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# Task-dependent mixtures of coordinate systems in visuomotor transformations

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**Abstract** In two experiments the involvement of relative and fixed coordinate systems in visuomotor transformations was examined. The experimental task required the successive performance of two movements in each trial, which had to "correspond" to different visual stimuli. One kind of visual display indicated target positions by way of different horizontal positions of a vertical line on a monitor (position mode), while the other indicated movement amplitudes by way of different lengths of a horizontal line (amplitude mode). Formal analysis of variances and covariances of successive individual movements led to the conclusion that in the position mode visuomotor transformations were based on a mixture of relative and fixed coordinate systems, while in the amplitude mode only a relative coordinate system was involved. Thus, visuomotor transformations can be characterized as mixtures of different coordinate systems, and their respective weights in the mixtures are task-dependent.

**Key words** Visuomotor transformation · Sensorimotor integration · Reference systems · Human

## Introduction

Movement of the hand to an object in space or movement of a computer mouse so that the cursor reaches a certain target on the screen involves the transformation of a visual stimulus into an appropriate movement. Behavioral (Flanders et al. 1992) as well as physiological data (Andersen et al. 1993; Lacquaniti 1996) suggest the involvement of multiple coordinate systems in such transformations. Although at the neural level a multitude of complex and diverse spatial representations of visual stimuli and movements in different cortical and subcortical areas have been identified, at the level of overt behavior movements can be related to the visual stimuli in simple, well-defined coordinate systems. These reference systems can be conceived of as emergent properties, that is, they may not actually be represented at any level of neural activity, but they are the cooperative result of several different coding schemes. They are fundamental in that they characterize the relation between sensory location and spatial movement control at a global level and thus the behavioral outcome of distributed neural processing.

Recent evidence as to the nature of the fundamental coordinate system has led to discrepant conclusions when different types of task were analyzed. For example, on the one hand the critical role of a shoulder-centered coordinate system has been suggested (Soechting and Flanders 1989; Flanders et al. 1992), but on the other hand the critical role of a hand-centered coordinate system is favored (Bock and Eckmiller 1986; Gordon et al. 1994). In more general terms, these systems represent examples of fixed and relative coordinate systems. A fixed reference system such as the shoulder-centered one does not change across a series of movements (as long as there is no movement of the shoulder girdle), while a relative system such as the hand-centered one changes its origin with each movement in the sequence. The distinction between fixed and relative coordinate systems for visuomotor transformations is analogous to the distinction between the use of position and distance information (Bock and Eckmiller 1986; Abrams and Landgraf 1990; Bock and Arnold 1993). However, it reflects better the operational distinction between different fundamental coordinate systems, which is typically based on the principle that error distributions should remain invariant against shifts or rotations of potential reference systems when the errors are measured in the functionally effective coordinate system, but not when measured with respect to some other reference. Thus, the two types of reference systems have different implications for movement errors.

Discrepant conclusions on the nature of the fundamental coordinate system suggest task dependency or, more generally, flexibility (see Soechting et al. 1990). In addition, such flexibility is not necessarily limited to using one or another coordinate system exclusively. In principle it seems that various characteristics of a motor pattern can

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be represented simultaneously (Heuer 1989), and, for endpoint and amplitude in particular, studies of motor memory indicate that the remembered movement reflects a task-dependent mixture of these two characteristics (Laabs 1974; Gundry 1975; Jaric et al. 1994). Such mixtures between representations in different coordinate systems could also be involved in visuomotor transformations, and some evidence for this has been reported (Carrozzo and Lacquaniti 1994). The purpose of the present study is to explore not only the existence of such mixtures, but also their potential dependency on the mode of presentation of the visual target, which was either presentation of start and end positions (position mode) or presentation of the length of a line that indicated the required movement amplitude (amplitude mode). With the first type of display, the involvement of a fixed reference system is a priori more likely than with the second display, which specifies only the amplitude of a movement relative to the current position of the hand.

The method that we used is based on the formal analysis of error propagation across successive movements. It is less general than the analysis introduced by Bock and Arnold (1993) in that it is unidimensional rather than three-dimensional; however, it can be generalized to two or three dimensions. On the other hand, it is more general than the Bock and Arnold analysis in that it takes account of possible variations in scaling factors or visuomotor gains. Such variations are likely to become especially important in tasks with fairly arbitrary visuomotor gain, for example in controlling a cursor on a computer screen by means of a mouse. In manual-control tasks of this type, the link between visual and motor representations is likely to be less tight than in direct-pointing tasks. In our experiments we used a task of this type, which is representative for the use of tools, to leave room for the variability of visuomotor gain.

Although we used a task in which variability of visuomotor gain was likely to be of particular importance because of an arbitrary definition of the correct gain and little practice of the subjects, variability of visuomotor gain may also be present in direct, open-loop pointing tasks. In this case the procedure of Bock and Arnold (1993) will result in spurious estimates of error propagation, as is illustrated in the Appendix. The size of the errors depends on the direction of the second movement relative to the first one, and also on the difference in amplitude. Thus, errors resulting from a confound of the effects of variable visuomotor gain with error propagation proper could have contributed to the dependency of measured error propagation on movement direction, which has been observed by Bock and Arnold (1993).

## Materials and methods

### Subjects

Sixteen men and eight women, aged 18–53 years (mean 25.2, SD 7.2 years), took part in two very similar experiments. In part, subjects were staff members, otherwise they were paid volunteers. All of them were unaware of the purpose of the study.

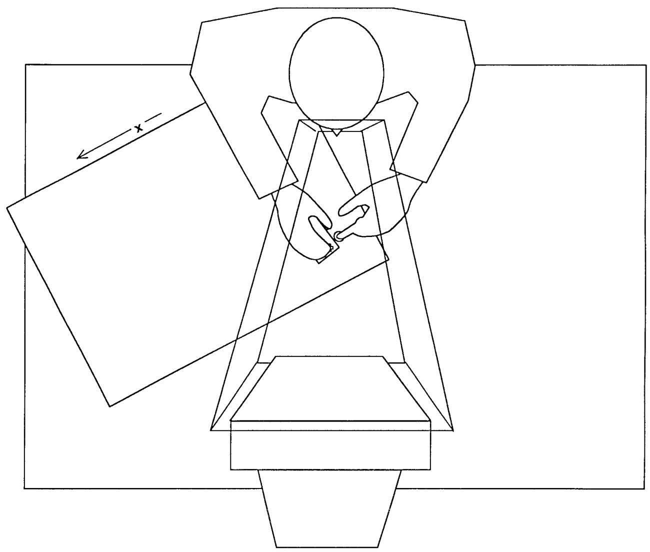

**Fig. 1** The experimental setup

### Apparatus

Figure 1 shows the experimental setup. Subjects sat at a table in a dimly lit room with their heads supported by a chin rest. They viewed a monitor at 82 cm distance with the line of sight tilted downward by about 18°. A viewing tube extended from the head of the subjects to the monitor so that the visual stimuli appeared in a dark field; full dark adaptation was prevented by exposing the subjects to the dim room light about every 3 min (between blocks of trials).

Subjects moved a modified, commercially available cursor (width 40 mm, length without crosshairs 105 mm, height 15 mm) on a digitizing tablet (Summasketch II; 46 × 31.9 cm). The cursor was mounted on a Plexiglas plate of 100 × 130 mm, which was equipped with four Teflon bases to reduce friction. At the front, another Plexiglas plate protruded with a trough, in the center of which were the crosshairs. At the left side of the cursor an additional key was located. The cursor was grasped with the thumb and the middle, ring, and little fingers, which rested on the Plexiglas plate, while the bent index finger was placed in the trough. The additional key was operated with the thumb.

The right elbow was placed on a pad (filled with fine-grained sand) on the table. For each subject the placement of the pad was adjusted such that the right index finger was located about 14 cm from the upper edge and 2.5 cm from the left edge of the digitizing tablet. This position was about 13 cm to the right of the midsagittal plane. The digitizing tablet was oriented such that the rotation of the lower arm around the resting elbow was associated with a movement of the index finger essentially parallel to the $x$-axis of the digitizing tablet. Finger position was monitored with a sampling rate of 115 Hz, and the start and end positions of each movement were stored. The left arm rested on the table with the index finger in a fixed position that was close to the left endpoint of the movement range; it remained in this well-defined position during each block of trials.

### The task

The task was to produce pairs of successive, smooth open-loop movements that corresponded to the visual stimuli. The movements varied in amplitude, and the second movement was in the same or the opposite direction as the first movement. In the instruction it was emphasized that it was the subjective relation between visual stimuli and movements that was of interest and that there were no "right" or "wrong" movements. The end of each movement was indicated by the subject by pressing the key with the thumb, and for each movement 350–5000 ms were available; when this range was exceeded, the trial was stopped and started anew. Two successive movements were performed in each trial to allow for an examination of error propagation.

At the start of each trial, the start position was shown on the screen (vertical line) and subjects were guided to the corresponding position of the index finger. Visual information thereafter was presented in two different ways. In the *position mode,* the end points of the first and second movement were indicated by two different positions of the vertical line (which, of course, also were at a certain distance from the previous position). In the *distance mode,* the required amplitude of the movement was indicated by the length of a horizontal line that was always centered on the screen, and the required direction was indicated by an arrow below the line.

## Design and procedure

Two experiments, each using 12 subjects, were run that differed only little: In experiment (Exp.) I the same start position was used for all trials of a subject, but for different subjects the start positions were different. In Exp. II each subject was exposed to different start positions from trial to trial.

Each subject performed four blocks of 72 trials each, two blocks in the position mode and two blocks in the amplitude mode in the sequence ABBA or BAAB. Each trial began with the presentation of a vertical line of length 1.2 cm, which appeared 8.4, 5.6, or 2.8 cm to the left of the screen center; in Exp. I this position was constant for each subject, but in Exp. II it varied randomly from trial to trial (with the constraint of equal frequencies in each block of trials). Below the line there was an outline rectangle of 1.6 cm width and 2.0 cm height, which was green with a green circle inside when the subject's index finger was in the initial position and red otherwise, with an arrow indicating the direction of the correction needed to reach the initial position. When the finger was in the initial position for 200 ms, the display was masked by a rectangle of width 25.2 cm and height 1.6 cm, with a pixel density of 33%, which was presented for 100 ms. The next stimulus appeared after a blank interval of 200 ms.

Depending on the display mode, the next visual stimulus was a vertical line 2.8, 5.6, or 8.4 cm to the right of the initial position or a horizontal line, centered on the display, of 2.8, 5.6, or 8.4 cm length, with a green rightward pointing arrow 2.1 cm below the line. This stimulus remained on until the subject pressed the key on the cursor to mark the end of the first movement. Following the masking stimulus, the vertical line was again presented, located 2.8 cm or 5.6 cm to the left or to the right of its previous position; in the amplitude mode a horizontal line of 2.8 cm or 5.6 cm length appeared, with a green rightward pointing arrow or a red leftward pointing arrow below it. Again this stimulus remained on until the subject pressed the key to mark the end of the corresponding movement and was followed by the mask.

When subjects are faced with the task to produce a movement that corresponds to a visual distance, they use quite variable gain factors. To reduce this variability, the experiment was preceded by a familiarization phase in which a step-tracking task was performed. A vertical line appeared in a random sequence of nine different positions (center of the screen, ± 2.8, ± 5.6, ± 8.4, ± 11.2 cm). The follower was a square, the position of which corresponded to the position of the index finger on the digitizing tablet. Whenever the target line was inside the square, the next target was presented, 100 in total. The display gain in the tracking task was 0.83, that is, a certain distance on the screen required a movement over a distance that was 1.2 times as long. This gain factor was the mean of the spontaneously chosen gain factors of five subjects, in a pilot study, who performed an open-loop tracking task.

With a constant start position, subjects did never experience the gain factor after the initial familiarization phase, but with variable start positions they did experience it across trials. The intention in running Exp. II with variable start positions was to obtain more stable results by stabilizing the display gain used by the subjects and thereby to replicate the main result of Exp. I, which was statistically slightly ambiguous.

## Data analysis

We analyzed the amplitudes of the first and second movement of each trial. The analyses were based on the means, variances, and covariances computed for each subject and each combination of display mode (2), amplitude of the first movement (3), direction (2), and amplitude (2) of the second movement. There were 12 trials for each of the 24 combinations for each subject. The main purpose was the determination of a parameter that characterizes the amount of error propagation. Error propagation is indicative of a relative coordinate system with its origin at the start of a movement, while lack of error propagation indicates the use of a fixed coordinate system that remains invariant across successive movements. When movement errors are determined by both types of coordinate system, the proportion of error of the first movement that is propagated can be considered as a parameter that characterizes the relative weight of the two types of coordinate system in the visuomotor transformation ("weighting parameter").

Our analysis is based on a limited set of plausible assumptions about the relation between the visual stimulus and the amplitude of the "corresponding" movement. Basically we assume that the amplitude $a_i$ of a movement that corresponds to a visual stimulus $v_i$, with $v_i$ as the length of a line or the distance between two visually registered positions, can be written as $a_i = \alpha_i v_i$, with $\alpha_i$ as the visuomotor gain. To increase generality, we allow $\alpha_i$ to vary across different display modes, different visual stimuli, and different directions of movement. Thus our analysis imposes no constraints on the functional relation between visual stimuli and the amplitudes of corresponding movements. In particular we assume no linear relation, because $\alpha_i$ is allowed to vary across different target amplitudes.

Amplitudes of movements vary from trial to trial, and we assume that two such sources of variability do exist; the one produces slow variations and the other more rapid ones. Operationally this difference is captured by the assumption that the first source of variability affects both movements of a trial in the same way, but the second source affects the first and second movement of a trial independently. For this specific error, caused by variability of the second type, we allow different distributions for the first and second movement as well as for different directions and amplitudes of them. This error may originate in the process of matching movement amplitude to the visual stimulus, but also in the production of the corresponding movement.

Our assumptions about the common source of variability are slightly more constraining. We assume an additive component of this variation, so that both amplitudes of a trial can be reduced or increased by a certain amount independent of the visual stimuli, and we assume a multiplicative component, which has the effect of reducing or increasing each amplitude in proportion to the product of $v$ and its associated visuomotor gain $\alpha$. Constraints on the data structure are imposed by the assumption that the distributions of the additive and multiplicative components of the common variability are independent of the specific combination of first and second amplitude and direction.

From these considerations the amplitude of a movement, which is now a random variable, can be written as:

$$A_{msi} = K\alpha_{msi}v_{msi} + F + E_{msi} \quad (1)$$

In this equation, $m$ = 1,2 designates the position of the movement in a trial (first or second movement). The index $s$ indicates the direction: $s$ = 1 for a leftward movement and $s$ = 2 for a rightward movement; first movements were always to the right, $s$ = 2, so $s$ =1 for the second movement also indicates a backward movement and $s$ = 2 a forward movement relative to the first one. Finally, the index $i$ designates the target amplitude as specified by the visual stimulus ($i$ = 1, 28 mm, $i$ = 2, 56 mm, $i$ = 3, 84 mm); for the first movement, $i$ = 1, 2,

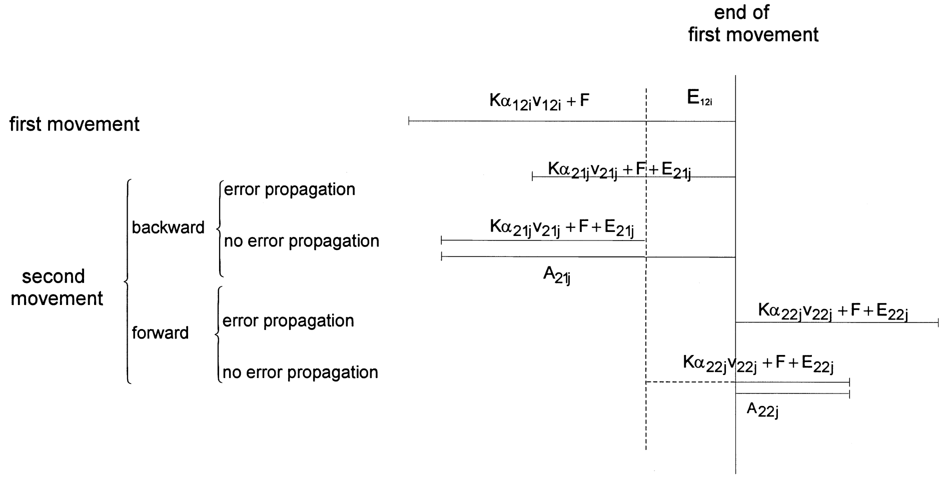


**Fig. 2** The effects of propagation of the specific error of a first movement ($E_{12i}$) on the amplitude of a second movement in the opposite (*backward*) or same (*forward*) direction as the first one. With full error propagation, the amplitude of the second movement is independent of the error $E_{12i}$, but without error propagation it is added or subtracted to the amplitude of the second movement, depending on its direction (see Data analysis, in the Materials and methods section)

3; for the second movement, i = 1, 2. $K$ is the multiplicative component of the common variation with $E(K) = 1$, and $F$ is the additive component of the common variation with $E(F) = 0$. $E_{msi}$ is the specific error with $E(E_{msi}) = 0$. The random variables $K$, $F$, and $E_{msi}$ are assumed to be independent so that their covariances are zero.

Equation 1 holds for first movements of each trial and also second movements, as long as the specific error $E_{12i}$ is fully propagated, as is illustrated in Fig. 2. (In this figure, indices $i = 1, 2, 3$ and $j = 1, 2$ are used to designate the amplitudes of the first and second movement, which can be different.) Error propagation indicates the involvement of a relative coordinate system with the origin at the start of the second movement, which is identical with the end of the first one. However, when the endpoint of the second movement is not represented in a coordinate system with its origin in the start position, but in a fixed coordinate system that is independent of the amplitude of the first movement, it will not be affected by the specific error of the first movement. Thus, the second movement would be performed to an end position that has a certain distance not from the end of the first movement (or the start position of the second one), but from the end position of the first movement minus the specific error (dotted vertical line in Fig. 2). From Fig. 2 it is clear that the effect of such a lack of error propagation is an increase in the measured amplitude $A_{2ij}$ of second movements in the backward direction by the specific error $E_{12i}$ of the first movement, and a corresponding decrease in the measured amplitude of second movements in the forward direction.

Taking variable proportions of error propagation into account, the amplitude of the second movement becomes

$$A_{2sj} = K\alpha_{2sj}v_{2sj} + F + E_{2sj} + d_s c E_{12i} \quad (2)$$

with $j = 1, 2$ designating the amplitude of the second movement and $i = 1, 2, 3$ the amplitude of the first one. The parameter $c$ gives the proportion of the specific error of the first movement that is propagated, more precisely, the complement thereof: $c = 0$ for full error propagation, which is indicative of the involvement of only a relative coordinate system, $c = 1$ for lack of error propagation, which is indicative of the involvement of only a fixed coordinate system. Intermediate values of this parameter characterize the relative weight of a fixed coordinate system in the visuomotor transformation; $c$ will be called the "weighting parameter." From Fig. 2 it is apparent that $d_1 = 1$ (for leftward or backward second movements) and $d_2 = -1$(for rightward or forward second movements).

From Eqs. 1 and 2, together with the simplifying assumptions about means and covariances of errors, the means, variances, and covariances of the amplitudes of the first and second movements of each trial can be derived straightforwardly:

$$E(A_{12i}) = \alpha_{12i}v_{12i} \quad (3)$$

$$E(A_{2sj}) = \alpha_{2sj}v_{2sj} \quad (4)$$

$$\mathrm{var}(A_{12i}) = \alpha_{12i}^2 v_{12i}^2 \mathrm{var}(K) + \mathrm{var}(F) + \mathrm{var}(E_{12i}) \quad (5)$$

$$\mathrm{var}(A_{2sj}) = \alpha_{2sj}^2 v_{2sj}^2 \mathrm{var}(K) + \mathrm{var}(F) + \mathrm{var}(E_{2sj}) + c^2 \mathrm{var}(E_{12i}) \quad (6)$$

$$\mathrm{cov}(A_{12i}, A_{2sj}) = \alpha_{12i}v_{12i}\alpha_{2sj}v_{2sj}\mathrm{var}(K) + \mathrm{var}(F) + d_s c\,\mathrm{var}(E_{12i}) \quad (7)$$

Equations 5–7 were fitted simultaneously to the variances and covariances that were observed for the 12 combinations of three amplitudes of the first movement, two directions of the second movement, and two amplitudes of the second movement, separately for the position mode and the amplitude mode. To reduce the number of free parameters, Eqs. 3 and 4 were used to estimate $\alpha_{12i}v_{12i}$ and $\alpha_{2sj}v_{2sj}$. There remained ten free parameters, $c$, var($K$), var($F$), var($E_{12i}$) for $i = 1, 2, 3$, var($E_{2sj}$) for $s = 1, 2$ and $j = 1, 2$, which were determined by minimizing the summed squared deviations of the predicted variances and covariances from the 36 observed ones. In addition to the least-squares criterion, a robust procedure was used that gave less weight to outliers.

## Results

### Mean amplitudes

Each subject performed 144 trials in the position mode and 144 trials in the amplitude mode, 12 trials for each combination of the amplitude of the first movement and the direction and amplitude of the second movement. Means were computed for each set of 12 trials, and the means across subjects are shown in Fig. 3 for the amplitude of the first movement. For each target amplitude, four bars are shown, one for each of the four direction and amplitude combinations of second movements that followed a first movement with a certain amplitude. Our assumptions made for the analysis of variances and covariances imply that the amplitudes of the first movement are independent of the nature of the second movement (see Eq. 3). This is more or less a trivial assumption, because in the experiment in each trial the direction and amplitude of the second movement were presented only after the end of the first movement, and their sequence was random. Any dependency of the first amplitude on the second movement should therefore be a chance result.

From Fig. 3 it appears that the amplitude of the first movement shows some variation across the four different second movements, but without any obvious consistency across display modes and experiments. The data of each experiment were subjected to an ANOVA with the factors

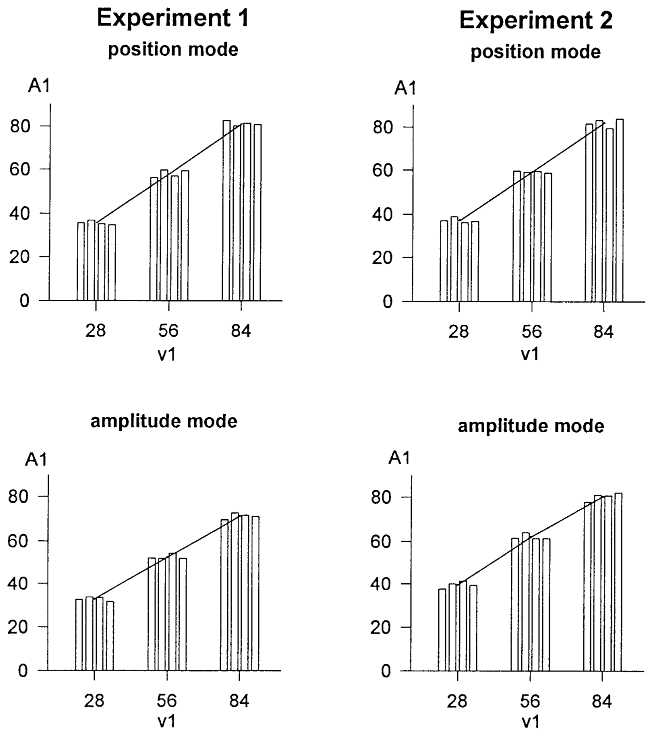


**Fig. 3** Mean amplitudes of first movements in experiment 1 and experiment 2 as a function of target amplitude $v_1$ (*v1*). For each experiment, display mode (position mode and amplitude mode) and target amplitude, the *four bars* give the mean amplitudes of first movements followed by long backward movements, short backward movements, short forward movements, and long forward movements (*from left to right*). *Continuous lines* indicate the means across different second movements

Display mode, First target amplitude, Second target direction, and Second target amplitude. Regarding the effects of the second movement on the first amplitude, there was a significant four-way interaction, $F_{2,22} = 3.6$, $P < 0.05$, in Exp. I as well as a significant main effect of the Second target amplitude, $F_{1,11} = 5.4$, $P < 0.01$, which, although statistically significant, amounted to only 0.8 mm. In Exp. II the interaction of Second target direction and Second target amplitude reached significance, $F_{1,11} = 7.6$, $P < 0.05$; the range of the four means amounted to only 1.9 mm. Thus, although in both experiments the assumption that the amplitude of the first movement does not depend on the direction and amplitude of the second movement was violated, the violations were of small size and exhibited different and erratic patterns in the two experiments.

In both experiments there was the trivial effect of the target amplitude. In Exp. I the mean amplitudes were 35.7, 58.1, and 81.4 mm in the position mode, and in the amplitude mode the range was somewhat reduced, 32.6, 52.4, and 71.3 mm; the interaction of First target amplitude and Display mode reached significance ($F_{2,22} = 5.0$, $P < 0.05$). In Exp. II the mean amplitudes were 37.1, 59.3, and 82.0 mm in the position mode and 39.5, 62.0, and 80.3 mm in the amplitude mode; the interaction was not significant.

Our assumptions for the analysis of variances and covariances also imply that the mean amplitudes of the second movement are independent of the first movement (see Eq. 4). Effects of the first movement on the amplitude of the second one can easily occur, because the location of the second movement in the workspace depends on the amplitude of the first movement.

The mean amplitudes of second movements are shown in Fig. 4. For each combination of direction and amplitude, three bars are shown, one for each target amplitude of the first movement (28, 56, and 84 mm from left to right). The variation across amplitudes of the first movement does not exhibit an obvious consistency. Again the data of each experiment were subjected to an ANOVA with the factors Display mode, First target amplitude, Second target direction, and Second target amplitude. In Exp. I no effect that involved the factor First target amplitude reached significance. The results of Exp. II were somewhat less conforming to our assumptions in that, in the position mode, the amplitude of the long backward movement decreased noticeably when the first movement became longer (Fig. 4, right upper graph). This gave rise to a number of significant interactions that involved the amplitude of the first movement. Thus, the assumption that the mean second amplitudes are independent of the first movement is violated only in Exp. 2 and mainly for the long backward movement in the position mode.

In both experiments there was the trivial effect of the target amplitude. In both experiments also the main effects of Second target direction were significant ($F_{1,11} = 11.6$, $P < 0.01$ for Exp. I; $F_{1,11} = 15.4$, $P < 0.01$ for Exp. II). In Exp. I the mean amplitudes in the backward direction were 38.6 mm and 61.1 mm, but in the forward direction only 29.6 mm and 48.3 mm; the interaction between Second target direction and Second target amplitude reached significance ($F_{1,11} = 7.4$, $P < 0.05$). In Exp. II the mean amplitudes in the backward direction were 40.7 mm and 60.6 mm, but in the forward direction only 31.2 mm and 52.0 mm; there was no significant interaction of Second target direction and Second target amplitude. The larger amplitudes in the backward than in the forward direction were perhaps related to the fact that the movements involved the left half of the total range more frequently than the right half.

The mean amplitudes of the second movement depended not only on the target amplitude and direction but also on the display mode. In Exp. I they were 35.6 mm and 58.0 mm for the position mode and 32.7 mm and 51.4 mm for the amplitude mode. The main effect of Display mode did not reach significance, but the interaction with Second target amplitude did ($F_{1,11} = 12.2$, $P < 0.01$). In Exp. II the mean amplitudes were 38.1 mm and 61.6 mm for the position mode, and 33.9 mm and 54.9 mm for the amplitude mode. In this experiment the main effect of Display mode reached significance ($F_{1,11} = 9.4$, $P < 0.05$), but not the interaction with Second target amplitude.

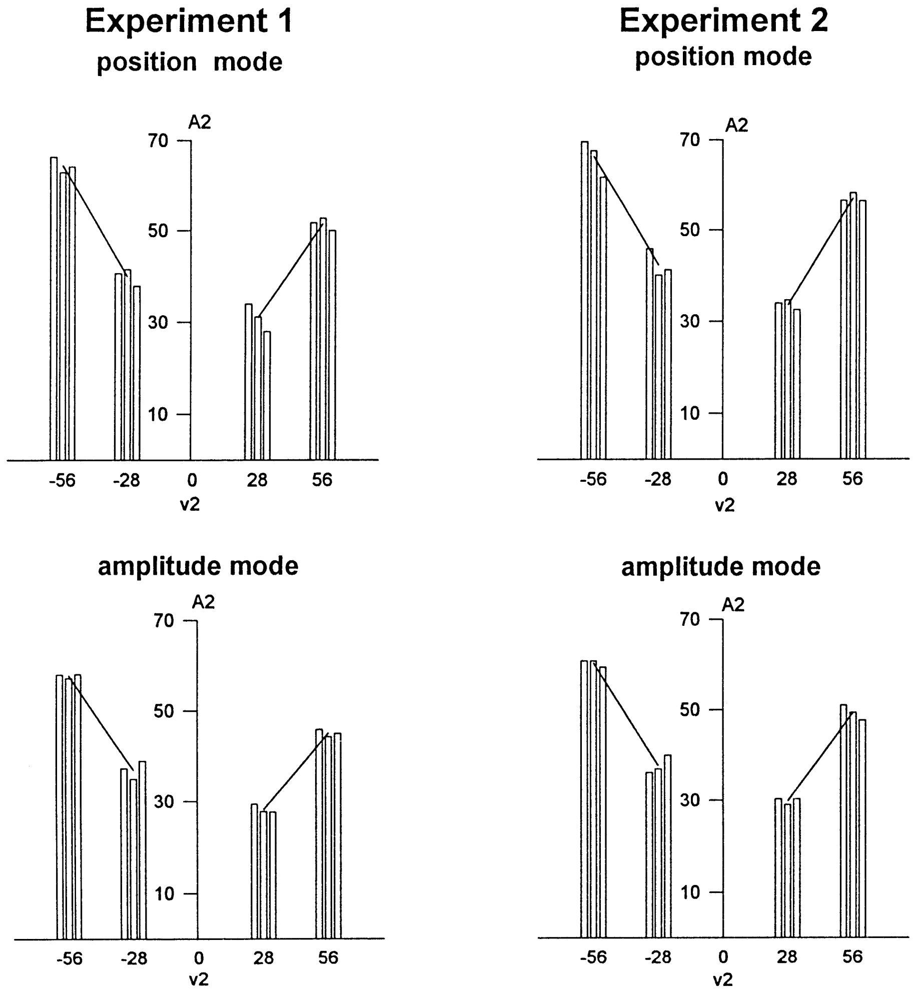


**Fig. 4** Mean amplitude of second movements in experiments 1 and 2 as a function of direction and target amplitude $v_2$ (*v2*); negative values of $v_2$ indicate backward direction, positive values indicate forward direction. For each experiment, display mode, and target amplitude, the *three bars* give the mean amplitudes of second movements preceded by first target amplitudes of 28, 56, and 84 mm (*from left to right*). *Continuous lines* indicate the means across different first movements

Variances and covariances

Our analysis of variances and covariances was somewhat affected by minor violations of the assumptions. All in all, the violations were small and inconsistent and will be treated as noise; this seems the more justified as the variances and covariances, each of which is based on only 12 data points for each subject, are themselves quite noisy. (For illustration, the 95% confidence interval for the variance of 100 of a normally distributed variable, computed from only 12 observations, ranges from about 50 to about 290.)

Some important characteristics of the covariation of the amplitudes of the first and second movement are shown in Fig. 5. These are data of a single subject of Exp. I from trials in which the target amplitude of the first movement was 56 mm. In each graph, the amplitude of the second movement is shown as a function of the amplitude of the first movement, for second movements in the forward and in the backward direction. In the upper two graphs, the visual stimuli were in the position mode, in the lower two graphs they were in the amplitude mode; in the two left graphs, the target amplitude for the second movement was 28 mm, in the two right graphs it was 56 mm.

Overall, Fig. 5 shows a considerable scatter of the data points from individual trials and positive covariation of the amplitudes of both movements. Thus, across trials there was variability in a factor that affects both amplitudes; in our formal analysis we capture this factor as the common variability with var($K$) for the multiplicative and var($F$) for the additive component. Figure 5 also shows that the increase in the second amplitude with the first one depended on the direction of the second movement: it was stronger for backward movements than for forward movements, and this difference seems to be less consistent in the amplitude than in the position mode. In the position mode with the short second movement, the amplitude of forward movements even decreased when the first amplitude increased. These differences in the slopes of the regression lines of Fig. 5 are related to error propagation.

From Fig. 2 it is apparent that with full error propagation ($c$ = 0), as with a relative coordinate system, any increase in the second amplitude with the first one should be independent of the direction of the second movement: covariation depends only on the common variability, and there is no direction-specific influence. Such a situation is present in the lower right graph of Fig. 5. However, without error propagation ($c$ = 1), as with a fixed reference

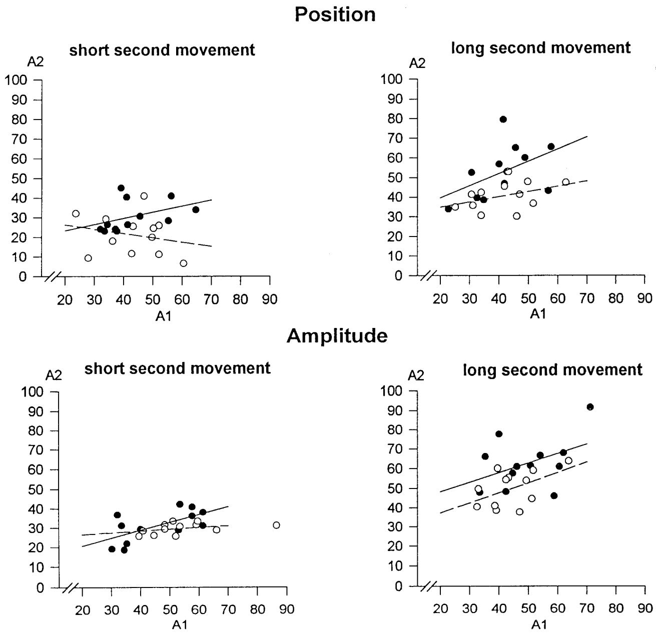


**Fig. 5** Bivariate distributions of amplitudes of first (*A1*) and second movements (*A2*) of a single subject under two display modes (position mode, *upper two graphs*; amplitude mode, *lower two graphs*) with fitted linear regression lines. Target amplitude of the first movement was 56 mm, target amplitude of the second movement was 28 mm (*left two graphs*) and 56 mm (*right two graphs*). *Filled circles* and *continuous lines* are for second movements in the backward direction, *open circles* and *broken lines*, for second movements in the same direction

system, the amplitude of the backward movement is increased when the specific error of the first movement becomes larger, which enhances the positive covariation, and for the forward movement it is reduced, which results in a reduction of the positive covariation or even a negative one, as in the upper left graph of Fig. 5. From Eq. 7 it is evident that a direction-dependent covariation will result whenever $c > 0$, because $d_1 = 1$ (for backward movements) and $d_2 = -1$ (for forward movements).

Differences between regression lines are dependent on factors other than error propagation. The slopes of regression lines equal the covariance divided by the variance of the independent variable, in the particular instance the covariance of the amplitudes of both movements divided by the variance of the amplitudes of the first movements. Provided that amplitude variability depends on mean amplitude, as is typically the case (see Schmidt et al. 1979), second movements in the forward direction would have smaller variability than movements in the backward direction because of their smaller amplitude. This would result in a smaller covariance and also a smaller slope of the regression line, even without any difference in error propagation. Considerations like this led us to apply the more formal analysis described in the Materials and methods section.

Tables 1 and 2 illustrates the results of this analysis for the same subject of which partial data are shown in Fig. 5. For the position mode and the amplitude mode, the observed variances of the amplitudes of the first, var($A_1$), and second movement, var($A_2$), are given as well as the covariance, cov($A_1$, $A_2$). Equations 5–7 were fitted simultaneously to the 36 variances and covariances by minimizing summed squared deviations in a ten-dimensional parameter space. After initial exploration of the space to determine whether there were problems with local minima, we used a simple search procedure that, at each step, proceeded in the direction of steepest descent. By this procedure a first set of parameters (Estimate 1 in Table 2) was obtained together with a first set of predicted values (Prediction 1 in Table 1). In searching for the minimum in the parameter space, no boundaries were set for the values of the parameters.

A straightforward characteristic of Eq. 5 is that the predicted variances of the first movement are independent of direction and amplitude of the second movement. The scatter of variances of the amplitude of the first movements gives some indication of the noise in the individual data. To ameliorate the effects of extreme variances and covariances on the parameter estimates, we also computed a robust regression of our predicted values on the observed ones, using a procedure described by Cleveland (1979). This procedure, which gives less weight to larger deviations between observed and predicted values, was repeated three times, giving progressively less weight to outliers with large deviations from predicted values. The robust estimates of the parameters are also given in Table 2 (Estimate 2), and in Table 1, the variances and covariances predicted from them (Prediction 2).

Obviously, with such noisy data as the present ones (for each individual subject) serious deviations of the predicted from the observed values are to be expected. Nevertheless, there are some typical characteristics of the pattern of variances and covariances that can be seen in the predicted values and – of course with more violations – also in the observed ones: (1) as already mentioned, the variance of the amplitude of the first movement is independent of the direction and amplitude of the second movement, but increases with target amplitude; (2) the variance of the amplitude of the second movement increases with target amplitude and is smaller for forward movements than for backward movements; (3) the same basic pattern as in the variances of the second movement can also be seen in the covariances. In terms of the parameters, the typical observations are an increase in the variance of the specific error of the first movement with target amplitude [var($E_{123}$) > var($E_{122}$) > var($E_{121}$)], an increase in the specific-error variance of the second movement with target amplitude [var($E_{212}$) > var($E_{211}$), var($E_{222}$) > var($E_{221}$)], and a larger specific-error variance for second movements in the backward than in the forward direction [var($E_{211}$) > var($E_{221}$), var($E_{212}$) > var($E_{222}$)]. (In Table 2 the position mode var($E_{221}$) is particularly large, so the typical pattern is disturbed here.)

In Table 2 the estimate of var($F$) is negative for the amplitude mode. Of course, such negative estimates of variances represent noise, and they can occur when the true variance is small. This is generally the case for var($F$), the estimate of the variance of the additive com-

**Table 1** Observed and predicted variances and covariances of amplitudes of first and second movement [var($A_1$), var($A_2$), cov($A_1$, $A_2$)]. Predicted values are based on parameters from least-squares fit (*Pred. 1*) and robust least-squares fit (*Pred. 2*). Values are given for all combinations of target amplitudes of first movements (28, 56, and 84 mm), directions of second movements (backward and forward) and target amplitudes of second movements (28 and 56 mm). Data are from a representative subject of Exp. I.

| | | 28 | | | | 56 | | | | 84 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Backward | | Forward | | Backward | | Forward | | Backward | | Forward | |
| | | 56 | 28 | 28 | 56 | 56 | 28 | 28 | 56 | 56 | 28 | 28 | 56 |
| Position mode | | | | | | | | | | | | | |
| Var($A_1$) | Observed | 42 | 102 | 53 | 64 | 105 | 106 | 119 | 117 | 137 | 152 | 224 | 257 |
| | Pred. 1 | 67 | 67 | 67 | 67 | 113 | 113 | 113 | 113 | 191 | 191 | 191 | 191 |
| | Pred. 2 | 63 | 63 | 63 | 63 | 112 | 112 | 112 | 112 | 157 | 157 | 157 | 157 |
| Var($A_2$) | Observed | 197 | 85 | 20 | 48 | 178 | 59 | 108 | 51 | 109 | 57 | 70 | 150 |
| | Pred. 1 | 161 | 66 | 65 | 82 | 162 | 67 | 66 | 83 | 163 | 68 | 67 | 84 |
| | Pred. 2 | 185 | 66 | 72 | 49 | 186 | 66 | 73 | 50 | 186 | 67 | 73 | 50 |
| Cov($A_1$, $A_2$) | Observed | 37 | 65 | 1 | 0 | 66 | 33 | –26 | 31 | 52 | 71 | 18 | 52 |
| | Pred. 1 | 33 | 25 | 4 | 11 | 58 | 41 | 9 | 25 | 84 | 58 | 9 | 32 |
| | Pred. 2 | 34 | 25 | 2 | 10 | 63 | 43 | 7 | 24 | 85 | 56 | 13 | 39 |
| Amplitude mode | | | | | | | | | | | | | |
| Var($A_1$) | Observed | 90 | 81 | 43 | 34 | 134 | 158 | 164 | 78 | 211 | 334 | 353 | 270 |
| | Pred. 1 | 61 | 61 | 61 | 61 | 133 | 133 | 133 | 133 | 293 | 293 | 293 | 293 |
| | Pred. 2 | 60 | 60 | 60 | 60 | 136 | 136 | 136 | 136 | 306 | 306 | 306 | 306 |
| Var($A_2$) | Observed | 148 | 50 | 56 | 273 | 168 | 66 | 8 | 83 | 185 | 112 | 52 | 227 |
| | Pred. 1 | 167 | 76 | 39 | 194 | 167 | 76 | 39 | 194 | 167 | 76 | 39 | 194 |
| | Pred. 2 | 167 | 75 | 39 | 250 | 167 | 75 | 39 | 250 | 167 | 75 | 40 | 250 |
| Cov($A_1$, $A_2$) | Observed | 79 | 54 | 19 | 30 | 65 | 65 | 15 | 41 | 126 | 52 | 62 | 150 |
| | Pred. 1 | 49 | 26 | 24 | 43 | 83 | 45 | 42 | 73 | 126 | 67 | 67 | 115 |
| | Pred. 2 | 49 | 27 | 24 | 43 | 83 | 45 | 42 | 73 | 125 | 67 | 67 | 114 |

**Table 2** Estimated parameters from least-squares fit (*Estimate 1*) and robust least-squares fit (*Estimate 2*)

| | $c$ | Var($K$) | Var($F$) | Var($E_{121}$) | Var($E_{122}$) | Var($E_{123}$) | Var($E_{211}$) | Var($E_{212}$) | Var($E_{221}$) | Var($E_{222}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Position mode | | | | | | | | | | |
| Estimate 1 | 0.156 | 0.017 | 6 | 55 | 76 | 118 | 42 | 101 | 51 | 45 |
| Estimate 2 | 0.187 | 0.019 | 4 | 52 | 74 | 79 | 41 | 121 | 58 | 10 |
| Amplitude mode | | | | | | | | | | |
| Estimate 1 | –0.060 | 0.028 | –2 | 39 | 68 | 139 | 39 | 49 | 17 | 120 |
| Estimate 2 | –0.053 | 0.028 | –1 | 38 | 72 | 154 | 38 | 50 | 17 | 176 |

ponent of the common variability. The estimate of var($K$), the multiplicative component of the common variability, appears neglible, but it is not. The unit of all other variance estimates is millimeters squared, but var($K$) is dimensionless. It characterizes the proportional dependence of variances and covariances on mean amplitudes. For example, when var($K$) = 0.0225, the standard deviation of the multiplicative component of the common error is 0.15 around a mean of 1, which is not really as small a variability as could be suggested by the small estimates of var($K$).

Of main interest are the estimates of the weighting parameter $c$. In the subject whose data are shown in Tables 1 and 2, the weighting parameter was larger in the position mode than in the amplitude mode, conforming to expectations. Overall, these estimates, in particular their differences between position mode and amplitude mode, appeared fairly robust against variations in the details of the procedure used for estimating them. As for the variances, estimates of the weighting parameter can become negative because of the noise inherent to the individual data.

Tables 3 and 4 summarize the results of the analysis of variances and covariances of Exp. I. Shown are the medians of the observed variances and covariances as well as the median deviations of the predicted values from the observed ones, with the predicted values of both the least-squares fit (Deviation 1 in Table 3) and the robust least-squares fit (Deviation 2 in Table 3). Predicted values were compared with observed values by a series of Wilcoxon signed-rank tests, and significant deviations are marked by asterisks. Their number is very small and within the range that can be expected by chance. Overall, as can be judged from the mean absolute median deviations, computed separately for the variances of each movement and the covariance, the robust least-squares procedure achieved a slightly better fit.

The main interest is in the weighting parameter $c$ (Table 4) and its difference between the position mode

**Table 3** Medians of observed variances and covariances (Exp. I), var($A_1$), var($A_2$), cov($A_1$, $A_2$), and median deviations of predicted values from the observed ones (*Dev. 1* and *Dev. 2*); predicted values are based on parameters from least-squares fit (*Dev. 1*) and robust least-squares fit (*Dev. 2*). Median deviations marked by *asterisks* are significantly different from zero. *Right-most column* gives the means of the median deviations across all combinations of amplitude of the first movement (28, 56, and 84 mm), direction (backward and forward) and amplitude (28 and 56 mm) of the second movement

| | | 28 | | | | 56 | | | | 84 | | | | Mean absolute deviation |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Backward | | Forward | | Backward | | Forward | | Backward | | Forward | | |
| | | 56 | 28 | 28 | 56 | 56 | 28 | 28 | 56 | 56 | 28 | 28 | 56 | |
| Position mode | | | | | | | | | | | | | | |
| | Observed | 82 | 117 | 103 | 86 | 167 | 261 | 132 | 211 | 356 | 281 | 254 | 256 | |
| Var($A_1$) | Dev. 1 | 7 | 0 | −9 | −8 | −26* | 7 | −7 | 13 | 13 | −43 | 29 | −22 | 15.3 |
| | Dev. 2 | 7 | 5 | −7 | −12 | −17* | 9 | −6 | 27 | 18 | −5 | 44 | −16 | 14.4 |
| | Observed | 256 | 96 | 92 | 151 | 203 | 130 | 101 | 184 | 160 | 101 | 85 | 145 | |
| Var($A_2$) | Dev. 1 | 27 | 5 | −7 | −24 | −16 | 16 | 4 | 5 | −40 | −14 | 1 | −4 | 13.6 |
| | Dev. 2 | 8 | 5 | −7 | 1 | 3 | 15 | −1 | −2 | −30 | −6 | −1 | −5 | 7.0 |
| | Observed | 98 | 58 | 17 | 8 | 153 | 117 | 0 | 41 | 180 | 66 | 16 | 45 | |
| Cov($A_1$, $A_2$) | Dev. 1 | 10 | 5 | 12 | −7 | 42 | 13 | −22 | 9 | 5 | −19 | −6 | −14 | 10.5 |
| | Dev. 2 | 21 | 4 | 5 | −9 | 0 | 9 | −23 | 8 | 6 | −16 | −6 | −17 | 10.3 |
| Amplitude mode | | | | | | | | | | | | | | |
| | Observed | 57 | 36 | 45 | 40 | 100 | 94 | 110 | 83 | 160 | 140 | 169 | 237 | |
| Var($A_1$) | Dev. 1 | 8 | −5 | −5 | −4 | −7 | −4 | 7 | 8 | −7 | −14 | −7 | −2 | 6.5 |
| | Dev. 2 | 19* | −4 | −3 | 1 | −1 | 4 | 7 | 7 | −2 | 8 | −2 | −6 | 5.3 |
| | Observed | 137 | 31 | 37 | 78 | 112 | 50 | 28 | 78 | 130 | 63 | 23 | 91 | |
| Var($A_2$) | Dev. 1 | −3 | −5 | 8 | 3 | −8 | −6 | −2 | −9 | 7 | 8 | −4 | 7 | 5.8 |
| | Dev. 2 | 2 | −4 | 8* | 3 | 3 | −5 | −2 | −5 | 4 | 7 | −5 | −2 | 4.2 |
| | Obsered | 39 | 14 | 16 | 27 | 50 | 42 | 20 | 45 | 104 | 53 | 27 | 57 | |
| Cov($A_1$, $A_2$) | Dev. 1 | 5 | −3 | −3 | −6 | −14 | 4 | −2 | −5 | 4 | −10 | −2 | 3 | 5.1 |
| | Dev. 2 | 7 | −6 | −3 | −5 | −6 | 3 | −2 | −2 | 4 | −1 | −2 | 2 | 3.6 |

**Table 4** Medians of estimated parameters from least-squares fit (*Estimate 1*) and robust least-squares fit (*Estimate 2*). Medians marked by *asterisks* are significantly different from zero

| | $c$ | Var($K$) | Var($F$) | Var($E_{121}$) | Var($E_{122}$) | Var($E_{123}$) | Var($E_{211}$) | Var($E_{212}$) | Var($E_{221}$) | Var($E_{222}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Position mode | | | | | | | | | | |
| Estimate 1 | 0.208* | 0.027* | 4 | 66* | 79* | 126* | 48* | 97* | 58* | 50* |
| Estimate 2 | 0.249* | 0.023* | 2 | 61* | 77* | 108* | 39* | 81* | 68* | 52* |
| Amplitude mode | | | | | | | | | | |
| Estimate 1 | −0.041 | 0.014* | 6 | 18* | 47* | 80* | 19* | 45* | 5 | 33 |
| Estimate 2 | −0.050 | 0.012* | 9* | 18* | 52* | 82* | 20* | 47* | 4 | 33* |

and the amplitude mode. In the position mode, the two estimates were 0.208 and 0.249, and both of them were significantly larger than zero as indicated by one-sided Wilcoxon signed-rank tests ($T(12) = 1$, $P < 0.01$; $T(12) = 0$, $P < 0.01$). In the amplitude mode, the median estimates were −0.041 and −0.050; these values were remote from any statistical significance. Thus, in the amplitude mode there was full error propagation, as expected for a relative coordinate system, but in the position mode error propagation was incomplete, indicating some influence of a fixed coordinate system. Although the weighting parameter was significantly larger than zero in the position mode, but not in the amplitude mode, direct (one-sided) tests to compare the parameters between the two conditions failed to reach significance ($T(12) = 23$, $T(12) = 20$, $P < 0.10$) for the least-squares estimates and the robust least-squares estimates, respectively. Thus the results of Exp. I are somewhat inconclusive.

Tables 5 and 6 summarize the results of the analysis of variances and covariances of Exp. II. Again there were only few significant deviations of the predicted variances and covariances from the observed ones, and the means of the absolute median deviations between predicted and observed values indicated again a slightly better fit obtained with the robust estimation procedure.

The medians of the weighting parameter $c$ (Table 6) essentially replicated the results of Exp. I. In the position mode, the estimates were 0.265 and 0.215, both being significantly larger than zero ($T(12) = 1$, $P < 0.01$; $T(12) = 3$, $P < 0.01$). In the amplitude mode, the estimates were 0.055 and 0.055, and both failed to reach significance. In contrast to Exp. I, the prediction of a smaller amount of error propagation in the position mode was also con-

**Table 5** Medians of observed variances and covariances (Exp. II), var($A_1$), var($A_2$), cov($A_1$, $A_2$), and median deviations of predicted values from the observed ones (*Dev. 1* and *Dev. 2*); predicted values are based on parameters from least-squares fit (*Dev. 1*) and robust least-squares fit (*Dev. 2*). Median deviations marked by *asterisks* are significantly different from zero. *Right-most column* gives the means of the median deviations across all combinations of amplitude of the first movement (28, 56, and 84 mm), direction (backward and forward) and amplitude (28 and 56 mm) of the second movement

| | | 28 | | | | 56 | | | | 84 | | | | Mean absolute deviation |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Backward | | Forward | | Backward | | Forward | | Backward | | Forward | | |
| | | 56 | 28 | 28 | 56 | 56 | 28 | 28 | 56 | 56 | 28 | 28 | 56 | |
| Position mode | | | | | | | | | | | | | | |
| | Observed | 77 | 174 | 83 | 78 | 190 | 137 | 132 | 144 | 204 | 202 | 274 | 218 | |
| Var($A_1$) | Dev. 1 | −17 | 24 | −23* | −1 | 20 | −9 | −23 | −7 | −14 | −6 | 32* | −2 | 14.8 |
| | Dev. 2 | −5 | 26 | −14 | 3 | 21 | −1 | −7 | −9 | −11 | −8 | 11 | 1 | 9.8 |
| | Observed | 187 | 86 | 79 | 124 | 177 | 80 | 72 | 123 | 137 | 112 | 74 | 142 | |
| Var($A_2$) | Dev. 1 | 1 | 10 | −5 | −16 | 30 | −17* | −4 | −16 | −37* | −10 | 0 | 35 | 15.1 |
| | Dev. 2 | 8 | 10 | 3 | 0 | 19 | −11 | −1 | −7 | −17* | −4 | −3 | 14 | 8.1 |
| | Observed | 60 | 72 | 4 | 20 | 97 | 45 | −8 | −1 | 70 | 79 | 35 | 3 | |
| Cov($A_1$, $A_2$) | Dev. 1 | 6 | 2 | −1 | 10 | 14 | −18 | −14 | −18 | −2 | 8 | 22 | −13 | 10.7 |
| | Dev. 2 | 13 | 7 | 3 | −1 | 29 | −11 | −11 | −14 | 0 | 12 | 27 | −12 | 11.7 |
| Amplitude mode | | | | | | | | | | | | | | |
| | Observed | 77 | 67 | 58 | 44 | 104 | 151 | 179 | 155 | 252 | 213 | 215 | 255 | |
| Var(A1) | Dev. 1 | 1 | 0 | −7 | 6 | −18 | 0 | 31 | 11 | −9 | −22 | 18 | −5 | 10.7 |
| | Dev. 2 | 1 | 2 | −5 | 7 | −7 | 8 | 19 | 12 | 10 | −10 | 5 | 3 | 7.4 |
| | Observed | 147 | 50 | 31 | 76 | 94 | 48 | 41 | 63 | 149 | 77 | 33 | 86 | |
| Var(A2) | Dev. 1 | 17 | −6 | 0 | 14 | −36* | −10 | 5 | −19 | 23 | 16 | −4 | 1 | 12.6 |
| | Dev. 2 | 22 | −6 | 0 | 13 | −8 | −6 | 4 | −11 | 14 | 4 | −4 | 6 | 8.2 |
| | Observed | 61 | 26 | 14 | 28 | 68 | 29 | 43 | 47 | 116 | 76 | 33 | 107 | |
| cov(A1,A2) | Dev. 1 | 9 | 1 | −9 | −6 | −5 | −9 | 11 | −20 | −14 | −2 | 1 | 10 | 8.1 |
| | Dev. 2 | 5 | 0 | −7 | −1 | −1 | −6 | 9 | −4 | −2 | 0 | −2 | 3 | 3.3 |

**Table 6** Medians of estimated parameters from least-squares fit (*Estimate 1*) and robust least-squares fit (*Estimate 2*). Medians marked by *asterisks* are significantly different from zero

| | $c$ | Var($K$) | Var($F$) | Var($E_{121}$) | Var($E_{122}$) | Var($E_{123}$) | Var($E_{211}$) | Var($E_{212}$) | Var($E_{221}$) | Var($E_{222}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Position mode | | | | | | | | | | |
| Estimate 1 | 0.265* | 0.010* | 30* | 77* | 111* | 181* | 55* | 86* | 25* | 66* |
| Estimate 2 | 0.215* | 0.007 | 14* | 51* | 119* | 175* | 48* | 82* | 23* | 70* |
| Amplitude mode | | | | | | | | | | |
| Estimate 1 | 0.055 | 0.014* | 19 | 27* | 63* | 85* | 18* | 67* | 6 | 31* |
| Estimate 2 | 0.055 | 0.013* | 18 | 26* | 68* | 56 | 15* | 39* | 5 | 24* |

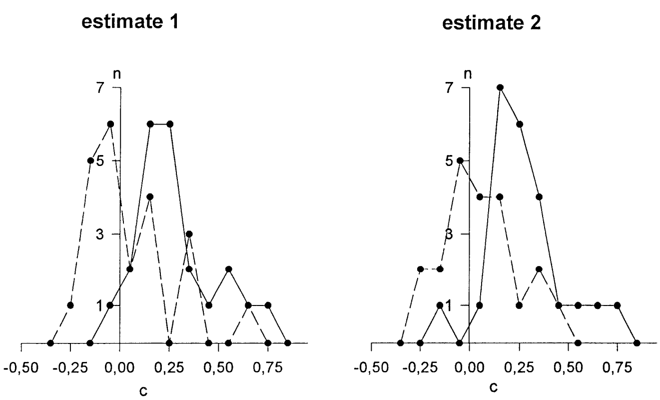


**Fig. 6** Distributions of individual weighting parameters ($c$) obtained with least-squares estimation (*estimate 1*) and robust least-squares estimation (*estimate 2*) Position mode, *continuous lines*; amplitude mode, *broken lines*

firmed in direct comparisons: one-sided Wilcoxon signed-rank tests indicated a significantly larger weighting parameter in the position mode for both estimates ($T(12) = 0$, $P < 0.01$; $T(12) = 16$, $P < 0.05$).

From Tables 4 and 6 it is apparent that the estimates of the weighting parameter $c$ in the two experiments were very similar. A comparison was performed between the two experiments, separately for the two estimation procedures and the two display modes, by means of Mann-Whitney tests. The difference between experiments never approached significance. The same was true when the difference between display modes was compared between experiments. Therefore the weighting-parameter estimates of the two experiments were collapsed. The distributions of the estimates are shown in Fig. 6. For the position mode, the distributions were clearly centered above zero, while for the amplitude mode they were centered close to zero. With both estimation procedures, there were a few subjects who provided estimates that can be considered as outliers, and these are omitted in Fig. 6. (For the least-squares estimates there were three values of more than 1.0, two in the position mode and one in the amplitude mode, one value of less than –0.3 in the amplitude mode; for the robust estimates there was one value of more than 1.0 in the position mode and one value of less than –0.3 in the amplitude mode.) Overall, the distributions had some positive skew. Estimates for the position mode and the amplitude mode were not correlated ($r = 0.05$ and 0.11 for estimates 1 and 2, respectively), indicating that there were no stable interindividual differences with respect to the weighting parameter across the different display modes.

## Discussion

Our results give clear evidence that visuomotor transformations can be characterized in terms of mixtures of different fundamental coordinate systems. The weighting factor that we observed with the position display was smaller than 0.5, indicating that the weight of relative coordinate systems in the mixture was stronger than the weight of fixed coordinate systems. Mixtures of multiple reference systems, as can be inferred from the analysis of movement errors, of course do not imply that the neural processing involves a mixture operation of two different kinds of visuomotor mapping. More likely the mixtures are emergent properties of distributed neural representations in different reference systems – or without any well-defined coordinate system (Zipser and Andersen 1988).

Our results also clearly indicate that mixtures of different fundamental coordinate systems are task-dependent. In particular, we found no influence of a fixed reference system when the visual stimulus was a line, the length of which indicated the required amplitude of the movement. With such a visual stimulus, a relative (hand-centered) coordinate system appears to be the most natural one to use, because the visual distance can be mapped straightforwardly into a distance from the origin. We found a weak influence of a fixed reference system when the visual stimulus was a marker, the position of which indicated the required end position of a movement. With similar visual stimuli, but a task that required direct open-loop pointing to the target, previous studies have found evidence for the decisive influence of relative reference systems (Bock and Eckmiller 1986; Gordon et al. 1994). However, there have also been some indications of an influence of fixed coordinate systems (Bock and Arnold 1993). Nevertheless, with such a type of visual display, representing the target relative to the start position does not appear to be more straightforward than representing it relative to some fixed origin. The comparatively weak influence of a fixed coordinate system in this type of task is the more remarkable as studies of motor memory fairly consistently show a stronger weight of a fixed reference system than of a relative one (Jaric et al. 1994; Heuer 1983, for a review of older studies). Thus, strong weights of relative coordinate systems are perhaps specific to immediate visuomotor transformations and will not be found in memory tasks such as the ones of Soechting and Flanders (1989); according to recent evidence (Bridgeman et al. 1997), the nature of visuomotor transformations changes as the delay between stimulus presentation and movement is increased.

The demonstration of task-dependent mixtures of fundamental coordinate systems in visuomotor transformations makes inconsistencies between inferences drawn from different experimental paradigms understandable. However, some conceptual confusions might also contribute. As an example, consider the following set of findings. Heuer (1981) analyzed the timing of acceleration profiles of rapid movements with the left and right arm to the left and right. He found that up to peak deceleration the timing was determined by the spatial direction of the movement, being similar for movements to the right and left, respectively, but dissimilar for flexions and extensions, while for the later part of the movements this pattern was reversed. These findings are consistent with a two-process model of motor control such as the one of Ghez (1979), according to which a dynamic phase, for which a certain force pattern is specified, is followed by a static phase, during which the movement reaches a specified location. This type of model, according to which amplitude information is critical for the initial part of a movement, but location information for the terminal part, has also found support in a series of studies by Abrams et al. (1990, 1994). Using different manipulations (e.g., smooth pursuit movement or saccade to the target position or induced motion added to real target motion), they varied perceived distance and found strong effects on the amplitude of primary submovements, but only smaller or no effects on terminal accuracy.

These data and conclusions seem to be at variance with the present results and those of Bock and Eckmiller (1986) as well as Gordon et al. (1994), according to which a relative (hand-centered) coordinate system is critical for final movement errors, but not a fixed coordinate system. However, this discrepancy only exists when one conceptually equates the use of amplitude information with the use of a relative coordinate system, with its origin in the start position, but the use of location information with the use of a fixed coordinate system, the origin of which is independent of the start position. Conceptually the use of different types of information seems to be related additionally to different mechanisms of motor control, which are based on specifications of movement amplitudes (Meyer et al. 1982) and movement end positions (Polit and Bizzi 1979), respectively (see Abrams et al. 1994).

The inconsistencies between the findings and conclusions disappear when one dissociates the issue of amplitude and location information from the issue of relative and fixed coordinate systems (or, more generally, from the issue of the origin and type of the fundamental coordinate system in visuomotor transformations). For example, when reaching from an initial position of the hand in the lap to the intersections of shafts and arrowheads of a Müller-Lyer figure (Mack et al. 1985) or to the final position of a target that has moved an illusory distance in the frontoparallel plane (Bridgeman et al. 1981; Honda 1985), a fixed reference system or a relative reference system might be used, and amplitude or final location might be specified in this system. In no case should the movement be affected by the visual illusion, because the illusory, perceived allocentric visual distance is simply irrelevant for the visuomotor transformation.

When the start position of the hand is aligned with the initial position of the visual target, in contrast, as in pointing from one intersection of the Müller-Lyer figure to the other one (Elliott and Lee 1995), the reported results are somewhat more variable in that with some illusions the final position of the hand is affected, but with others it is not. In addition the effect of the illusion depends on whether the task is instructed with reference to amplitude or final position (Abrams and Landgraf 1990). Such results suggest that distance and location can be dissociated, even though they are registered in the same coordinate system (see Abrams and Landgraf 1990); in fact, at the level of single-unit behavior, they are dissociated. For example, Fu et al. (1993, 1995) found single-cell activity in the primary motor cortex and the premotor area to be correlated with several movement characteristics, direction, and target location as well as amplitude. On the behavioral level an example of a dissociation has been reported by Drain and Reuter-Lorenz (1996). The stimulus was a vertical line that was interrupted at some point close to its center. Subjects had either to judge the position of the interruption (above or below the center) or the lengths of the line segments above and below the interruption (one longer or shorter than the other). The position of the interruption that appeared in the center of the line turned out to be higher than the position of the interruption that produced two equally appearing line segments. Similarly, Mateeff et al. (1990) found a stronger shortening of the perceived distance moved by a fixated target when distance estimates were required than when distance was computed from position estimates; in particular the increase in the shortening effect with target velocity was stronger for distance judgements than for position judgements. Thus, in registering distances and locations in a certain reference system, the brain does not necessarily obey the geometric relations between them, so that dissociations do not necessarily imply the involvement of different coordinate systems.

**Acknowledgement** We thank Patricia Tegtmeier for collecting the data.

## Appendix

The procedure of Bock and Arnold (1993) uses error propagation as an indicator for the involvement of a relative reference system. The purpose of this appendix is to demonstrate that the measures of error propagation used are sensitive not only to error propagation proper but also to variations in visuomotor gain. Therefore we have generated artificial data, using a fixed reference system and variable visuomotor gains, and performed an analysis according to Bock and Arnold (1993), restricted, however, to two dimensions.

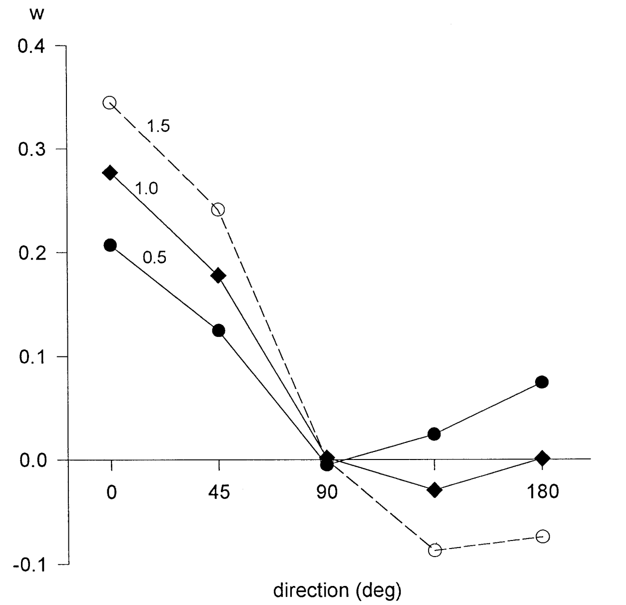


**Fig. A1** Effects of variability of visuomotor gain on estimates of error propagation ($w$) by the method of Bock and Arnold (1993) as a function of direction and amplitude of the second movement. Direction is given as the angle of the second movement with the first one, amplitude as the proportion of the second amplitude relative to the first one

Consider two target positions in a plane, $P_1 = (x_{T1}, y_{T1})$ and $P_2 = (x_{T2}, y_{T2})$. Two successive movements end at positions $M_1 = (X_{R1}, Y_{R1})$ and $M_2 = (X_{R2}, Y_{R2})$, where $X_{R1}$, $X_{R2}$, $Y_{R1}$, and $Y_{R2}$ are random variables that take different values when the sequence of the two movements is repeated. The procedure of Bock and Arnold (1993) is based on a coordinate system with origin in $(\overline{X}_{R1}, \overline{Y}_{R1})$ and the abscissa running through $(\overline{X}_{R2}, \overline{Y}_{R2})$, where these two points are the bivariate means of the two distributions of endpoint positions. In this coordinate system $X'_{R1}$ is the error of the first movement in the mean direction of the second one, and $X'_{R2}$ is the amplitude of the second movement in the same direction. Adding an error term to the regression equation, the determination of error propagation is based on

$$(A1) X'_{R2} = w \cdot X'_{R1} + \overline{X}'_{R2} + E_{R2}$$

where $\overline{X}'_{R2}$ is the mean amplitude of the second movement in the $x$ direction. Thus, $w$ is a measure of error propagation, while $E_{R2}$ represents the variability of $X'_{R2}$, which is independent of the preceding error $X'_{R1}$. Of course, the use of $w$ as a measure of error propagation implies a causal effect of the first error on the second one; however, $w$ is also affected when both errors depend on a third variable as the visuomotor gain.

We generated artificial data based on a fixed reference system for the visuomotor transformation, which implies that these data do not exhibit error propagation proper. The origin of the fixed reference system was arbitrarily placed in the start position of the first movement, and endpoint distributions were generated as $X_{R1} = K \cdot x_{T1} + E_{x1}$, $Y_{R1} = K \cdot y_{T1} + E_{y1}$, $X_{R2} = K \cdot x_{T2} + E_{x2}$, and $Y_{R2} = K \cdot y_{T2} + E_{y2}$ with $K$, $E_{x1}$, $E_{y1}$, $E_{x2}$, and $E_{y2}$ as normally distributed random variables; $E(K) = 1$ and $E(E) = 0$. $K$ represents the visuomotor gain and $E$ the specific error. For the simulations we set $\mathrm{var}(K) = 0.0004$ and $\mathrm{var}(E) = 0.0025$. We set $P_1 = (1,0)$ and varied $P_2$ such that the second movement had target amplitudes of 0.5, 1.0, and 1.5 units and directions of 0°, 45°, 90°, 135°, and 180° relative to the first movement.

We estimated $w$ for sets of 100 repetitions, and Fig. A1 shows the mean estimates of $w$ computed from 1000 such runs. Even without error propagation proper – in the sense that the second error is determined by the first one – the estimator $w$ can be larger or smaller than zero: the second error is predictable from the first one because both depend on the visuomotor gain. In particular at angles of 0° and 45° the value of $w$ is positive and high; this implies that the observation of Bock and Arnold (1993) that error propagation is reduced after changes of direction of 90° and more could result from such an artifactual increase in $w$ at smaller angles. The effects of direction changes become stronger when the variability of the visuomotor gain is increased relative to error variability.

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