensitivity of the tVOR for a remembered target situated at about 35 cm from the eyes (target 1) would be about 3° at most (see Fig. 5 in Medendorp et al. 2002). For targets 2 and 3—at distances on average of about 50 and 60 cm, respectively—the sideward errors should be even smaller (since the deficiency in sensitivity increases with decreasing target distance). However, the observed sideward gaze errors in this study are much larger than this (10, 5, and 5° for targets 1, 2, and 3, respectively, see Fig. 7). Therefore the constant gaze errors along the step direction cannot be fully explained by deficiencies in tVOR.

Since neither the gaze drift nor the tVOR could explain the sideward component of the constant gaze errors during and at the end of the step, we speculate that the constant errors also depend on underestimation of the step size (see Medendorp et al. 1999), possibly related to errors in the use of proprioceptive signals and efference copies, in line with suggestions by Medendorp et al. (2002) to explain the differences between gaze control for passive and active head movements while fixating a visual or a remembered visual target.

Relation between gaze and pointing

Previous studies have shown that variable errors in pointing to remembered targets are related to the variability in gaze at the time of pointing even without a step (e.g., Admiraal et al. 2003; Bock 1986; Enright 1995; Henriques et al. 1998; Medendorp and Crawford 2002; Van Donkelaar and Staub 2000). In this study, which included a step, the relation between variability in fixation position and pointing may be more difficult to detect, because of the mutual dependence on the step. Figure 10 schematically shows how the step-dependent constant error in pointing (or fixation), as described above, may lead to a co-variation between the step and pointing (or fixation). The figure shows an example of two steps, 50 and 45 cm (black arrows). If only 80% of the step is accounted for, as argued by Medendorp et al. (1999), the pointing movement will be based on the erroneously perceived location of the subject’s shoulder after the step (white arrows) and the (remembered) target position, which results in an incorrect pointing position (squares). Consequently, this explains why the variability in pointing positions is related to the variability in the step. The same argument may explain why underestimation of the step causes similar errors in binocular fixation. The influence of the step on the variability of pointing and fixation could be estimated from the linear relation between the step on the one hand and pointing and gaze on the other hand. This

FIG. 10. Schematic illustration of how underestimation of the step size may lead to a co-variation between the pointing positions (white squares) and the step. Two steps (black arrows) of different size and direction are underestimated, such that only 80% of the step is accounted for (white arrows). The planned pointing movement corresponds to the vector from the perceived endpoint of the step (tip of the white arrow) toward the target (dashed lines), but originates from the actual position (tip of the black arrow). Two ellipses represent the estimated distributions of the step endpoints and the distribution of the corresponding pointing positions.
linear relation was used to correct the variable errors for any direct influence of the step.

After eliminating the influence of the step from the variable error of pointing and fixation, neither pointing nor fixation is correlated to the step. However, the variability in fixation and pointing appeared to be significantly correlated: in all visual feedback conditions, the fixation position directly after the step co-varies with its concomitant pointing position. Moreover, the co-variance between fixation position and pointing increases gradually in the period between the end of the step and the time of pointing toward a maximum at the time when the pointing position is reached.

One explanation for the co-variance might be a common command signal that drives gaze and pointing toward the same target position. Variability in the common command signal will inevitably lead to a co-variance between fixation and pointing. Undoubtedly, such a common input signal will be there, since both pointing and gaze are directed toward the visually perceived initial target position. If the co-variance between fixation position and pointing were due only to such a common command signal, one would expect the gradual drift in fixation in the delay period to deteriorate the co-variance between pointing and fixation. This is obviously not the case, as is shown in Fig. 8, which shows that the co-variance increases rather than decreases in time. Thus a common input related to the remembered visual target cannot explain the increase in the co-variance between fixation and pointing during the delay period.

Therefore we hypothesize that fixation position affects the pointing movement, which is in agreement with previous studies that showed an effect of gaze on pointing accuracy (see Admiraal et al. 2003; Medendorp and Crawford 2002; Pouget et al. 2002). When fixation position at the time of pointing is used to define the pointing target, the gradual drift in fixation during the delay period toward the time of pointing results in an increasing co-variance during this period, which is indeed what we found.

In a previous study, Flanders et al. (1999) measured the orientation of the head in a pointing task that included a forward step. They reported that errors in pointing were geometrically related to the errors in head orientation during pointing. In this study, we not only measured head orientation, but also orientation of the two eyes throughout the trial. This allowed us to compare pointing and fixation both in direction and in distance. We found that the pointing position is related to the gaze direction, in agreement with Medendorp and Crawford (2002); however, we also found a strong relation to fixation distance. Therefore we conclude that pointing depends on the binocular fixation position.

Table 1 shows that the variability of pointing was more often correlated to the variability of the step for near targets (targets 1 and 2) than for the far target (target 3). This may be surprising since the suggestion that only 80% of the step size is incorporated in pointing would predict similar errors for far and near targets and therefore would predict a similar correlation between pointing and step for all targets. A possible explanation for this apparent discrepancy may be the following.

The data in Figs. 2 and 6 show that both the constant error in the direction of the step as well as the variable error in the direction of the step is about the same for targets 1 and 3, both for pointing (Fig. 2) and for gaze (Fig. 6). The main difference in pointing positions and gaze position is that it is in radial distance: the drift in gaze in radial direction during the step is smaller for target 3 than it is for target 1. Presumably, this is due to the fact that gaze in darkness tends to drift to a distance of about 80 cm (‘‘dark vergence’’, see Heuer and Owens 1989), and target 3 lies close to this preferred distance. As a consequence, gaze drift is almost absent for target 3 and the effect of the step on gaze may be relatively small. This might have led to a smaller effect of the step on pointing position and therefore to a smaller co-variance between step size and pointing position.

**Frame of Reference**

The improvement of pointing performance toward remembered targets in the presence of a (visual) environment led previous authors to question in what frame of reference the CNS plans goal directed movements and how the CNS copes with egomotion (Marteniuk et al. 2000; Medendorp et al. 1999; Pigeon et al. 2003; Pozzo et al. 1998). Since this study is the first to measure pointing movements along with three-dimensional gaze during a step, the finding that binocular fixation is involved in the planning of an arm movement after a step provides new insight in this discussion.

Medendorp et al. (1999) addressed the question of what coordinate frame could best be used to describe the pointing errors after a step. They tested a Cartesian model for errors in x-y direction in the horizontal plane and another model, which relates errors to spherical coordinates of the pointing position relative to the shoulder. The cross coupling between the x and y components (sideward and forward direction, respectively) in the description was not significantly different from zero, whereas there was a significant coupling between the r and φ components (for distance and azimuth, respectively) in the spherical description. This led these authors to the conclusion that the data were best described in Cartesian coordinates. The analysis by Medendorp et al. (1999) required a broad range of step sizes and target positions. Since we tested only a small range of step sizes in this study, the analysis by Medendorp et al. could not discriminate between the two hypotheses.

Some other recent studies asked subjects to pick up an object from the floor (Pozzo et al. 1998) or focused on reaching an object from a table while walking past it (Marteniuk et al. 2000). Both studies found that the planning of the reach included all segments of the body involved and that the trajectories of the hand or wrist in space were remarkably straight, indicating a movement planning in terms of the trajectory in allocentric coordinates. Pigeon et al. (2003) limited the movements of the whole body to a passive rotation around the vertical axis, while the trajectory of the wrist was evaluated during a reach. With different rotational velocities subjects used different configurations of the arm during the pointing movement. The trajectory of the wrist in space, however, was preserved, and a description in terms of allocentric coordinates was smoother and corresponded to a more bell-shaped velocity profile than a description in egocentric coordinates. Therefore these authors conclude that turn-and-reach movements are controlled in an allocentric frame of reference.
In this study, we showed that the underestimation of the step is less pronounced in the pointing responses when the environment is visible (FRAME condition) than after stepping in the dark (FINGER and DARK conditions). One explanation could be that the visual environment serves to store the target position in an allocentric frame of reference instead of an internal frame of reference, which is the only one available in the FINGER and DARK conditions. By doing so, the CNS no longer needs to rely solely on the vestibular, efferent, and proprioceptive signals related to the egomotion, which may be less accurate than vision of the continuously lit visual environment. However, since vision is most accurate in direction relative to the cyclopean eye and less so in distance, the improvement due to such a strategy will mainly result in an improvement in pointing direction relative to the FRAME condition relative to the FINGER and DARK condition and less so in distance (see Van Beers et al. 2002). The data shown in Figs. 2 and 6 clearly support this interpretation.

Another explanation for the smaller underestimation of the step in the FRAME condition, which does not exclude the explanation suggested in the previous paragraph, may be that vision of the environment during the step helps to improve the perception of the displacement. Such an effect may be reflected in a more correct location of three-dimensional fixation and pointing. We found that the visual frame causes significantly smaller errors in pointing, but did not reduce errors in fixation. Based on this finding, we suggest that the visual environment was sufficient to remember the target relative to the visual frame and that fixation was less important in the FRAME condition than in the FINGER and DARK condition.

From this study, it is difficult to come to a final conclusion concerning the frame of reference used to represent the target position in the various visual conditions. Moreover, many authors have indicated that the effects of more complex processes, such as the use of an alternative frame of reference for the storage of remembered target positions (McIntyre et al. 1998), the storage of relative sizes or positions of target objects (Carrozzo et al. 2002; Hu and Goodale 2000; Hu et al. 1999), become evident only after a delay of about 2 s. In our study, the interval between the offset of the target and the onset of the pointing movement lasted just about 2 s, in which subjects also performed the step. Therefore it is possible that these results reflect a combination of strategies, which makes it impossible to distinguish between separate strategies. This is compatible with the idea that the control of gaze and the coordination of reaching and gaze depends on the scale and complexity of the task space (see also Herst et al. 2001).

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