Exp Brain Res (1999) 125:50–60

RESEARCH ARTICLE

W.P. Medendorp · S. Van Asselt · C.C.A.M. Gielen

Pointing to remembered visual targets after active one-step self-displacements within reaching space

Received: 12 January 1998 / Accepted: 11 August 1998

Abstract We studied pointing movements to remembered visual targets in a completely darkened room with and without self-made step movements in order to investigate in which coordinate system and to what extent target representations relative to the body are updated for self-induced egomotion. A small red-light-emitting diode on the fingertip provided visual feedback about fingertip position at all times. We asked subjects to make pointing movements that started 2 s after disappearance of a visual target. In this interval of 2 s the subject did or did not make a step. The pointing errors without a step showed that subjects undershot faraway targets in a systematic way, whereas they sometimes overshot nearby targets. We found that the step causes larger pointing errors both in amplitude and direction with a bias in the direction of the step. We explored three different versions of a descriptive model in which polar coordinates were used to describe the pointing movement, and in which either Cartesian or polar coordinates were used to update target position relative to the shoulder for the step. The results suggest that incorporation of the step displacement in the new target position relative to the subject is done in a Cartesian frame of reference. Moreover, the amplitude of the step displacement tends to be underestimated by subjects.

Key words Pointing errors · Remembered target Navigation · Active self-movements · Human

Introduction

In many sensorimotor tasks, such as pointing to a visual target, various frames of reference are involved. Initially, visual information is encoded in a retinal coordinate system, when it enters the brain. For the process of translating the visual information about target position and arm position into appropriate motor commands, several hypotheses have been put forward proposing that end point position of reaching is specified in shoulder-centered coordinates (Soechting and Flanders 1989a, 1989b; Flanders et al. 1992), hand-centered coordinates (Flanders et al. 1992; Gordon et al. 1994), or viewer-centered (McIntyre et al. 1997) frames of reference. In most of these studies subjects did not move themselves relative to the targets but only made arm movements to point to the targets. However, in many normal conditions, subjects frequently move relative to targets in the environment before reaching or pointing to a target. In such a case, the internal representation of target position has to be updated for movements of the body in order to preserve a correct representation of target position relative to the subject. The present paper investigates the coordinate system used and the extent to which the internal representation of position of remembered visual targets is updated for self-initiated movements, by asking subjects to point to remembered targets without and after active movements (a step in one out of three orthogonal directions) of the subject.

Several studies have shown that pointing to visual targets without movements of the subject is complex by itself. For example, it is well known that subjects make consistent errors when asked to point to visual targets in space (Soechting and Flanders 1989a). Both undershoot (Soechting and Flanders 1989a; Darling and Miller 1993; Gentilucci and Negrotti 1996; McIntyre et al. 1997) and overshoot (Foley 1975; Berkinblit et al. 1995; McIntyre et al. 1997) of reaching movements have been reported in the literature. These errors are different in conditions when the visual target is visible throughout the movement and in conditions when subjects are asked to point to a remembered target position, i.e., when the target disappears before pointing to the target. These errors in pointing have been attributed to "errors in sensorimotor processes" (Soechting and Flanders 1989a, 1989b) and were found to depend critically on visual

W.P. Medendorp (✉) · S. Van Asselt · C.C.A.M. Gielen
Department of Medical Physics and Biophysics,
University of Nijmegen, Geert Grooteplein 21,
6525 EZ Nijmegen, The Netherlands
e-mail: pieter@mbfys.kun.nl
Tel.: +31-24-3614237, Fax: +31-24-3541435

feedback (Berkenblit et al. 1995), proprioceptive information (Soechting and Flanders 1989a, 1989b; Hocherman 1993), eye orientation (Enright 1995), and delay between target offset and pointing (McIntyre et al. 1997).

In all these studies it was found that the pointing errors were elliptically distributed where the orientation of the ellipse depends on the directon of the target. This was interpreted as evidence for independent parallel planning of movement for distance and direction in static pointing movements (Soechting and Flanders 1989a, 1989b; Bock and Arnold 1992; Gordon et al. 1994; Berkenblit et al. 1995). Moreover, as mentioned above, several studies have indicated that end point of reaching may be specified in shoulder-centered, hand-centered, or viewer-centered frames of reference. This means that a spherical coordinate system with an origin chosen at the shoulder, the hand, or the eyes may be more appropriate to study static pointing movements than an orthogonal Cartesian coordinate system. Based upon the results of Soechting and Flanders (1989a, 1989b), in the present study the errors during static pointing movements will be investigated in a shoulder-centered spherical frame of reference.

In this study, we were primarily interested in the problem of how target position relative to the body can be updated for self-induced egomotion. Therefore, we have studied reaching movements of subjects with and without a step, in as much as possible the same stimulus conditions. For this purpose, we instructed subjects to make reaching movements to a remembered visual target. A small visual target was presented in a completely darkened room for a period of 1 s and subjects were instructed to bring the tip of the index finger to the remembered target position about 2 s after offset of the visual stimulus. In the intervening period, subjects did or did not make a step. In this way, the delay between target offset and reaching was the same in both conditions. The latter is important since a recent study (McIntyre et al. 1997) showed that errors in pointing may depend on the time period between target offset and pointing movement.

Two main sources of errors can be distinguished in the finger position after pointing without a step, namely errors due to perception or memorization of target position and errors due to the pointing movement itself. In the step condition additional errors may be introduced, for example, errors related to the internal representation of the step and errors due to the computation of a new target position by incorporation of the step. The latter are equivalent to the computation of the new position of the subject relative to the target.

The problem of how subjects perceive egomotion is not new. Several studies in humans (Bloomberg 1991; Klatzky et al. 1990; Loomis et al. 1992, 1995; Mittelstaedt and Glasauer 1991; Israël et al. 1993; Israël et al. 1997; Amorim et al. 1997) have shown that subjects can estimate the traveled distance from self-generated information, i.e., without external sensory cues. For example, when subjects were walking with closed eyes to previously viewed targets in a well-lit environment their performance was quite accurate (Loomis et al. 1992; Rieser 1989). However, under dark viewing conditions it was recently found by Philbeck and Loomis (1997) that subjects when walking to targets in a range from 79 from 500 cm tend to overshoot the distance to near targets (they walked too far), whereas they undershoot the distance to far targets. Also Glasauer et al. (1994) found that subjects underestimated their displacement during active self-motion. However, when subjects were displaced passively (for example, subjects seated in a car) without any feedback or training, the target distance is undershot, indicating that subjects tend to overestimate their own displacement (Israël et al. 1993, 1997). Israël et al. (1997) showed that the performance of subjects in a car did not depend on whether subjects were displaced passively or actively by control of a joystick which could control velocity and direction of the car. The subjects in these studies on path integration and navigation could not use proprioceptive information from muscles and tactile receptors, which is directly related to egomotion. However, this information is available when subjects make voluntary steps. In order to allow the use of proprioceptive information, we asked subjects to make a step within reaching space and tested the accuracy of pointing without a step and after a step.

Until now, it has been unclear in which coordinate system target positions are updated for active displacements of the subject. In the present analysis, we explored a descriptive model in which polar coordinates are used to describe the pointing movement using either Cartesian or polar coordinates for the incorporation of the step in the pointing movement. We tested in which case the performance of the model (Cartesian or polar coordinates) was better by a goodness-of-fit analysis. Based upon this analysis we conclude that the incorporation of the step displacement in the new target position relative to the subject is done in a Cartesian frame of reference. Moreover, the results demonstrated that the step displacement tends to be underestimated by the subject.

Materials and methods

Subjects

Seven healthy adult volunteers (two women and five men, aged 21–45 years) participated in the experiment. Three of the subjects (P.M., S.A., and S.G.) were familiar with the purpose of the experiment. The results of these subjects were not different from those of the other subjects. All subjects gave informed consent to participate in the experiment. All subjects were right-handed, and were free of any known sensory, perceptual, or motor disorders. All pointing movements were made using the right (preferred) arm.

Experimental setup

Subjects stood erect in a completely darkened room and were tested with two different sets of target configurations. The targets of the first set (target set A) had fixed positions relative to the subject. Targets of the second set (target set B) appeared at various locations relative to the subject. In target set A four red-light-emitting diodes [LEDs, type HLMP 3762, 10 millicandela (mcd)] served as targets and were attached to a flat T-shaped mold. All “legs” of the T had equal length such that the three targets at the end of the legs were located at a distance of 35 cm from the central target. For each trial the mould was placed at a fixed position relative to the subject’s shoulder in a transversal plane at the subject’s shoulder height. Targets 1, 2, and 3 were on a straight line at a distance of 30 cm in front of the subject. The leftmost target (target 1) was in front of the subject’s eyes. Targets 2 and 3 were at 35 and 70 cm, respectively, to the right of target 1 (see target positions in Fig. 2). Target 4 was located at a distance of 35 cm from target 2, which is at a distance of 65 cm from the subject. After one of the four LEDs had been lit for 1 s, the experimenter withdrew the T-shaped mold such that the subject could not touch the targets when pointing to the remembered target position. Subjects were tested in two conditions as described below. Five out of the seven subjects were tested using target set A. All seven subjects were tested with target set B.

The targets of target set B were presented at various, quasi-random positions by the experimenter. The experimenter tried to restrict the targets to positions in a transversal plane at the subject’s shoulder height. Deviations from the transversal plane remained within 10° below or above the shoulder. The distance of the targets varied between 20 and 70 cm relative to the subject’s shoulder. The directions of the targets ranged from 60° medially to 60° laterally to the subject’s sagittal plane. As before, the target was an LED (HLMP 3762, 10 mcd) fixed at a little stick held by the experimenter. The experimenter switched on the LED for 1 s and then withdrew the target. All subjects participated in this version of the experiment (i.e., using target set B) and were tested in two conditions, a STATIC condition and a STEP condition (see below).

During the experiment, infrared-light emitting diodes (IREDs) were attached to the subject’s limb segments: shoulder (acromion) and elbow (lateral epicondyle) as well as on the nail of the right index finger and on the target LED. Furthermore, the subject wore a helmet with three additional IREDs to measure head position. All IRED positions were measured in three dimensions using an OPTOTRAK 3020 system (Northern Digital Inc.), which operates by tracking active IREDs in a precalibrated space by means of three lens systems. It provides the three-dimensional positions of the IREDs with an accuracy of about 0.1 mm in a range of about 2.3 m^3. The coordinates of the IREDs were transformed to a right-handed coordinate system with the x–y plane aligned with the subject’s transversal plane, and the z-axis orthogonal to this plane according to the conventions of a right-handed coordinate system. The positive x-axis was chosen to the right and the positive y-axis was pointing forward relative to the subject.

The positions of the IREDs were measured for a period of 1 s, both during the presentation of the target and when the subject had brought the fingertip to the remembered target position. To provide visual feedback about the subject’s finger position, another visible LED (the same type as the target LED) was placed on the fingertip. This LED was visible throughout the experiment. Since we were interested in the effect of the movement of the subject on pointing accuracy, which took place in the horizontal (x–y) plane, we only focussed our attention on the pointing accuracy in that plane. For that reason, the data will be treated as being two dimensional and will be analyzed in both polar and Cartesian coordinate systems according to the model described below. For reasons mentioned in the “Introduction”, we studied static pointing movements (i.e., without a step of the subject) in a spherical coordinate system using polar coordinates relative to the subject.

Paradigm

Subjects made pointing movements in two conditions: a STATIC condition and a STEP condition. Each trial started with the presentation of the target for 1 s, which then disappeared both visually and physically. This prevented the subject from touching the target, which would have provided feedback information about the location of the target.

STATIC condition

In this condition the subject was standing at a fixed position in the experimental room. After the target disappeared, the subject had to wait for 2 s before being allowed to bring the tip of the index finger to the remembered target location. No restrictions were imposed on head or eye movements. Measurement of head position revealed that during the experiment all subjects rotated their head in the direction of the target within the 1-s presentation of the visual target.

STEP condition

In this condition the subject was standing at a fixed starting position in the experimental room. After the target disappeared the subject made a step in one out of three directions. The direction of the movement, which actually was a step of less than 1 m, was verbally instructed by the experimenter, and could be sideward (left or right along the x-axis), or forward (y-direction). The step directions were equally distributed over the three directions. The subject was instructed not to turn the body during the self-displacement. Using target set A only steps in the rightward direction were made by the subject. The size of the step was left free to the subject, as long as he was able to point to the remembered target position in the new position. After each trial, the room lights went on such that the subject could return to the starting position, which was marked on the ground and which was the same position as the position in the static condition. This light also prevented the subject from losing his orientation for left, right and forward. In addition, the room light prevented adaptation to the dark room by the subject. Also in this condition there was no constraint on head or eye movements.

For reasons mentioned in the “Introduction”, the time delay between target offset and pointing movement (2 s) was the same in both the STATIC condition and the STEP condition. In the STEP condition the subject could make the step-movement in this 2-s time period, which enabled us to exclude any effect of time differences between the presentation of the target and the pointing moment in both conditions.

Data analysis

Static pointing data were analyzed in a spherical coordinate system with the origin at the shoulder. To characterize the shape of the distribution of the end points of the tip of the index finger for fixed targets (target set A) in the STATIC condition, we used a principal components analysis (Sokal and Rohlf 1981; Gordon et al. 1994; McIntyre et al. 1997). In this procedure two axes are determined: the principal axis corresponding to the direction with the largest variability and an axis orthogonal to this axis in the horizontal plane of target positions. The directions of these axes correspond to the eigenvectors of the covariance matrix of the end points of the tip of the index finger relative to the targets. The eigenvalues are equivalent to the variances along the corresponding eigenvectors of the matrix. The eigenvector with the largest eigenvalue (the direction with the largest variance) defines the principal axis of the distribution. The other axis is orthogonal to this principal axis. With the two axes an ellipse can be constructed which contains 95% of the end points.

In the case of target set B (i.e., various target locations), the static pointing results were analyzed by minimizing the residual error vector $\vec{\varepsilon}$ in the equation:

$$\vec{R}=A\vec{T}+\vec{C}+\vec{\varepsilon} \qquad (1)$$

where $\vec{R}$ and $\vec{T}$ represent the finger position and target location, respectively, in polar coordinates (r,φ) relative to an origin at the shoulder. A is a matrix, $\vec{C}$ is a constant vector, and $\vec{\varepsilon}$ is random noise with mean value zero. For an ideal subject, who made no errors (neither due to the pointing movement nor due to perception or storage of the target location), matrix A should be the identity matrix, the vector $\vec{C}$ should be zero, and the noise $\vec{\varepsilon}$ should be zero too.

To analyze the pointing results obtained with target set B in the STEP condition, we used a descriptive model (model 1), which is schematically illustrated in Fig. 1A. In this model we chose the origin at the right shoulder [S] of the subject. Vector $\vec{T}$ gives the location of the target [T] relative to the shoulder when it is briefly presented to the subject. The step displacement of the subject is given by vector $\vec{S}$. If the subject has a correct percept of target location T, as represented by $\vec{T}$, but does not account for the step $\vec{S}$ at all, the fingertip position at the end of the pointing movement will be incorrect as indicated by $\vec{N}$. However, if the subject pointed to the new target position after the step without any errors, he would have updated the internal representation of the remembered target position according to the relation $\vec{S}=\vec{T}-\vec{R}$. We, therefore, define the internal representation of the step displacement $\vec{S}_{int}$ of the subject by the relationship:

$$\vec{S}_{int}=\vec{T}-\vec{R} \tag{2}$$

such that when $\vec{S}_{int}=\vec{S}$ the subject has correctly updated the target position for his step displacement.

In this descriptive model (Eq. 2) it is assumed that all pointing errors are due to the step. This is a simplification, since subjects also make errors in static pointing movements. These errors can be due to either an erroneous percept or storage of the target location or due to errors in the motor planning of the pointing movement. When we assume that the errors in the STATIC condition are due to an erroneous percept or storage of the target position, the incorrectly memorized target position will induce errors in the pointing movement in the STEP condition. Accordingly, we can correct Eq. 2 by:

$$\vec{S}_{int}=\vec{T}'-\vec{R} \tag{3}$$

in which $\vec{T}'=A\vec{T}+\vec{C}$ represents the perceived or memorized target vector by the subject, according to Eq. 1. Figure 1B gives an illustration of Eq. 3, which will be referred to as descriptive model 2. In model 2 it is assumed that the values of matrix A and vector $\vec{C}$, as determined for each subject separately in the STATIC condition, also hold for the STEP condition.

When we assume that the errors in the STATIC condition are due to errors in the motor planning of the pointing movement, this will affect errors in the STEP condition in a different way. For this case, we have to correct Eq. 2 by:

$$\vec{S}_{int}=\vec{T}-\vec{R}' \tag{4}$$

in which $\vec{R}'=A^{-1}(\vec{R}-\vec{C})$ represents the pointing vector as corrected by Eq. 1 with values for A and $\vec{C}$ obtained in the STATIC condition for each subject separately. This descriptive model, designated as model 3, is illustrated in Fig. 1C.

The relationship between $\vec{S}_{int}$ and $\vec{S}$ in models 1–3 can be fitted in both Cartesian and polar coordinates by minimizing the residual error vector $\vec{\varepsilon}$ in a regression analysis by the equation:

$$\vec{S}_{int}=B\vec{S}+\vec{D}+\vec{\varepsilon} \tag{5}$$

in which $\vec{S}$ is the vector representing the actual step displacement made by the subject, B, a matrix which relates the actual step $\vec{S}$ to $\vec{S}_{int}$, $\vec{D}$ a constant vector, and $\vec{\varepsilon}$ random noise with mean value zero. For an ideal subject, who made no errors in incorporation of his egomotion displacement, B should be the identity matrix, the vector $\vec{D}$ should be zero, and the noise $\vec{\varepsilon}$ should be zero too. When subjects make errors, matrix B as well as vector $\vec{D}$ tell us how the internal representation of the step is related to self-induced displacements. The coordinate system which fits the data best using Eq. 5 is assumed to be the reference frame in which target representations are updated with respect to the body for self-displacements.

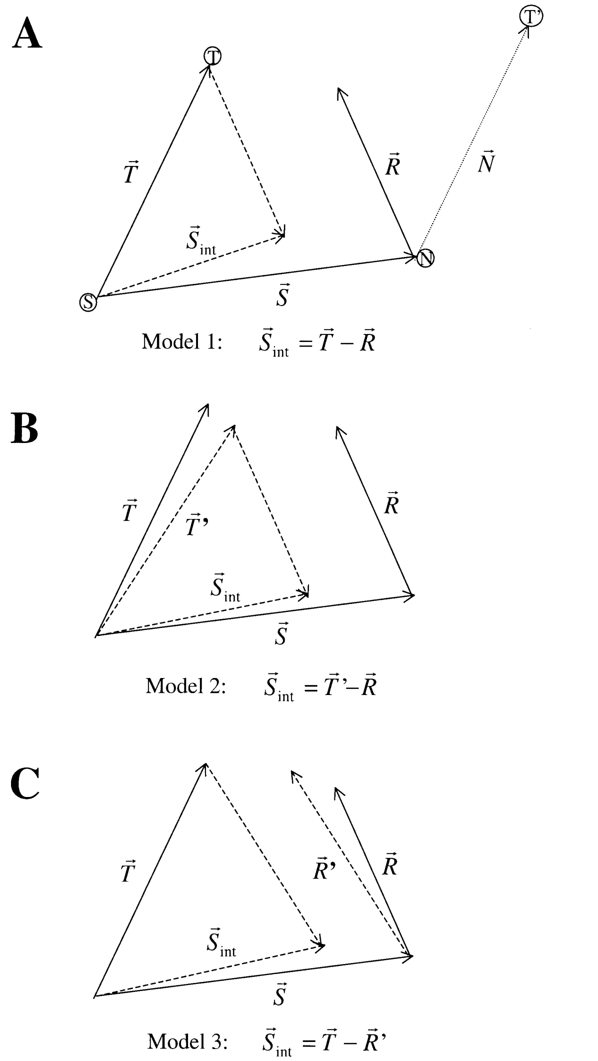

Fig. 1A–C Illustration of the descriptive models tested in this study. The vector $\vec{T}$ represents the position of the target (T) relative to the subject's shoulder (S) before he made a step. The vector $\vec{S}$ represents the new shoulder position (N) after the step relative to the shoulder position (S) before the step movement. The three models give different descriptions for the computation of the internal step displacement. **A** When the subject correctly perceives target location (T), but does not account for the step displacement at all, *Model 1* predicts that fingertip position after the pointing movement $\vec{N}$ will end up in (T'). When the subject performs perfectly, the internal representation of perceived step-displacement as given by the relationship $\vec{S}_{int}=\vec{T}-\vec{R}$ is equal to the actual step-displacement $\vec{S}$. **B** *Model 2* accounts for an erroneous percept or storage of target position as source of the errors in the static pointing task. **C** *Model 3* accounts for errors in motor planning of the pointing movement as being the source of the errors in the static pointing condition

Results

We shall now describe the results of the pointing experiments in the two conditions (i.e., for pointing to a target without and after a step) as described in the "Methods" section. As outlined in "Methods," subjects were given two different sets of target positions. The first (target set

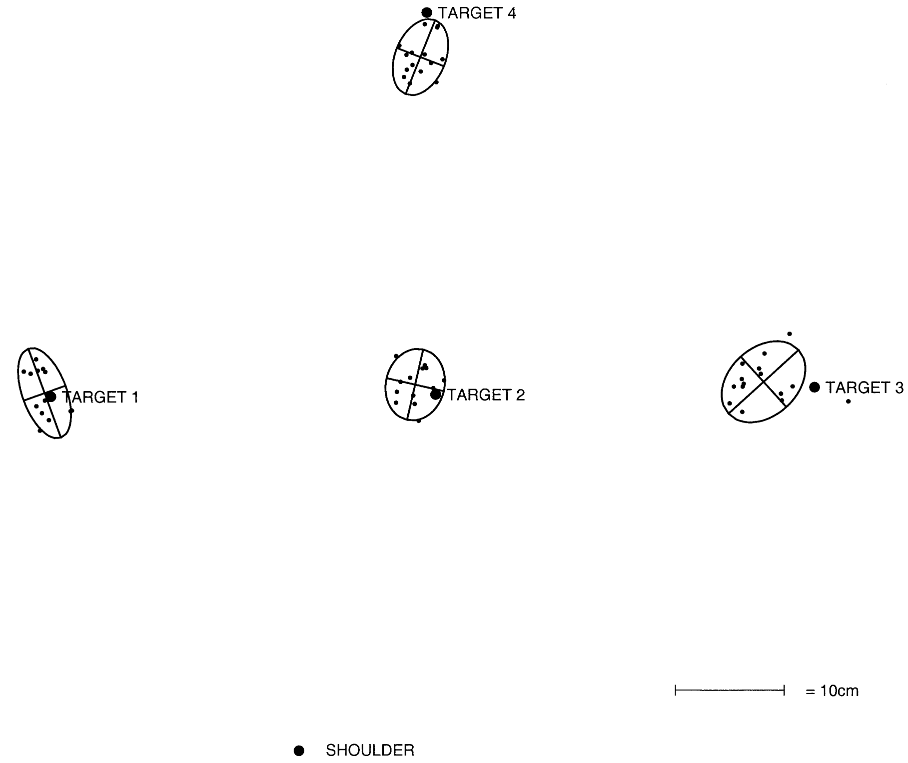

Fig. 2 End points of pointing movements for one subject to four remembered targets in the STATIC condition (target set A). The subject made 12–15 movements to each of the four targets. The end points of the pointing movements are elliptically distributed. The *thick dots* represent the target positions

A) with four fixed target positions was used to investigate the distribution of the pointing errors in the two conditions. The other set (target set B) with multiple target positions was used to test the descriptive models, defined by Eqs. 2–4 in both Cartesian and polar coordinates.

Static condition

Figure 2 presents data of a typical subject pointing to fixed target positions relative to the shoulder (target set A). Some small deviations of the mean end point relative to the target position can be observed for all targets. In all trials the subject undershot the distance of target 4. Also there is a small error in the pointing direction to targets 2 and 3. Furthermore, Fig. 2 shows that the ellipses, which indicate the area which contains 95% of the distribution of end positions of the index fingertip for each target, are more or less of equal size. The long axes of the ellipses are approximately oriented towards the subject, indicating that the variability in pointing distance is larger than the variability in pointing direction. The mean variable error across all subjects was 4.1 cm (SD=2.5 cm). In comparison with earlier studies (e.g., Gentilucci and Negrotti 1996; McIntyre et al. 1997), Fig. 2 shows no new features and just serves to illustrate the scatter of the pointing data.

To further investigate the effect of target position on pointing accuracy, Fig. 3 shows the data of all subjects pooled in polar coordinates for the STATIC condition for various target positions (target set B). Figure 3A shows

Table 1 Fit results of the parameters in Eq. 1 for the STATIC condition. Only the diagonal coefficients of matrix *A* are shown, since the values of the off-diagonal components were small and not significantly different from zero. After each value its standard deviation is given in *parentheses*. The goodness-of-fits R^2 were higher than 0.87, indicating that the data can be well described by the model

Subject	A_{rr}	$A_{\varphi\varphi}$	C_r (cm)	C_φ (deg)
S.A.	0.73 (0.02)	0.98 (0.01)	7.2 (1.8)	–4.7 (1.5)
M.S.	0.74 (0.04)	0.97 (0.01)	12.6 (2.3)	–7.1 (2.3)
M.Z.	0.91 (0.03)	0.99 (0.01)	4.1 (1.7)	–0.8 (1.4)
P.M.	0.81 (0.04)	0.95 (0.01)	8.9 (2.3)	–0.4 (2.2)
P.S.	0.69 (0.05)	0.98 (0.01)	11.3 (2.6)	–6.1 (1.8)
B.B.	0.80 (0.04)	0.99 (0.01)	6.4 (1.8)	–3.4 (1.6)
S.G.	0.78 (0.03)	0.96 (0.01)	3.6 (1.8)	–8.6 (1.3)
Pooled	0.77 (0.02)	0.97 (0.01)	8.2 (1.1)	–3.7 (0.8)

the target distance versus the distance of the fingertip at the end of the pointing movement, relative to an origin chosen at the shoulder. In agreement with the data shown in Fig. 2, Fig. 3 shows that targets at larger distances are undershot by the subject (sometimes more than 10 cm). This is obvious from the fact that the pointing data are in general located along a line with a slope smaller than 1. Figure 3B demonstrates that the directions of the targets are judged accurately. The data fall along a line that deviates only slightly from a line with slope 1 passing through the origin. Fitting Eq. 1 to the pooled data in polar coordinates reveals for the diagonal terms of matrix *A*, A_{rr}=0.77 (SD=0.02) and $A_{\varphi\varphi}$=0.97 (SD=0.01). The off-diagonal terms, which tell us something about the interaction between radial and azimuthal components of the pointing

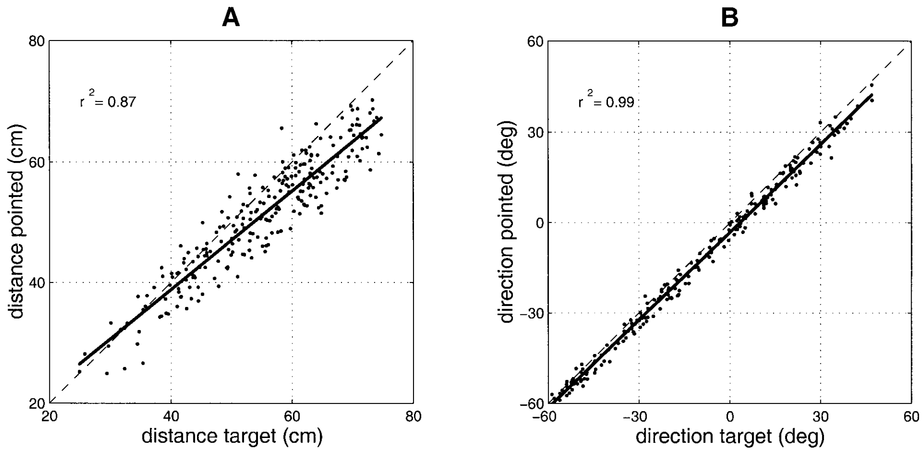

Fig. 3A,B Results of pointing movements for all subjects in polar coordinates. The measured position of the fingertip is plotted against the position of the target. Each data point represents the result of one trial. **A** shows an undershoot of pointing amplitude which is larger for targets far away from the subject. **B** shows the direction of pointing. These data points are scattered around the line $y=x$, indicating that the direction of the target is well judged by the subject. The goodness-of-fit R^2 is a measure of how well the data can be fitted by Eq. 1

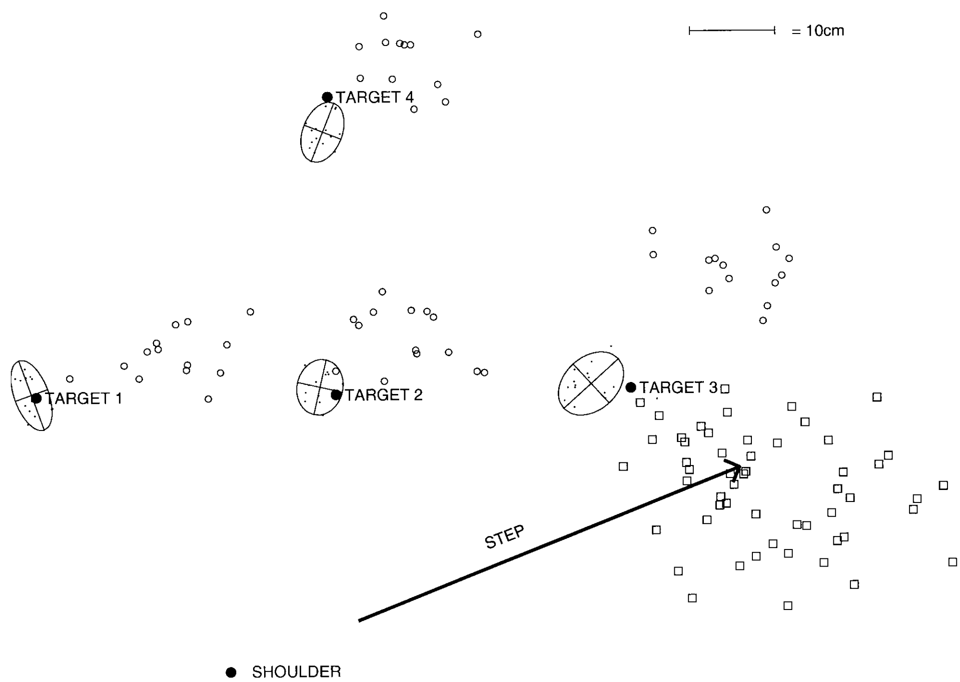

Fig. 4 End points of pointing movements without a step (*small thin dots near the ellipses*) and after a step (*open circles*) to targets represented by a *thick dot*. The data are from the same subject as in Fig. 2. The subject made 55 steps to the right. The shoulder positions after the step are represented by the *open squares at the lower right*, indicating the extent of variability in step size. The pointing results in the STEP condition (*open circles*) are shifted in a rightward direction relative to the target, which is in the same direction as the movement

vector $\vec{R}$ and target vector $\vec{T}$, were small ($A_{r\varphi}$=0.03±0.01 cm/deg and $A_{\varphi r}$=0.01±0.01 deg/cm). The components of vector $\vec{C}$ (C_r=8.2±1.1 cm and C_φ=–3.7±0.8 deg) reveal a bias component in both the radial and azimuthal direction which is significantly different from zero. These fit results indicate that the amplitude of the pointing movement by the subject depends on the target distance: an undershoot for large distances and hardly any undershoot and sometimes even an overshoot for small target distances.

The fit results of all subjects are listed in Table 1. The goodness of fit R^2 varied between 0.87 and 0.99 for the radial component and was near 0.99 for the azimuthal component for various subjects, indicating that, in general, Eq. 1 could account for more than 87% of the pointing errors. Since the off-diagonal terms, which describe the interaction between radial and azimuthal components of the pointing vector $\vec{R}$ and target vector $\vec{T}$, were small (mean values: $A_{r\varphi}$=–0.02±0.02 and $A_{\varphi r}$=0.05±0.06) and not significantly different from zero (*t*-test, *P*>0.05), these off-diagonal terms are not listed in the table and only the diagonal components of matrix *A* are presented. As shown in Table 1, both the A_{rr} and $A_{\varphi\varphi}$ components deviate significantly from 1 (χ^2-test for A_{rr}: $\chi^2_{(6)}$=392, *P*<0.01; and for $A_{\varphi\varphi}$: $\chi^2_{(6)}$=49, *P*<0.01). The components of vector $\vec{C}$ indicate a bias component and range from 3.6 to 12.6 cm in the radial direction and from –8.6 to –0.4 deg in the azimuthal direction. For the whole population of subjects these values were significantly different from zero in a χ^2-test (for C_r: $\chi^2_{(6)}$=4183, *P*<0.01; and for C_φ: $\chi^2_{(6)}$=136, *P*<0.01).

Step condition

Figure 4 shows the end positions of the pointing movements without a step and after a step for the same subject

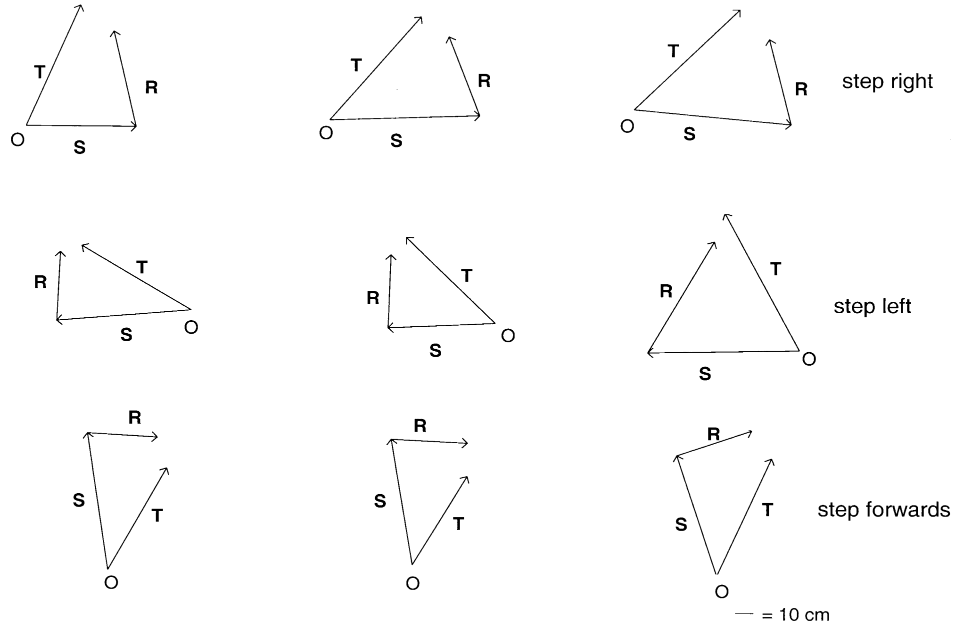

Fig. 5 Selection of pointing movements to illustrate the main findings for the STEP condition ($\vec{T}$, the vector representing the target position relative to the shoulder; $\vec{S}$, the vector which gives the movement of the subject; and $\vec{R}$, the vector denoting the fingertip position with respect to the shoulder). The *upper, middle, and lower figures* illustrate three pointing movements after a step in the right, left, and forward direction, respectively. This figure illustrates that the step gives rise to a bias in pointing in the direction of the step

as in Fig. 2. When a step was made, the direction of the step was in the rightward direction. The pointing results for the static condition are given by the tiny dots surrounded by the ellipses and are identical to the results shown in Fig. 2. The open circles represent the end points of the pointing movements for each target position after the subject has made a step. The open squares at the lower right give the shoulder positions of the subject after each sideward step. The data clearly show that the end points are consistently biased to the right of the targets, i.e., biased in the same direction as the step. Moreover, the scatter in the pointing data in the STEP condition is much larger than in the STATIC condition, indicating that the step contributes to a large extent to the pointing errors.

In order to test whether the bias in pointing accuracy after a step is related to the direction and size of the step, pointing accuracy to targets at different positions (target set B) was tested for steps of different amplitude in different directions. Some typical results are shown in Fig. 5, which shows the target position $\vec{T}$, step movement $\vec{S}$, and pointing movement $\vec{R}$ after the step for several trials. The upper panel illustrates three trials in which the subject made a step to the right. In all three trials the subject consistently pointed with a deviation to the right relative to the target. The middle panel shows three trials in which the subject made a step to the left. For this step direction there is a tendency for the subject to point with a deviation to the left of the target. The bottom panel shows data for step movements in the forward direction. In this case the end position of the pointing movement falls short of the target position. These data suggest that subjects do not correctly compute new target positions after self-induced egomotion, or correspondingly seem to underestimate their step size. To test in which reference frame the internal representation of the step is computed, we applied our descriptive models (see Eqs. 2–4) to the data and tested whether the data could be best described in Cartesian or polar coordinates.

Table 2 presents the mean values of all subjects for the diagonal components of matrix B and the components of vector $\vec{D}$ for both Cartesian and polar coordinates for the three models as outlined in the "Methods" section. As in Table 1, the off-diagonal terms of matrix B are not listed in the table. In Cartesian coordinates, the off-diagonal terms were not significantly different from zero in all subjects (i.e., no significant cross-talk between the x- and y-component). However, using the polar coordinates we found a small but significant coupling between the r-component and φ-component (range –0.62 to 0.66 mm/deg) in all subjects. The model performance is expressed by R^2 values, which are the goodness-of-fit values obtained by fitting Eqs. 2, 3, and 4 to the data. As shown in the table, the overall performance of all three models is better in Cartesian ($R^2 \approx 0.85$) than in polar coordinates ($R^2 \approx 0.70$). This is also illustrated by the large standard deviation of the components of bias vector $\vec{D}$ in polar coordinates. The bias in the r-component varied between –30 and 30 cm and the φ-component ranged between –23 and 7 deg among subjects. For Cartesian coordinates, the components of vector $\vec{D}$ as well as the diagonal terms of matrix B have much smaller standard deviations. The bias varied between +5 and –5 cm and is on average zero. The small range around zero for the bias components in the Cartesian coordinate system implies that the update of the target representations is completely described by matrix B. This makes sense since we expect that subjects do not perceive self-displacements for $\vec{S}=\vec{O}$, which implies a bias equal to zero. In summary, in order to preserve the representation of target positions relative to the subject, our data suggest a Cartesian reference frame in which internal representations of target positions are updated for movements of the body. Another criterion upon which the most prefera-

Table 2 Fit results and model performance expressed by R^2 values. After each value its standard deviation is given in *parentheses*. The R^2 values are shown separately for each component, i.e., (x,y) for Cartesian coordinates and (r,φ) for polar coordinates. The overall performance of all three models is higher in Cartesian than in polar coordinates. Model 2 performs slightly better compared to the other models in Cartesian coordinates

	Cartesian						Polar					
	B_{xx}	B_{yy}	$R^2{}_x$	$R^2{}_y$	D_x (cm)	D_y (cm)	B_{rr}	$B_{\varphi\varphi}$	$R^2{}_r$	$R^2{}_\varphi$	D_r (cm)	D_φ (deg)
Model 1	0.85 (0.10)	0.65 (0.11)	0.99 (0.01)	0.83 (0.16)	0.3 (2.8)	3.6 (2.7)	0.95 (0.28)	0.96 (0.04)	0.72 (0.18)	0.99 (0.01)	–6.5 (17.5)	–4.5 (6.9)
Model 2	0.90 (0.10)	0.75 (0.12)	0.99 (0.01)	0.87 (0.15)	0.3 (2.7)	–0.9 (1.3)	0.90 (0.25)	1.02 (0.02)	0.72 (0.23)	0.99 (0.01)	–1.2 (14.9)	–6.9 (8.3)
Model 3	0.88 (0.11)	0.70 (0.13)	0.99 (0.01)	0.83 (0.16)	0.4 (3.2)	–1.2 (1.6)	0.89 (0.31)	1.02 (0.02)	0.68 (0.26)	0.99 (0.01)	–2.2 (18.9)	–7.6 (9.6)

Table 3 Fit results of descriptive model 2. Only the diagonal coefficients of matrix *B* are shown, since the values of the off-diagonal components were small and not significantly different from zero. After each value its standard deviation is given in *parentheses*

Subject	B_{xx}	B_{yy}	D_x (cm)	D_y (cm)
S.A.	0.93 (0.02)	0.69 (0.04)	–3.9 (1.0)	–0.6 (0.9)
M.S.	0.77 (0.01)	0.54 (0.15)	1.5 (0.5)	–0.2 (0.4)
M.Z.	0.77 (0.01)	0.68 (0.03)	–2.2 (0.9)	–1.4 (0.6)
P.M.	0.99 (0.01)	0.68 (0.06)	–0.6 (0.7)	1.1 (0.6)
P.S.	1.01 (0.02)	0.88 (0.03)	1.6 (0.9)	–2.7 (0.7)
B.B.	0.92 (0.01)	0.82 (0.03)	1.8 (0.5)	–2.1 (0.6)
S.G.	0.90 (0.01)	0.85 (0.02)	4.0 (0.7)	–0.6 (0.6)

ble coordinate system might be chosen is that in which the amount of cross-coupling between the two components (represented by the off-diagonal terms of matrix *B*) is minimal. Also this criterion suggests a Cartesian frame of reference. From now on, we therefore continue our data analysis using a Cartesian model description to incorporate the step movements.

Since model 2 gives a slightly better fit than the other two models, we have shown interindividual differences among subjects in Table 3 using this model. Only the diagonal terms of the matrix were presented since the off-diagonal terms were small and not significantly different from zero. The mean values for the diagonal components of matrix *B* were 0.90 (SD=0.10) and 0.75 (SD=0.12) for B_{xx} and B_{yy}, respectively (see Table 2). Although these coefficients were not significantly different from the value 1 for each single subject (e.g., subjects P.M. and P.S. update target positions almost perfectly for steps in the *x*-direction), the data for the whole population revealed a statistically significant deviation from 1 (for B_{xx}: $\chi^2_{(6)}=1166$, $P<0.01$; and for B_{yy}: $\chi^2_{(6)}=425$, $P<0.01$). Furthermore, an ANOVA revealed significant differences between B_{xx} and B_{yy} (ANOVA $F_{(1,6)}=12.4$, $P<0.05$), indicating that the direction of the step did have an effect on the update of target position relative to the subject. With regard to vector $\vec{D}$, the data for the whole population revealed a rather small (less than 4 cm) but statistically significant deviation from zero (for D_x: $\chi^2_{(6)}=79$, $P<0.01$; and for D_y: $\chi^2_{(6)}=41$, $P<0.01$). The differences between D_x and D_y were not significant (ANOVA $F_{(1,6)}=1.1$, $P>0.05$). In summary, our data suggest that internal representations of step displacement depend almost entirely on the amplitude and direction of the actual body-displacement of the subject.

Discussion

In the present study we have investigated for the first time the ability of human subjects to account for self-initiated movements (steps) within reaching space when pointing to remembered target positions. We found that the step causes the pointing errors to increase in amplitude and to become biased in the same direction as the step (Fig. 4). Under the assumption that there is a linear relationship between the internal representation of the step displacement and the actual displacement of the subject, our descriptive models gave the best fits for a Cartesian frame of reference. Thus in order to preserve the target representation relative to the body, our data suggest that subjects compute the new target position in a Cartesian rather than a spherical reference frame. This is supported by the finding that the amount of cross-coupling between the two components is minimal for Cartesian coordinates. Furthermore, we found that our model 2 (which accounts for an erroneous percept of storage of remembered target position; see "Methods") gave a slightly better fit to the data than the other two models. This suggests that subjects account for the perceived or stored target position before the step, not the actual target position, after their step performance. The contribution to the pointing error by the step displacement denotes how well the step is incorporated in the pointing movement. Therefore, an undershoot was interpreted as an underestimation of the step amplitude. The underestimation of the step size could be 54% of the real step size. However, we also found two subjects (P.M. and P.S.) who incorporated their step displacement in the x-direction almost perfectly (see Table 3). This illustrates that the amount of underestimation varies among subjects. We never found that subjects overestimated their step size. In this respect the errors related to the step differ from errors in pointing for the static condition: step size is always underestimated, whereas in the static condition the pointing movement will reveal a smaller undershoot (and sometimes an overshoot!) for targets nearby. To further discuss the findings in the present study we will distinguish between the static pointing results (STATIC condition) and the pointing results after the step movement (STEP condition).

In general the results of the experiments in the static condition were in good agreement with findings reported in previous studies (Soechting and Flanders 1989a; Gordon et al. 1994; Berkenblit et al. 1995; Gentilucci and Negrotti 1996; McIntyre et al. 1997). The spatial distributions of the movement end points were elliptical in shape with a tendency of the major axis to be oriented towards the subject (Fig. 2). Based on these observations, we chose a spherical coordinate system with an origin at the shoulder (Soechting and Flanders 1989a, 1989b; Flanders et al. 1992) to analyze the static pointing data to various target positions. When analyzed in such a coordinate system we found that pointing movements showed an undershoot for targets faraway. This undershoot could be more than 10 cm. For nearby targets pointing movements were more accurate and for targets near the body pointing movements could even show a small overshoot. The finding of an overshoot for nearby targets and an undershoot for targets farther away might explain an apparent discrepancy between previous results in the literature: some authors reported an overshoot (e.g., Berkenblit et al. 1995), whereas others found an undershoot of target distance (e.g., Soechting and Flanders 1989a). This apparent discrepancy might well be explained by different target distances relative to the body in the various studies. With regard to pointing direction, we found that the direction of pointing was accurate for the static condition. These results support previous results (Soechting and Flanders 1989a, 1989b; Bock and Arnold 1992; Gordon et al. 1993) that distance and direction may be controlled independently.

There have been many suggestions as to the origin of the pointing errors. We cannot provide a full explanation for the pointing errors in our data. In the literature two hypotheses have been proposed which may be relevant. The first hypothesis is based on a nonlinear distortion of perceptual space. If perceptual space were to be distorted nonlinearly, as hypothesized by Wolpert et al. (1994), then the subject would have a wrong percept of target position in space. However, if the subject moves his finger to this incorrectly perceived target position in space, the finger may still end up in the actual target position. The nonlinear distortion hypothesis predicts that pointing errors after the step vary in a complicated way as a function of direction and amplitude of the step. Since our models (Eqs. 2–5 in Cartesian coordinates) are basically linear, the good fit of the models in explaining the relation between internal representation of the step and actual step displacement argues against a role of nonlinear distortion of perceptual space in the spatial updating of remembered target positions.

The other hypothesis proposes that errors in motor planning prevent the subject from pointing accurately to the remembered target position (Soechting and Flanders 1989a, 1989b). This may well explain the pointing errors obtained in the STATIC condition in the present study. This hypothesis also predicts that pointing error depends on target position relative to the body. Gentilucci and Negrotti (1996) suggested that the two processes of perception and visuomotor transformation share common mechanisms for distance reproduction. If that were true, more specific experiments would be necessary to locate the precise location of the origin of the various error components in the chain of sensorimotor transformations.

The descriptive models 2 and 3 that we used to explain our data assume that the errors related to pointing in the static condition persist in the STEP condition. In addition to errors in the update of step displacements, model 2 only incorporates errors due to an erroneous percept or storage of target position, whereas model 3 only incorporates errors in the pointing movement. We would like to emphasize that both corrections represent some extreme cases, since each correction (model 2 or model 3) attributes errors to a single factor (errors in target or in pointing movement). Presumably, a combination of both factors may be more realistic.

The diagonal components of matrix B, which represent the contribution of body displacement to the perceived step displacement, are all smaller than 1 for nearly all subjects. Two subjects (P.M. and P.S.) incorporate their step in the x-direction (not in the y-direction) in a nearly perfect way. The other subjects revealed an undershoot in the update of the remembered target position for their own displacements. For those subjects we found statistically significant differences in pointing error for steps in the *x*- and *y*-direction. We invariably found that the underestimation of the step was larger in the *y*-direction (forward) than in the *x*-direction (left/right direction).

The fact that the components of vector $\vec{D}$ are small (less than 4 cm) and on average near zero indicates that the perceived step displacement of the subject is almost entirely specified by the components of matrix *B*. This is in agreement with the fact that the subjects do not perceive a self-displacement without step displacements (i.e., for $\vec{S}=\vec{O}$).

As far as we know there are no studies which have investigated the effect of one-step self-displacements within reaching space on pointing movements to remembered visual targets. However, there are some reports on the percept of egomotion during walking and navigation to a target. We will first discuss the relevance of these papers for our results. Subsequently we will speculate about possible explanations and implications of our results.

Israël et al. (1993) did a study in which subjects were displaced passively on a sled which was linearly accelerated. Subjects had to push a button to indicate when they thought the sled had traveled a particular distance. Their results showed that subjects pushed the button too soon, suggesting that they overestimated the traveled distance for relatively small distances (about 0.8 m). The explanation for the apparent overestimation of displacement provided by Israël et al. is based on the abrupt onset of acceleration which induces a transient in otolith output. Glasauer et al. (1994) did an experiment in which they asked subjects to walk blindfolded to a previously seen target on the ground. These subjects walked too far, corresponding to an underestimation of their displacement during active self-motion. According to Glasauer et al. (1994), the vestibular system does not play a major role in active displacements, where proprioception is apparently more important. This finding corresponds with our observations and contributes to the notion that the abrupt acceleration in the experiment by Israël et al. may be responsible for the apparently discrepant overestimation of self-motion. An underestimation of distance walked was also found by Amorim et al. (1997). Also recently, Philbeck and Loomis (1997) found that subjects underestimated their walking distance under dark viewing conditions. Taken together, these studies indicate that subjects underestimate self-motion both during active walking and navigation, as well as in pointing.

With regard to possible implications of our findings we would like to discuss two other observations. Rossetti et al. (1995) argued that a weighted fusion of visual and proprioceptive information about hand position is used in pointing movements with the hand. One could speculate that when visual information is not available [as was the case in our study and in those of Glasauer et al. (1994) and Philbeck and Loomis (1997)], the absence of visual information in the weighted fusion may give rise to a decreased amplitude of perceived target distance. In another study investigating navigation of subjects towards a target in a complex environment, Amorim et al. (1997) made a distinction between two so-called processing modes used to update target location and orientation. When the subject had to keep track with the target position relative to his own position all the time during navigation (the object-centered mode), the errors were much smaller than in the mode in which the subject focused on the path he walked during the trajectory towards the target (trajectory-centered mode). The authors concluded that the type of cognitive task might affect the accuracy of updating the orientation and location of a target. Based on this result, one could argue that most of the subjects in our experiment used the trajectory-centered mode.

Acknowledgements We would like to thank Jan Van Gisbergen for useful suggestions and helpful comments on the text. We also appreciate the suggestions of two anonymous reviewers which led to valuable improvements of the manuscript.

References

Amorim MA, Glasauer S, Corpinot K, Berthoz A (1997) Updating object's orientation and location during nonvisual navigation: a comparison between two processing modes. Percept Psychophys 59:404–418

Berkinblit MB, Fookson OI, Smetanin B, Adamovich SV, Poizner H (1995) The interaction of visual and proprioceptive inputs in pointing to actual and remembered targets. Exp Brain Res 107:326–330

Bloomberg J, Melvill Jones G, Segal BN (1991) Adaptive modification of vestibularly perceived rotation. Exp Brain Res 84:47–56

Bock O, Arnold K (1992) Motor control prior to movement onset: preparatory mechanisms for pointing at visual targets. Exp Brain Res 90:209–216

Darling WG, Miller GF (1993) Transformations between visual and kinesthetic coordinate systems in reaches to remembered object locations and orientations. Exp Brain Res 93:534–547

Enright JT (1995) The non-visual impact of eye orientation on eye-hand coordination. Vision Res 35:1611–1618

Flanders M, Tillery SIH, Soechting JF (1992) Early stages in a sensorimotor transformation. Behav Brain Sci 15:309–362

Foley JM (1975) Error in visually directed manual pointing. Percept Psychophys 17:69–74

Gentilucci M, Negrotti A (1996) Mechanisms for distance reproduction in perceptual and motor tasks. Exp Brain Res 108:140–146

Glasauer S, Amorim MA, Vitte E, Berthoz A (1994) Goal directed linear locomotion in normal and labyrinthine-defective subjects. Exp Brain Res 98:323–335

Gordon J, Ghilardi M, Ghez C (1994) Accuracy of planar reaching movements: I. Independence of direction and extent variability. Exp Brain Res 99:97–111

Hocherman S (1993) Proprioceptive guidance and motor planning of reaching movements to unseen targets. Exp Brain Res 95:349–358

Israël I, Chapuis N, Glasauer S, Charade O, Berthoz A (1993) Estimation of passive linear whole body displacement in humans. J Neurophysiol 70:1270–1273

Israël I, Grasso R, Georges-Francois P, Tsuzuku T, Berthoz A (1997) Spatial memory and path integration studied by self-driven passive linear displacement. I. Basic properties. J Neurophysiol 77:3180–3192

Klatzky RL, Loomis JM, Golledge RG, Cicnelli JG, Doherty S, Pellegrino JW (1990) Acquisition of route and survey knowledge in the absence of vision. J Mot Behav 22:19–43

Loomis JM, Da Silva JA, Fujita N, Fukusima SS (1992) Visual space perception and visually directed action. J Exp Psychol Hum Percept Perform 18:906–921
Loomis JM, Klatzky RL, Golledge RG, Cicnelli JG, Pellegrino JW, Fry PA (1995) Nonvisual navigation by blind and sighted: assessment of path integration. J Exp Psychol Gen 1:73–91
McIntyre J, Stratta F, Lacquaniti F (1997) Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. J Neurophysiol 78:1601–1618
Mittelstaedt ML, Glasauer S (1991) Idiothetic navigation in gerbils and humans. Zool Jahrb Physiol 95:427–435
Philbeck JW, Loomis JM (1997) Comparison of two indicators of perceived egocentric distance under full-cue and reduced-cue conditions. J Exp Psychol Hum Percept Perform 23:72–85
Rieser JJ (1989) Access to knowledge of spatial structure at novel point of observation. J Exp Psychol Learn Mem Cogn 15: 1157–165
Rossetti Y, Desmurget M, Prablanc C (1995) Vectorial coding of movement: vision, proprioception, or both? J Neurophysiol 74:457–463
Soechting JF, Flanders M (1989a) Sensorimotor representations for pointing to targets in three-dimensional space. J Neurophysiol 62:582–594
Soechting JF, Flanders M (1989b) Errors in pointing are due to approximations in sensorimotor transformations. J Neurophysiol 62:595–608
Sokal R, Rohlf F (1981) Biometry, 2nd edn. Freeman, New York
Wolpert DM, Ghahramani Z, Jordan MI (1994) Perceptual distortion contributes to the curvature of human reaching movements. Exp Brain Res 98:153–156