Gaze affects pointing towards remembered visual targets after a self-initiated step

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ABSTRACT

We have investigated pointing movements towards 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 covariance increases during the delay period after the step, reaching a highly significant value at the time of pointing. The significant covariance 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 covariance 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.

Keywords:
Reaching, ego-motion, frame of reference
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 in order to preserve a correct representation of the target position relative to the subject. If the pointing movement is made towards a remembered visual target and when 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 and colleagues (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 few studies have investigated gaze control in subjects who made active movements. During active body motion, visual, vestibular, proprioceptive information, and possibly also corollary discharges are available to assist the control of gaze for target fixation.

In a recent study Medendorp and colleagues (2002a) 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) 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 ego-motion. 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 towards 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 covariance in gaze and pointing accuracy. An alternative hypothesis, that gaze would affect the accuracy of pointing, would also cause a covariance 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 covariance 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 covariance 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 covariance between gaze and pointing due to the step and the hypothesis, that gaze affects pointing, by subtracting any covariance of gaze and pointing signal with the step signal from gaze and pointing. Any covariance, which is left after correcting for any covariance 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; Philbeck 2000; Panerai et al. 2002), 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). In order 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 in order 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. In order 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. Secondly, 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 covaries with the change of gaze in time. Since gaze changes in time, we tested whether the covariance between fixation and pointing, if any, is strongest in the delay period near target offset or near pointing.
METHODS

Six subjects (aged 21-49 years) 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 x 90 x 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 the present 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 Figure 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 in order to keep the duration of the experiment under 45 minutes. The 45-minute 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 downwards along the body. Each trial started with the onset of one of the three target LEDs for a period of one second. The targets appeared in front of the subject with the center target about 50 cm to the left of the subject (see Fig. 1). 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 downwards along a horizontal axis by approximately 135 deg 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 about 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 which prevented any change of hitting the frame during the step. Two seconds after target disappearance, an auditory signal cued the subject to start the movement 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 half 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 at least 13 trials per target. Blocks with different visual feedback conditions were presented in randomized order. A block of 20 trials typically lasted about three minutes, and after each block the room lights were switched on for about one minute 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 m³ (see Admiraal et al. 2003). The positions of ireds were measured with a sampling frequency of 100Hz.

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 3-D 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 (Remmel Labs). This system consists of a cubic frame of welded aluminum of 3 x 3 x 3 m³, 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. In order 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 were 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° to +40° in both elevation and azimuth (for the full calibration procedure: see Admiraal et al. 2003). For each eye, the two-dimensional calibration errors -defined as twice the standard deviation of the data relative to the calibration fit- were typically about 0.5° in azimuth and 1° in elevation on average; resolution was less than 0.04°. The errors in 3-D fixation position within the target range tested here were on average about 0.6° and 1.1° in azimuth and elevation, respectively, and 3 cm in radial distance from the cyclopean eye. Coil signals were sampled at 500 Hz. In offline analyses, the coil signals were resampled 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 ired on the tip of the index finger at the end of the pointing movement towards 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 towards that target, and the variable error, which reflects the distribution of the pointing positions towards a target relative to the average pointing position to that target. The distribution of the pointing positions for target \( i \) is described by the 3-D covariance matrix \( S_i \): 

\[
S_i = \frac{\sum_{j=1}^{n} \pi^i_j (\pi^i_j)^T}{n - 1}
\]

where \( n \) is the number of trials to target \( i \) and \( \pi^i_j = p^i_j - \bar{p}^i \) is the deviation of the finger position in trial \( j \) to target \( i \) relative to the mean pointing position \( \bar{p}^i \) to target \( i \). The three orthogonal
eigenvectors of the covariance 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 eigenvalues of the covariance 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 more than 3 SD from the ellipsoid fitted to the pointing positions, we left out these pointing positions and derived the covariance matrix again. Due to this rejection procedure, less than 3% of the data was not incorporated in further analyses.

We tested whether variability in the pointing position was correlated to variability in the step. When the covariance 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 $\sum_{i,j} (e_{ij})^2$ in:

$$\pi_j^i = \tau \cdot \sigma_j^i + \epsilon_j^i$$

where $\sigma_j^i = s_j^i - \bar{s}^i$ is the deviation of the step in trial $j$ relative to the mean step $\bar{s}^i$ for pointing to target $i$. Since, by the above definitions, $\pi_j^i$ and $\sigma_j^i$ have mean values equal to zero, $\epsilon_j^i$ 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 ($\tau \cdot \sigma_j^i$) was subtracted from the pointing position data $p_j^i$. 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 covariance with the step. A $\chi^2$-test demonstrated 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 section).

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 $e^{-(3.75)^2}$ 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 covariance 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. In order 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 covariance between fixation position and pointing position was then derived between the resampled fixation data and the corresponding pointing position for that trial for each sample $i$ (with $i$ between 1 and 300). This procedure revealed the changes in the covariance 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 towards 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 near here

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 Figures 2A, 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 cm, 11 cm and 7 cm for the DARK, FINGER and FRAME condition, respectively (range 6 to 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 cm (SD= 3.5) and 10 cm (SD= 3.4), 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 cm (SD= 3.1), 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, Figure 2A and B) compared to that in the FRAME condition (Figure 2C). Averaged 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 Figure 2 (JV) tended to step slightly backwards by about 5 cm. Some subjects systematically stepped slightly backwards, whereas others stepped slightly in forward direction. 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 Figure 2), for targets 1, 2 and 3 (left, middle and right column) in sideward and forward direction separately (top rows and bottom rows, respectively). This figure shows that for this subject, the pointing variability revealed a significant covariance in the sideward or forward direction for each target: Targets 1 and 3 show a significant covariance for the forward direction, whereas target 2 shows a significant covariance for the sideward direction (p<0.05).

The covariance between step-size and pointing position was positive for almost all subjects in all conditions. A Wilcoxon-Signed Rank test showed that the covariance 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 covariance, 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 covariance, although significantly positive across all subjects and conditions, was not always significant because of the scatter in the data (see e.g. Figure 3). A Rank-Sum test (Krauth, 1988) revealed that more subjects showed a significant covariance for targets 1 and 2, than for target 3 (p<0.05, see also Table 1). Averaged over all cases, where the
covariance was significant, the mean covariance was 0.69 (SD=0.18), 0.60 (SD=0.23) and 0.64 (SD=0.25) for the FINGER, DARK and FRAME conditions, respectively. These values were not significantly different for the three conditions.

Figure 3 near here

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Table 1

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 (SD= 0.23, range 0.32 to 1.19) in the DARK condition, and 0.69 (SD= 0.18, range 0.40 to 0.95) in the FINGER condition. In the FRAME condition, the subjects accounted almost correctly for the step size in pointing. As a consequence, the covariance between the variability of pointing and step variability was low (below 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 to the linear regression. This test demonstrated 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 (Henriques et al. 1998, Medendorp et al. 2003, Admiraal et al. 2003). Therefore, we investigated gaze during and after the step in order to see whether errors in pointing could be related to errors in fixation. We will first show the average trajectory of fixation for one typical subject. Since the exact timing of the onset and end of the steps relative to disappearance of the target varied, we resampled the fixation data from step onset until step offset before averaging over trials (see Methods).

Figure 4 near here

Figure 4 shows the average trajectory of fixation starting at target offset until the end of the step for subject MA in the DARK, FINGER and FRAME conditions in Figures 4A, B and C, respectively. At the end of target presentation, fixation is on target (filled dot) for all conditions. During the step, however, fixation does not remain on target, but moves away, mainly in radial direction relative to the subject as indicated by the arrows. At the end of the step, fixation is at a position behind the target, and to the left of the target. We will refer to this type of movement as “drift” to indicate a gradual displacement of the fixation position over distances of about 10 cm or more. This does not relate to the slow random eye movements in the frequency range of 2-5 Hz with amplitudes of the order of 1-5’, which is usually called “drift” in the oculomotor literature (see e.g. Carpenter 1977).

Remarkably, the presence of a visual background during the step in the FRAME condition does not prevent gaze from drifting during the step, as is the case for the DARK and FINGER condition. Deviations of fixation position from target at the end of the step are similar in the FRAME condition and the DARK and FINGER conditions (compare the ends of the traces in Figure 4C with those in Figures 4A and B).
The open symbols in Figure 4 indicate the fixation position at the end of the pointing movement when the index finger has reached the pointing position. Fixation while pointing (open symbols) is closer to the target than fixation at the end of the step in the FINGER and FRAME conditions, indicating that fixation has returned from the far fixation position at the end of the step to a distance closer to the subject at the time of pointing. At the end of the step, the distance between fixation and target position is 32 cm (SD=7 cm), 33 cm (SD=7 cm) and 35 cm (SD =8 cm) for the DARK, FINGER, and FRAME condition, respectively, averaged over all subjects. The distance becomes 23 cm (SD=7 cm), 14cm (SD=4 cm) and 18 cm (SD=4 cm) at the time of pointing. In the DARK condition -when the finger is not visible during pointing- fixation position remains far from the target relative to the subject, close to the position of fixation at the end of the step (compare the open symbols and the ends of the trajectories in Figure 4A).

Figure 5 near here

Figure 4 only shows the spatial trajectories of fixation position during the step, but it does not give detailed temporal information about the changes in binocular fixation position during and after the step. The temporal aspects of the fixation position are displayed in Figure 5, where we compare the measured gaze direction and fixation distance with the gaze direction and fixation distance that are required to keep fixation on the target. Since the required gaze direction and fixation distance depend on the size and direction of the step, and thus varies slightly between trials, we have plotted the measured fixation position in terms of its deviation from the required fixation position, i.e. the error in gaze direction and fixation distance. These deviations are averaged over all trials and displayed for the same subject as in Figure 4 (subject MA).

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

Figure 6 near here

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° (SD= 11°) and 12° (SD= 8°) to the left for the DARK and FINGER condition, 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 (SD= 17) in the FRAME condition and 13 (SD= 11) and 5 (SD= 15) cm in the DARK and FINGER condition, respectively.

The top panels in Figure 6 (panels A to C) clearly show 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 Figures 6A 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 Figure 6E), which is easily understood, since the tip of the finger is visible in this condition. In the FRAME condition (Figure 6F), fixation returns only partly towards the pointing position.

The mean constant errors for pointing and fixation for all subjects are shown in Figure 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 lower 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 (Figures 7A-C). Mean distance errors are (averaged over all subjects) $10 \text{ cm (SD = 4.5 cm)}$ and $13 \text{ cm (SD = 4 cm)}$ in the DARK and FINGER conditions, respectively, and somewhat larger in the FRAME condition ($21 \text{ cm (SD = 5.5 cm)}$). In all feedback conditions, directional fixation errors at the end of the step are largest for target 1 (mean over all subjects $9^\circ$; SD = $2^\circ$) and smaller for targets 2 and 3 (mean $5^\circ$; SD=2$^\circ$). At the time of pointing, the distribution of the fixation errors in the DARK and FINGER condition clearly depends on the target position: for the most distant target (target 3) fixation distance is underestimated by $4 \text{ cm (SD=2 cm)}$ and $5 \text{ cm (SD=2.5cm)}$ (averaged over all subjects) for the DARK and FINGER condition, respectively, whereas the fixation distance towards the two proximal targets (targets 1 and 2) is overestimated, by $7 \text{ cm (SD=3 cm)}$ for target 1 and by $14 \text{ cm (SD = 3.5 cm)}$ for target 2 (see Figures 7D-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 (on average over all subjects $17 \text{ cm (SD= 2 cm), 13 cm (SD=2 cm)}$ and $6 \text{ cm while pointing to targets 1, 2 and 3,}$
respectively, compared to 24 cm (SD=5 cm), 27 cm (SD=6 cm) and 10 cm (SD=3 cm) at the end of the step.

For an easy comparison between fixation and pointing, the lower panels in Figure 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.

The relation between pointing and fixation

In order to remove the effect of the step on the relation between pointing position and fixation position, we corrected the fixation position directly after the step for the influence of the variability of the step by fitting a linear relation, like we did for the pointing position. Similar to the pointing positions, fixation variability sometimes correlates significantly to the variability in the step (see Table 2). However, this is less often the case than for the covariance between the variability of pointing position and step variability (compare data in Table 1 and 2).

<table>
<thead>
<tr>
<th></th>
<th>DARK</th>
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<tr>
<td>target 2</td>
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<tr>
<td>target 3</td>
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Table 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 covariance of fixation and step in most subjects, most often in the DARK and FINGER condition. 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 covariance is positive, and for those that were significant the average linear regression has a slope of about 0.80.
In order 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 covariance between step variability and pointing or fixation variability was significant. When the covariance was not significant, no correction was made.

In the following we will consider the covariance 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 covariance 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 ms (SD= 350 ms). In order 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 covariance between fixation position and pointing position. Figure 8 shows the resulting covariance as a function of time, for the DARK, FINGER and FRAME condition (left, middle and right panels, respectively). The covariance between fixation and pointing for distance (R) and direction (ψ) 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 grey 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.

Figure 8 near here
In the FINGER condition, only two subjects showed a significant covariance 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 covariance was found for four subjects (Figure 8B). Two subjects never showed a significant covariance between radial distance of fixation and pointing in the FINGER condition. In the DARK and FRAME conditions, the average covariance in radial distance per subject was slightly (but not significantly) lower than in the FINGER condition. For two subjects, the covariance did never reach significance. These subjects were not the same as the subjects that did not show a significant covariance in the FINGER condition.

The largest covariance was found for the directional components of fixation position and pointing position (Figures 8D, E and F). The bottom panels clearly show a highly significant (p<0.01) covariance directly after completion of the step. This covariance tends to increase to larger values by the time of pointing. The covariance for the directional component found in the FINGER condition (panel D) is significantly higher (p<0.05) than in the other conditions (panels E and F), which may not be very surprising since in this condition, subjects tend to redirect gaze towards 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 towards the index finger (see e.g. Figure 6).
DISCUSSION

In this study we have investigated the performance of binocular fixation and pointing towards remembered visual targets in 3-D 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 covariance 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 towards remembered visual targets without a step (e.g. Soechting and Flanders 1989; McIntyre et al. 1997; Admiraal et al. 2003) and after a step (Medendorp et al. 1999; Flanders et al. 1999; Daghestani 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 errors 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 e.g. errors in Figures 2 and 7 in this study with those in Figure 3 of Admiraal et al. 2003). In agreement with previous authors (Medendorp et al. 1999; Flanders et al. 1999; Daghestani
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 to 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 Figure 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 the present 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 illustrated schematically in Figure 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 Figure 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 Figure 9 we also included two of the typical trajectories for fixation during the step from Figure 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 end point lies too far to the left of the measured position.

The scheme in Figure 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 illustrated by the trajectories in Figure 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 illustrate that a radial drift in gaze alone can not 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 (Medendorp et al. 2002a; Crane and Demer 1997). 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. 2003). 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; Medendorp et al. 2002a; Gielen et al. 2003). 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 standard deviation 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 standard deviation of about 4°.

Can the results of Crane and Demer (1997) and Medendorp and colleagues (2002a) explain the present results? If we consider the step—which typically had a duration of about 1 s—as half of a periodic back-and-forth movement of 0.5 Hz—as studied by Crane and Demer (1997) and Medendorp et al. (2002a)—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 Figure 5 in Medendorp et al. 2002a). For targets 2 and 3—at distances of on average 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 the present study are much larger than this (10°, 5° and 5°, for targets 1, 2 and 3, respectively, see Figure 7 in the present study). Therefore, the constant gaze errors along the step direction can not be fully explained by deficiencies in tVOR.

Since neither the gaze drift, not 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. (2002a) 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. Bock (1986); Enright (1995); Henriques et al. 1998; Van Donkelaar and Staub 2000; Medendorp and Crawford 2002b; Admiraal et al. 2003). In the present 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 illustrates how the step-dependent constant error in pointing (or fixation), as described above, may lead to a covariance between the step and pointing (or fixation). The figure shows an example of two steps, of 50 cm and 45 cm, respectively (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 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. Yet, the variability in fixation and pointing appeared to be significantly correlated: In all visual feedback conditions, the fixation position directly after the step covaries with its concomitant pointing position. Moreover, the covariance between fixation position and pointing increases gradually in the period between the end of the step and the time of pointing, towards a maximum at the time when the pointing position is reached.

One explanation for the covariance might be a common command signal that drives gaze and pointing towards the same target position. Variability in the common command signal will inevitably lead to a covariance between fixation and pointing. Undoubtedly, such a common input signal will be there, since both pointing and gaze are directed towards the visually perceived initial
target position. If the covariance 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 covariance between pointing and fixation. This is obviously not the case, as is shown in Figure 8, which shows that the covariance increases, rather than decreases in time. Thus, a common input related to the remembered visual target cannot explain the increase in the covariance 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, which demonstrated an effect of gaze on pointing accuracy (see e.g. Pouget et al. 2002; Medendorp and Crawford 2002b; Admiraal et al. 2003). When fixation position at the time of pointing is used to define the pointing target, the gradual drift in fixation during the delay period towards the time of pointing results in an increasing covariance 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 the present 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 (2002b), but 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 Figures 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 (Figure 2) and for gaze (Figure 6). The main difference in pointing positions and gaze for
targets 1 and 3 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 covariance between step size and pointing position.

Frame of reference

The improvement of pointing performance towards 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 ego-motion (Medendorp et al. 1999; Pozzo et al. 1998; Marteniuk et al. 2000; Pigeon et al. 2003). Since the present study is the first to measure pointing movements along with 3-D 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 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 ψ 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 the present study, the analysis by Medendorp et al. applied to our data could not discriminate between the two hypotheses.

Some other recent studies asked subjects to pick up an object from the floor (Pozzo and colleagues 1998), or focused on reaching an object from a table while walking past it (Marteniuk et
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 ego-motion, 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 in 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 Figures 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 3-D 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 the present 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 (Hu et al. 1999; Hu and Goodale 2000; Carrozzo et al. 2002) 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 2s, in which subjects also performed the step. Therefore it is well possible that the present 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).
ACKNOWLEDGEMENTS

We thank Martha Flanders for useful discussions about the interpretation of the data and Pieter Medendorp for useful comments on the manuscript.
REFERENCES


LEGENDS TO FIGURES

Figure 1:
Experimental setup with the position of the subject before (dashed lines) and after (solid lines) the step. An L-shaped obstacle attached to the floor indicated the start position before the step. After the step, the subject stood with the cyclopean eye at a distance of about 25 cm in front of the position halfway between targets 1 and 2. Targets (black symbols) were located at a height of about 15 cm above the shoulder; target 2 (black dot) was placed 25 cm to the left relative to target 1 (black triangle), and target 3 (black square) was positioned 25 cm behind target 1. Thus the workspace of the right shoulder ranged on average from about 28 cm (targets 1 and 2) to 52 cm (target 3) in distance. Azimuth angles from the shoulder to the targets were on average -27° for target 1, +27° for target 2 and -14° for the most distant target 3 (negative azimuth angles indicate positions to the right). Since the size and direction of the step varied slightly between trials, the distances of the targets relative to the shoulder varied as well. After target extinction the framework was canted away (arrow). Solid grey lines indicate the 90 x 90 x 90 cm frame, which was illuminated in the FRAME condition.

Figure 2
Top view of the pointing positions for subject JV in the FINGER condition (A), DARK condition (B) 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). The pointing positions are indicated with the small open symbols corresponding to the target. 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).

Figure 3
Example of the relation between the variability in pointing and the variability of the step, for subject JV (same data as in Figure 2) in the FINGER condition, for targets 1 (left column), 2
(middle column) and 3 (right column), respectively. Regression plots are shown for the variability in the step and pointing for sideward direction (top rows) and forward direction (bottom rows) separately. A regression fit is only displayed, when the relation between pointing and the step is significant (p<0.05).

**Figure 4**
Top view of the average trajectories of fixation from step onset to step offset for subject MA in the FINGER condition (A), DARK condition (B) and FRAME condition(C). Target positions are indicated with filled dots. Arrows indicate the evolution of the gaze trajectories in time. Open symbols indicate gaze position at the time of pointing (about 1s after step offset): a triangle for target 1, a dot for target 2 and a square target 3. For clarity, the trajectory for target 3 is indicated by a thin line, whereas the trajectories for targets 1 and 2 are indicated by a thick line.

**Figure 5**
Difference between average fixation relative to perfect fixation as a function of time for target 1 (thin line), target 2 (normal line) and target 3 (bold line). Standard deviations are indicated by an error bar at the time when the target is fixated (t= 0.5 s), just before the cue to start the movement (t= 2.5 s) and when the subject points to the target (t= 4.5 s). Vertical grey bars represent the interval of target presentation (0.0 s < t < 1.0 s) and the interval of pointing (4.1 s < t < 5.1 s). The vertical line at t= 3 s indicates the presentation of the auditory tone that indicated the end of the delay period.

**Figure 6**
Top view of fixation position at the end of the step (A-C) and at the time of pointing (D-F) for subject JV in the DARK condition (left column), FINGER condition (middle column) and FRAME condition (right column). Target positions are indicated by filled symbols: a triangle (target 1), a dot (target 2) and a square (target 3). The gaze positions at the time of pointing are indicated by small
open symbols corresponding to the target symbol. Ellipses show the 95% confidence distribution of the corresponding pointing positions.

**Figure 7**
Overview of the constant errors of gaze relative to the target position directly after the step (A-C), and at the time of pointing (D-F). Constant pointing errors are shown in panels G-I. Different symbols refer to data from different subjects (see inset). Symbol fillings correspond to the target (filled for target 1, dot for target 2, open symbol for target 3). The location of the targets is indicated by a small black dot. The constant errors are displayed for the DARK condition (left column), the FINGER condition (middle column) and the FRAME condition (right column), separately.

**Figure 8**
Covariance between pointing and gaze after correction for a mutual correspondence to step size as a function of time from the end of the step to the end of the pointing movement for distance (panels A, B, and C in top row) and direction (panels D, E and F in bottom row) relative to the cyclopean eye, for all subjects separately. The number of trials differs slightly between subjects (overall range: 26 to 40 trials) and consequently so does the 95% confidence value. In each panel, the grey horizontal bars covers the 95% confidence values for all subjects within the condition. The covariance is displayed for the DARK condition (left columns), the FINGER condition (middle column) and the FRAME condition (right column), separately. Different labeling of the lines refers to the covariance traces of different subjects (see caption).

**Figure 9**
Simulated trajectories of gaze during the step for a constant radial drift in gaze (bold trajectories), and the measured trajectories taken from Figure 3A (thin trajectories). The simulated trajectory is constructed at 5 equidistant time intervals during the step, which result in equally sized drift-segments, indicated by dots along the simulated trajectory. The simulated trajectory starts at the target (thick black dot). The end of the simulated trajectory is chosen such that the forward
component of the simulated end point corresponds to the forward component of the end point of the measured gaze drift (open circle). The cyclopean eye position (which serves as the origin of the radial drift) translates with a bell-shaped velocity profile, which results in 4 translational segments corresponding to equal time intervals but of different length along the line from the cyclopean eye position before the step to its position after the step. Dashed lines indicate the direction of the radial drift, which changes according to the position of the cyclopean eye during the step.

**Figure 10**
Schematic illustration of how underestimation of the step size may lead to a covariance 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 end point of the step (tip of the white arrow) towards the target (dashed lines), but originates from the actual position (tip of the black arrow). Two ellipses represent the estimated distributions of the step end points and the distribution of the corresponding pointing positions.
LEGENDS TO TABLES

Table 1
Number of subjects that showed a significant covariance between the variability of pointing and stepping. Subjects are counted if the covariance was significant either in forward direction, in sideward direction or in both. In each condition, six subjects participated.

Table 2
Number of subjects that showed a significant covariance between the variability in fixation at the end of the step and stepping. Subjects are counted if the covariance was significant either in forward direction, in sideward direction or in both. In each condition, six subjects participated.
Figure 1
Figure 2
sideward

forward

Figure 3
Figure 4
Figure 5
Figure 6
Figure 7
Figure 8
Figure 9
Figure 10