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Arm Trajectory Modifications During Reaching Towards Visual Targets

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Abstract

■ In this paper we study the question of how an aimed arm movement is modified in response to a sudden change in target location occurring during the reaction or movement time. Earlier monkey and human studies demonstrated that aimed arm movements can be elicited in quick succession, without appreciable delays in responding to the target displacement, beyond the normal reaction time. Nevertheless, it is not yet clear how this motor task is performed. A first guess is that when a new visual stimulus appears the old plan is aborted and a new one conceived. Upon analyzing human arm movements, however, we find that the observations can be well accounted for by a different movement modification scheme. It appears that a new plan is vectorially added to the original plan. Among the implications of this result is the possibility of parallel planning of elemental movements and further support for the idea that arm movements are internally represented in terms of hand motion through external space. ■

INTRODUCTION

Even the generation of simple reaching movements toward a static visual object (e.g., a cup of coffee) requires extremely complicated and as yet poorly understood computations such as the encoding of target position, the coordination between the motions of several limb segments, and the generation of appropriate muscle activation patterns. Very often, the locations of visual objects may unexpectedly change, or more accurate information about target location may become available and, as a result, ongoing motor commands must be modified. This paper reports new results concerning the question of what strategies are employed in the trajectory modification task.

Earlier monkey and human studies demonstrated that aimed arm movements can be elicited in quick succession, without appreciable delays in responding to the target displacement, beyond the normal reaction time (Megaw, 1974; Georgopoulos, Kalaska, & Massey, 1981; Soechting & Lacquaniti, 1983; Gielen, Van den Heuvel, & Denier Van der Gon, 1984; Vicario & Ghez, 1984). This is in contrast to the prolonged delays in response initiation [the so called "psychological refractory period" (PRP)] that were often observed in motor tasks involving the use of two anatomical units, such as two fingers or two hands (Gottsdanker, 1967; Poulton, 1981). Generally, the explanation given for the presence of a PRP is that the brain has a limited processing capacity and cannot cope simultaneously with the stimulus–response requirements of two or more stimuli. Hence, it was suggested that the lack of a PRP when the required responses are movements of the same hand aimed at successively presented targets may reflect the strong similarity between the ways that visual targets and aimed arm movements are internally coded (Georgopoulos, Kalaska, & Massey, 1981). Still lacking, however, is an explicit hypothesis regarding the mechanisms subserving arm trajectory modification.

Earlier studies of horizontal planar reaching movements toward static targets have shown that for the same set of movements, while the hand trajectory through external space remains essentially invariant (i.e., it follows a straight path with a bell-shaped velocity profile), the rotations of individual joints vary considerably with the locations of the movement end-points (Morasso, 1981; Flash & Hogan, 1985; Hogan & Flash, 1987). This observation was interpreted to suggest that motion planning takes place in terms of spatial hand coordinates rather than in terms of joint rotations (Morasso, 1981). In the absence of any overriding accuracy demands, the shape of the hand velocity profiles was found to be unaffected by changes in the temporal and spatial scales of execution (i.e., movement duration and amplitude) or by target locations (Hollerbach & Flash, 1982; Flash & Hogan, 1985). For example, if movements of different speeds, performed between the same target pair, are normalized with respect to speed, and then coaligned, they coincide exactly (Hollerbach & Flash, 1982; Atkeson & Hollerbach, 1985; see also Fig. 4).

The above kinematic features of planar horizontal reaching movements were successfully accounted for by a model that suggests that a major objective of motor coordination is to generate maximally smooth hand trajectories (Flash & Hogan, 1985). Equating this objective with the minimization of integrated hand jerk (rate of change of acceleration), hand motions were described by the following fifth-order polynomials:

$$x(t) = x_A + (x_B - x_A)(10\tau^3 - 15\tau^4 + 6\tau^5), \qquad (1)$$

$$y(t) = y_A + (y_B - y_A)(10\tau^3 - 15\tau^4 + 6\tau^5)$$

$$\text{where } \tau = \frac{t}{t_f}$$

In (1), $(x_B - x_A)$ and $(y_B - y_A)$ are, respectively, the x and y components of the displacement vector between target positions A and B, and t_f is the movement duration. These hand trajectories are invariant under translation, rotation, amplitude, and time scaling.

Taken together, the above observations and results from both behavioral and modeling studies were consistent with the notion that the construction of motor acts involves different hierarchical levels of organization (Bernstein, 1967). Hence, the same general internal representation of motion is used each time a movement is about to be generated, with the spatial and temporal parameters (i.e., movement amplitude, duration, and end-point locations) chosen for that particular movement (Keele, 1981; Flash & Hogan, 1985).

One plausible strategy for motion modification when the target location is suddenly changed may involve the replacement of the rest of the initially planned response by a new motion between the expected hand position at the time of the switch and the second target location. For the two motions to be smoothly joined together, information about the kinematic state of the hand at the time of trajectory modification should be available to the system. Since motion planning precedes its execution, such information cannot be derived from vision or proprioceptive feedback but might be obtained from efference copies of past motor commands (McCloskey, 1981). This study presents a simpler trajectory modification strategy that does not require a detailed record of the kinematic state of the evolving initial motion plan. It is suggested that the initial trajectory plan continues unmodified until its intended completion and is vectorially added to a second trajectory plan for moving between the first and second target locations. Thus, this strategy involves the superposition of two trajectory primitives. To test its validity, the superposition scheme was mathematically modeled and the predicted behavior was compared to experimentally measured arm movements.

Modeling Rationale and Analysis

To investigate what mechanisms might be possibly involved in the movement modification task, human arm trajectories, recorded in double-step target displacement trials (Megaw, 1974; Georgopoulos et al., 1981; Soechting & Lacquaniti, 1983; Gielen, Van den Heuvel, & Denier Van der Gon, 1984) were kinematically analyzed. As described in Methods, in these experiments, the hand is initially at rest at some specified location A. At time $t = 0$, a target located at position B is illuminated. It either remains lit (control condition), or may shift again following an *interstimulus interval* (ISI) to its final location C (double-step condition). The subject is instructed to move his/her hand toward the one lit target.

We wished to test whether the modified motions may emerge from the vectorial summation of two independent trajectory plans. The first one is the initial unmodified (control) trajectory plan AB. The second is a time-shifted "control-like" trajectory plan that starts and ends at rest and has the same amplitude and kinematic form as a simple point-to-point movement between targets B and C.

Although the idea that more complex motor behaviors might be constructed from the superposition of simpler movements has already been hypothesized in the context of speech (Munhall & Lofqvist, 1987), locomotion (Flashner, Beuter, & Arabyan, 1988), and both single-joint (Adamovitch & Feldman, 1984) and complex arm trajectories (Morasso & Mussa-Ivaldi, 1982), the elementary building blocks cannot be easily identified in these tasks. This hypothesis was also tested for the arm trajectory modification task, but was found to be incompatible with the observed behavior (Massey, Schwartz, & Georgopoulos, 1986). However, in that study it was assumed that the superimposed trajectories must have the same durations as those of the corresponding point-to-point movements AB and BC that were separately generated by the same subject during control trials. Since in the study of Massey et al. (1986) motion speed following the modification time was found to be substantially higher than during the corresponding control trials, simulated trajectories obtained by superimposing average, measured control movements AB and BC failed to match the observed trajectories. Consequently, these authors suggested a different strategy involving the application of large forces to break the first movement, if needed, and the implementation of a new movement as fast as possible.

Motion speed may vary between trials, or may increase with practice (Gottlieb, Corcos, Jaric, & Agarwal, 1989), and in the modification task the speed might also be affected by the mechanical state of the muscles at the modification time. However, as previous studies have demonstrated, the general features of point-to-point movements, and, in particular, their kinematic form, are generally unaffected by changes in speed. Consequently, in contrast to the study of Massey et al. (1986), we do not make any a priori assumption about the durations of the added trajectory units. Instead, we wished to test whether the added elemental trajectories, regardless of their durations, might obey the same law of motion as obeyed by simple reaching movements [i.e., Eq. (1)].

For each (not average) measured modified motion, the following analysis was first separately applied to the

x and y components of the recorded trajectory, and the results were then combined to simulate the entire emerging movement.

1. A point-to-point minimum jerk trajectory AB between the initial hand position A (taken from the data) and the first target location B was appropriately time-scaled to coincide with the initial part of the measured velocity profile. This was taken to be the first trajectory unit. In an alternative procedure, the velocity profiles of the measured control movements AB were normalized with respect to time. This was done by compressing the time axis and multiplying the velocities by the scaling factor v_{ref}/v_{max}, where v_{max} is the measured peak velocity of each profile and $v_{ref} = 0.5$ m/sec. An average control velocity profile was then obtained and was used instead of the minimum jerk movement to derive the first trajectory unit. This procedure gave similar results to the one described above.

2. The time t_s of the first detectable deviation of the measured speed profile from that of the first movement unit was extracted.

3. From this time on, the position components of the modified movement were assumed to be represented by the algebraic summation of the position components of the initial unmodified trajectory unit with the corresponding position components of an added trajectory unit. The latter were described by general fifth-order polynomials. Hence, the expression used to describe the x component of the added motion units was

$$x(t) = (x_C - x_B)(a_3T^3 + a_4T^4 + a_5T^5), \qquad (2)$$

$$\text{where } T = \frac{t - t_s}{t_f - t_s}$$

In Eq. (2), $(x_C - x_B)$ is the x component of the displacement vector between target position B and the final hand location C, and t_f is the duration of the entire modified movement. Both x_C and t_f were derived from the data. The expression for $y(t)$ was analogous to Eq. (2). At t_s, the trajectories described by Eq. (2) have zero positions, velocities, and accelerations. Thereafter, since a_3, a_4, and a_5 are unspecified coefficients, these trajectories may have many possible kinematic forms.

4. To determine which specific polynomial among this entire family, when added to the initial trajectory, can best describe the entire modified movement following t_s, the values of a_3, a_4, and a_5 for both the x and y components were determined using a least-squares best-fit method (Marquardt, 1963) based on the position error between the simulated and measured data points.

RESULTS

The hand trajectories recorded in the control (i.e., single-step target displacement) trials were roughly straight with bell-shaped speed profiles (for typical examples see left column of Figs. 1, 2, 3, and 4). The mean reaction time in these trials was 330 ± 111 msec ($N = 991$). The mean movement time was 544 ± 112 msec ($N = 991$).

In the double-step target displacement trials, the change in target location elicited a graded movement toward target B, followed by a change in movement direction and a subsequent motion toward target C (e.g., Figs. 2 and 3). The duration of the initial movement monotonously increased with ISI. As was previously reported (Gielen et al., 1984; Van Sonderen, Denier Van Der Gon, & Gielen, 1988), occasionally, for short ISIs, the hand initially moved either toward target C or along some intermediate direction in between targets B and C. Of 1557 trajectories recorded in the double displacement trials, the percentage of movements initially directed toward the first target, the second target, and along an intermediate direction were for ISI = 50 msec, 56%, 35%, and 8%, respectively; for ISI = 100 msec, 80%, 11%, and 9%, respectively; and for ISI = 150 msec, 86%, 6%, and 8%, respectively.

The mean reaction time to the first stimulus (RT_1) was 326 ± 91 msec ($N = 1557$). The mean reaction time to the second stimulus (RT_2) was 406 ± 164 msec ($N = 1557$). For short ISIs, the values of RT_2 were slightly longer than those of RT_1. Nevertheless, these values were still significantly smaller than those expected according to the single-channel theory, which postulates that two consecutive stimuli are treated sequentially and without overlap (Poulton 1981). This assumed successive processing of information results in a delay of the response to the second stimulus by an amount of time approximately equal to RT_1 − ISI, for the case that the second stimulus is presented before the motion has begun (Davis, 1956). Thus, our results are in agreement with previous findings that have shown that the mean reaction time to the second stimulus is not substantially different from the normal reaction time (Georgopoulos et al., 1981).

The Superposition Scheme

Based on the analysis described in the Introduction, the calculated mean values of the three coefficients of the polynomials describing the added trajectory units were found to be $a_3 = 9.85 \pm 1.51$, $a_4 = -14.64 \pm 3.44$, and $a_5 = 5.90 \pm 1.50$ ($N = 64$). The hypothesis that these mean values are equal to those of the corresponding minimum-jerk coefficients for a control movement ($a_3 = 10.0$, $a_4 = -15.0$, $a_5 = 6.0$) was accepted on the basis of Student's t test at the 0.05 level. Thus, our findings show that the added trajectories have the same amplitude and kinematic form as that of a simple point-to-point trajectory between targets B and C.

Using steps (1), (2), and (3) of the analysis procedure (see in Modeling Rationale and Analysis), the durations of the two trajectory units were inferred from the data. The duration of the first trajectory unit corresponded to the time interval between movement initiation and the time at which the velocity of the first unit becomes zero. The duration of the second trajectory unit was derived by subtracting the modification time (t_s) from the duration of the measured modified movement (t_f). The mean value of the movement durations of the initial trajectory units was found to be 522 ± 135 msec (N = 64). The mean value of the movement durations of the added (second) trajectory units was found to be 542 ± 138 msec (N = 64). Thus, the average movement times of the two superimposed trajectory units AB and BC were roughly equal and not much different from the average movement time of the control movements (544 ± 112 msec, N = 991).

To test the success of the superposition scheme in accounting for the kinematic features of the modified movements, trajectories simulated on the basis of the superposition scheme were compared with the measured ones. In Figures 1–3 the hand paths and velocity profiles of the measured and simulated movements are marked by solid and dashed lines, respectively. The hand paths and velocity profiles of the two superimposed trajectory units are marked by alternating dots and dashes. The initial hand position and the first and final target locations are marked by A, B, and C, respectively.

Figure 1 describes typical results from trials in which both the first and second target displacements were coaligned with a line passing parallel to the x axis (a one-dimensional target configuration). The (x, y) coordinates (in cm) of targets A and B in Figure 1, with respect to the shoulder, were (7.0, 47.5) and (−6.6, 47.5), respectively. The left panel shows a control movement. The middle panel shows a continuation movement with ISI = 100 msec, recorded in a trial in which both the first and second target displacements were in the same direction [the coordinates of C were (−20.7, 47.5)]. The right panel shows a reversal movement with ISI = 100 msec, recorded in a trial in which the first and second target displacements were in opposite directions with respect to each other [the coordinates of C were (21.1, 47.5)]. Hand paths of the measured and simulated movements and of the two superimposed trajectory units are shown in the top row of Figure 1. The corresponding velocity profiles (V_x) are shown in the bottom row. As can be seen from this figure, there is a good qualitative and quantitative agreement between the measured and predicted trajectories.

Figure 2 shows typical examples from two trials in which either one or both target displacements were obliquely oriented with respect to the orthogonal coordinate system located at the shoulder. Hand paths for two different target configurations are shown in the top row of this figure. The targets A and B were located (in cm) at (14.1, 44.2) and (−6.6, 50.4) with respect to the shoulder. Shown from left to right, are the hand paths of a control movement AB and of two modified motions (ISI = 50 msec) with the final target C located either at (−27.5, 43.1) (middle figure) or at (−6.6, 29.6) (right figure) with respect to the shoulder. The added trajectory units are plotted beginning at the position that the hand occupied at the modification time (t_s). The corresponding velocity components are shown in the middle (V_x) and bottom (V_y) rows.

As Figures 1 and 2 demonstrate, the fit between the simulated and real trajectories was equally good for different trials, regardless of the direction and amplitude of the second target displacement.

We were also able to account for the variability in hand trajectories generated by different subjects or by the same subject in trials involving the use of the same target configuration but different ISIs. This is illustrated by the results shown in Figure 3 taken from a single subject. In the top row, the measured hand paths are shown. The locations of A, B, and C with respect to the shoulder (in cm) were (−6.7, 33.6), (14.2, 40.9), and −6.7, 54.5), respectively. Shown from left to right are the paths of a control and three modified movements for ISI = 50, 200, and 300 msec, respectively. The corresponding

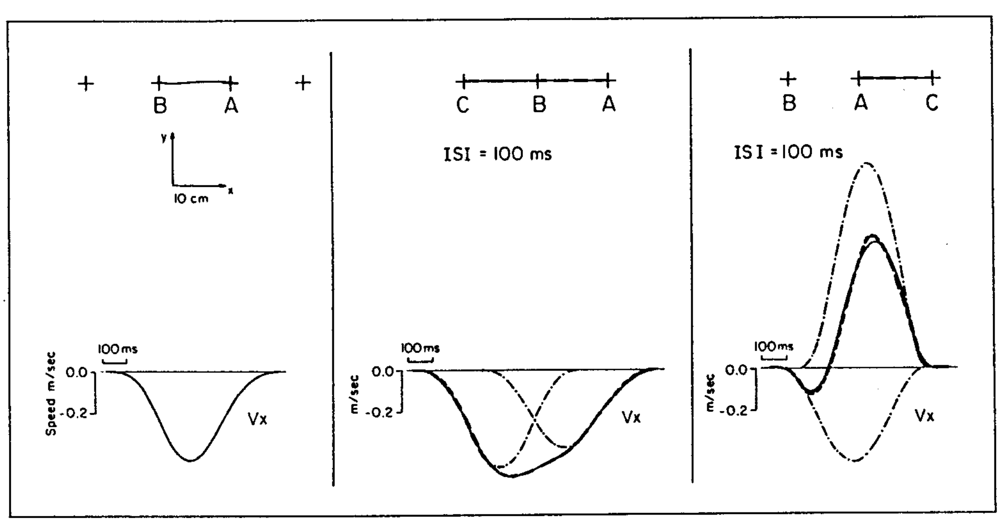
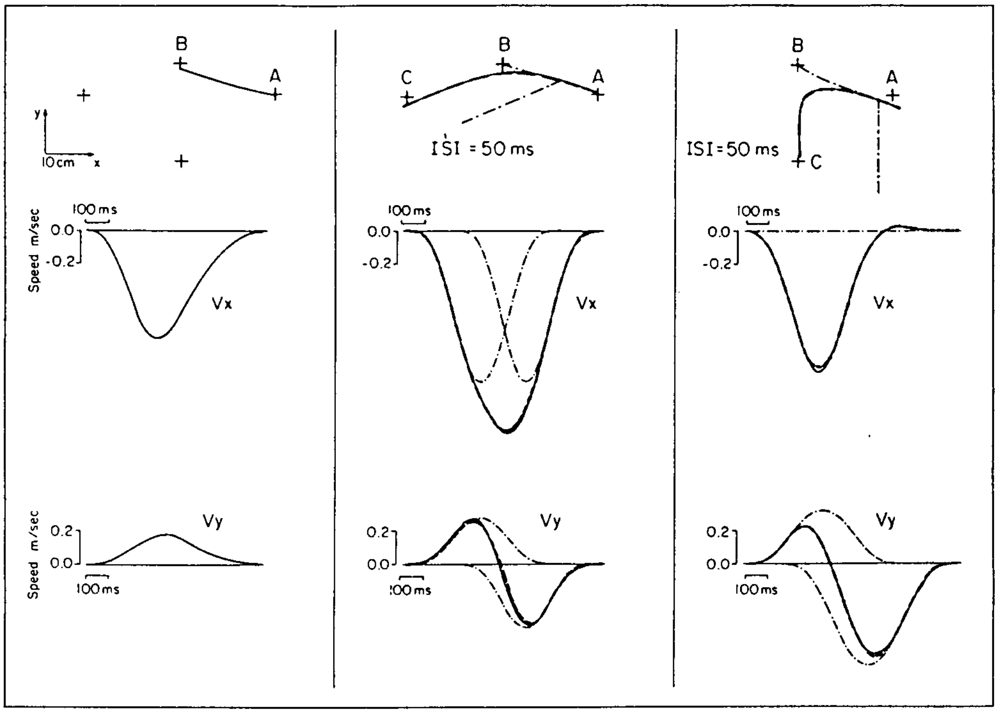


Figure 1. The superposition scheme: one-dimensional target configurations. Representative examples of comparisons between measured one-dimensional movements and the corresponding movements resulting from the superposition scheme. Shown are the measured (solid lines), simulated (dashed lines), and two trajectory units (alternating dots and dashes). Shown are the hand paths (top row) and the x components of velocity (V_x, bottom row), of a control (left), a continuation (middle), and a reversal (right) movement with ISI = 100 msec.

Figure 2. The superposition scheme: two-dimensional target configurations. Representative examples of comparisons between measured two-dimensional movements and the corresponding movements resulting from the superposition scheme for two different target configurations. Shown are, from left to right, hand paths of a control and two modified movements with ISI = 50 msec. The second trajectory unit is plotted beginning at the position that the hand occupied at the modification time. The corresponding velocity components are shown in the middle (V_x) and bottom (V_y) rows. See Figure 1 for legend description.



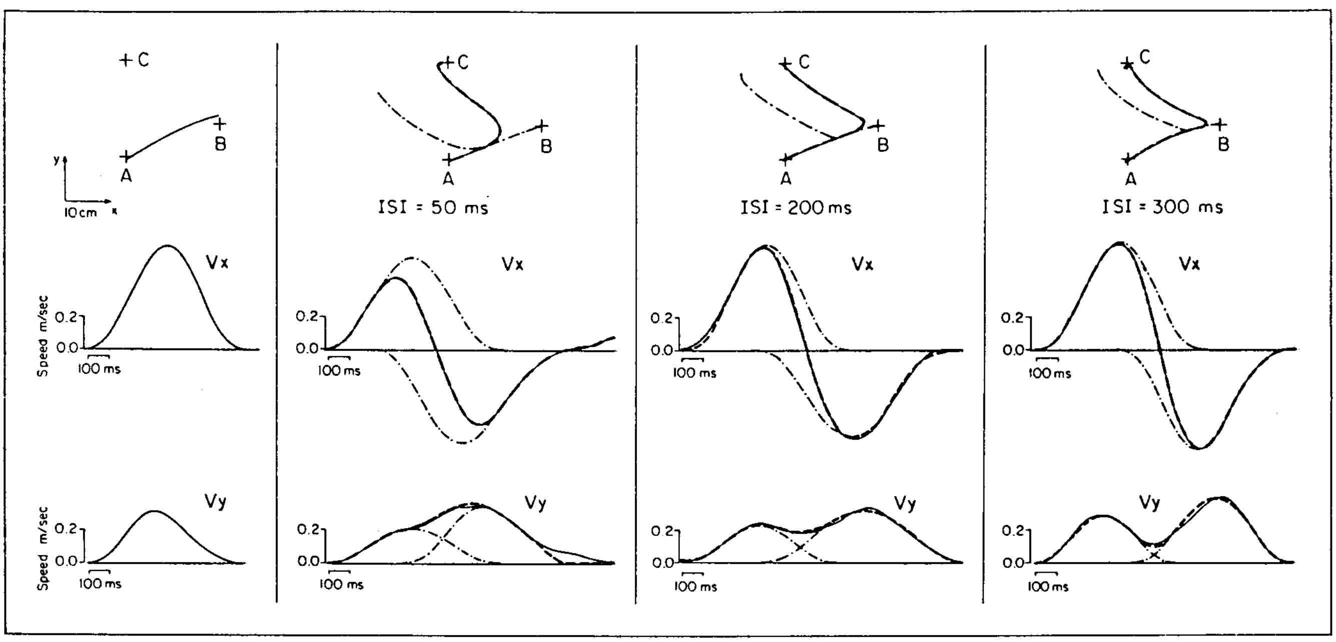


Figure 3. Various ISIs. Hand trajectories as in Figure 2 for a different two-dimensional target configuration and for different ISIs. Shown from left to right are a control and three modified movements for ISI = 50, 200, and 300 msec. Hand paths are shown in the top row. The second trajectory unit is plotted beginning at the position that the hand occupied at the modification time. The corresponding hand velocity components are shown in the middle (V_x) and bottom (V_y) rows. See Figure 1 for legend description.

hand velocity components are shown in the middle (V_x) and bottom (V_y) rows. Notice the differences between the kinematic details of the hand paths and velocity profiles of these three measured movements and their good agreement with the simulated ones. Also plotted in this figure are the simulated trajectories resulting from the superposition scheme and the trajectories of the two superimposed units. The added trajectory units are plotted beginning at the position that the hand occupied at the modification time. Since the amplitudes of the superimposed trajectory units are assumed to be equal to those of the corresponding target displacement steps, they did not vary among the three movement modification trials shown in Figure 3. Given, however, the differences among the durations of these units, and among the time delays between their initiation, their vectorial summation resulted in kinematically different modified movements. Similarly, movement variability of trajectories generated by the same subject on successive trials with the same ISI could result from the variability in RT_1 and RT_2 and in the durations of the superimposed trajectory units.

As the results shown in Figures 1–3 illustrate, the simulated movements were found to be in good agreement with the measured ones for both one-dimensional and two-dimensional target configurations, for different ISIs, and for movements measured across different trials with a fixed target configuration and the same ISI. Hence, the whole spectrum of hand paths and velocity profiles was successfully accounted for by the superposition scheme.

Is the Initial Motion Plan Aborted?

One of the basic hypotheses of the superposition scheme is that the initial trajectory is neither aborted nor modified following the target switch. Further confirmation for this hypothesis was provided by the analysis of movements recorded for right-angle target configurations. An example of such target configuration is shown in Figure 4. The targets were located (in cm) at A (−6.7, 33.6), B (−6.7, 54.5), and C (20.6, 54.6), with respect to the shoulder. Typical examples of measured hand paths of both control and modified movements for this target configuration are shown in the top row of Figure 4. In these and in similar movements, the initial trajectory units AB were fully represented by the measured (i.e., not mathematically derived) y components of the recorded modified movements. In the bottom row, on the left, the average velocity profile for 63 time-scaled control movements for this target configuration is shown. Time scaling was again performed (see Modeling Rationale and Analysis) by compressing the time axis and multiplying the velocities by the same scaling factor with v_{ref} = 0.5 m/sec. The lengths of the vertical bars indicate the magnitude of 1 standard deviation of the average control velocity profile. In the bottom row on the right, 15 speed-scaled and coaligned y components of the velocity profiles for the measured modified movements are shown, together with the standard deviation bars of the average control velocity profile. As the results described in this figure show, the coaligned, time-scaled, velocity profiles of these components lie within 1 standard deviation of the average velocity profile of the corresponding time-scaled control movements. These results demonstrate that the initial trajectory units have the same kinematic form as that of a control movement, thus indicating that the initial trajectory plan is neither aborted nor modified following the target switch.

The Alternative Abort–Replan Scheme

The validity of the alternative abort–replan modification strategy was also tested. This scheme was mathematically modeled by assuming that following the target switch the initial trajectory is aborted and that the motion from t_s and until target C is reached can be represented by a new trajectory smoothly joined with the initial one. Both the x and y components of this new trajectory were described by general fifth-order polynomials. For each measured movement, the values of the six polynomial coefficients of each trajectory component were derived using two alternative methods. In Method I, the hand was assumed to reach the measured final position with zero velocity and acceleration, thus dictating the values of three of the six unspecified polynomial coefficients. The values of the remaining coefficients were derived using the same least squares best-fit method as the one applied above (Marquardt, 1963). In Method II, the values of all six polynomial coefficients were determined using

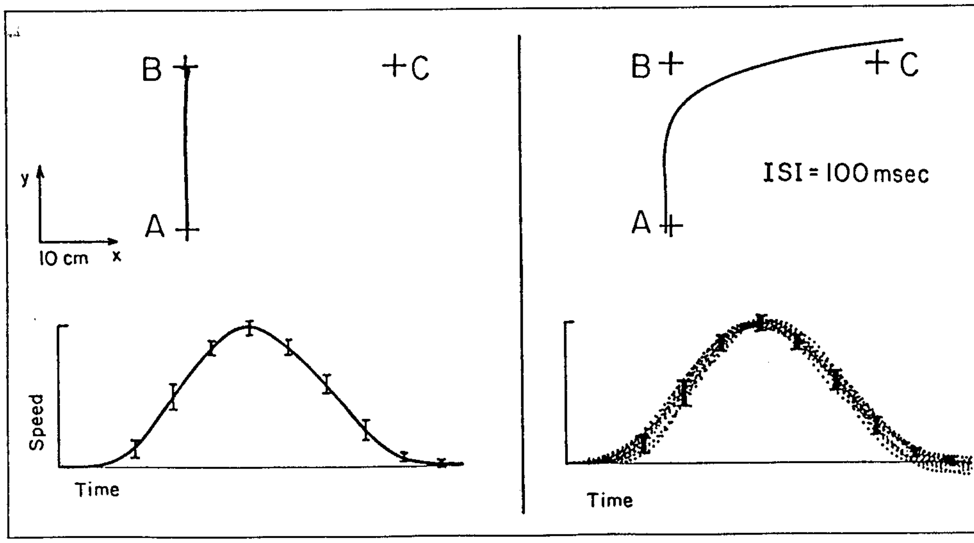


Figure 4. Evidence for the hypothesis that the initial trajectory plan is neither aborted nor modified. In the top row, typical measured hand paths of a control (left) and a modified (right) movement for a right-angle target configuration are shown. In the bottom row, on the left, the average velocity profile for 63 time-scaled control movements for this target configuration is shown. The vertical bars indicate one standard deviation of the average control velocity profile. On the right, 15 speed-scaled and coaligned y components of the velocity profiles for the modified movements are shown, together with the standard deviation bars of the average control velocity profile.

the measured values of hand positions, velocities, and accelerations at t_s and at the movement end-point.

To test the success of this abort–replan scheme in accounting for the observed data, measured and simulated movements were quantitatively compared. Although the recorded paths were occasionally reproduced (more often with Method I), the majority of the velocity profiles simulated on the basis of the alternative abort–replan scheme showed substantial deviations from the measured profiles. This is illustrated in Figure 5, where velocity profiles of measured (solid lines) and simulated (dashed lines) trajectories resulting from the abort–replan scheme are shown. These velocity profiles correspond to the same one-dimensional reversal movement as in Figure 1 (right). On the left of Figure 5, a simulated velocity profile obtained by Method I is compared to the corresponding measured profile. Notice the discrepancy between the simulated and measured velocities at t_s. On the right of Figure 5, the same measured velocity profile is compared to the simulated velocity profile obtained from the use of Method II.

As comparison of Figures 5 and 1 illustrates, the superposition scheme has provided a better description of the data than the abort–replan scheme. This was also confirmed on the basis of formal statistical tests as follows. The sum of squares of the differences between the measured and simulated velocity profiles, normalized by the sum of squares of the measured velocities, was used as a numerical estimate of the degree of fit between the simulated and the measured movements. The mean values of these numerical estimates obtained for the superposition scheme, and for Methods I and II of the abort–replan scheme, were 0.0174 ± 0.0173, 0.0446 ± 0.0529, and 0.0318 ± 0.0262 ($N = 63$), respectively. Using Student's t test, the hypothesis that the differences between the numerical estimates obtained for the two abort–replan methods and the ones obtained for the superposition scheme are due to chance was rejected, at the 0.001 level, for both abort–replan modeling methods. Thus, the superposition scheme was found to be significantly better in accounting for the measured data than the alternative abort–replan strategy.

Algebraic analysis has further shown that the latter strategy is mathematically distinct from the superposition scheme and that the two are equivalent only when the two superimposed trajectory plans terminate at the same time.

The Level of Superposition

The execution of the desired hand trajectory plans requires the generation of appropriate joint rotations, joint torques, and muscle activation patterns. Therefore, an important question to be asked is at what level of the motor hierarchy (hand, joint, or muscle) are the basic trajectory units superimposed? As the results presented above have shown, superposition at the hand level can successfully account for the observed kinematic features of the modified trajectories. Nevertheless, we were still interested in testing whether superposition of the above elemental hand trajectory plans at the joint or torque levels might also be feasible.

To test the feasibility of joint level superposition, the basic hand trajectory units were transformed into the corresponding joint (shoulder and elbow) rotations using the inverse-kinematics calculations (Brady, Hollerbach, Johnson, Lozano-Pérez, & Mason, 1982). The transformation from hand to joint coordinates is configuration dependent and the trajectories resulting from the joint level superposition scheme must end at location C. Hence, the second trajectory unit was assumed to start at target location B. The joint trajectories corresponding to the second motion unit must have zero initial positions and their amplitudes must correspond to the differences in position between locations B and C expressed in joint coordinates. The shoulder and elbow angles associated

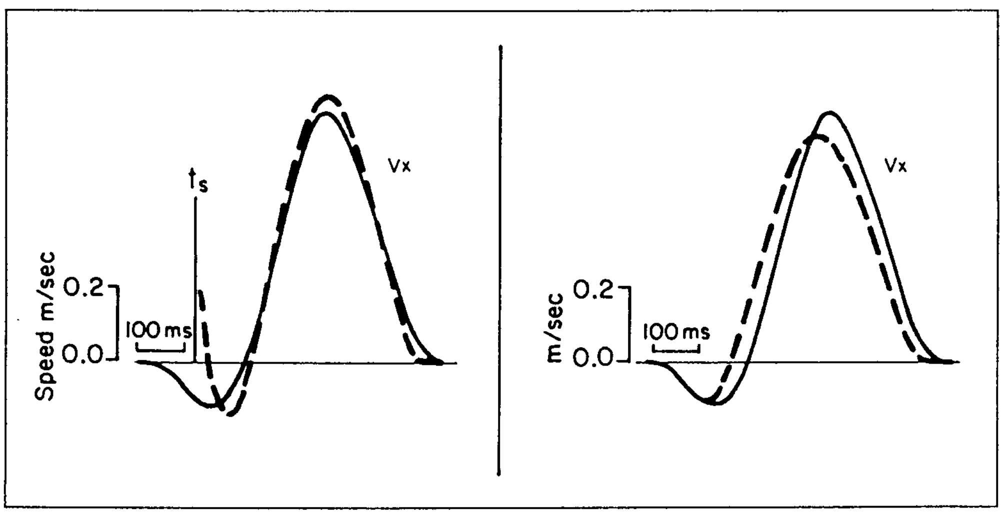


Figure 5. Velocity profiles resulting from the alternative abort–replan scheme. The x components of velocity profiles of measured (solid lines) and simulated (dashed lines) trajectories resulting from the alternative abort–replan modification scheme. The velocity profiles shown correspond to the same one-dimensional reversal movement as in Figure 1. The simulated trajectories were obtained from the use of Method I (left) and Method II (right).

with position B were therefore subtracted from the joint profiles derived from the above kinematic transformations. The resulting profiles were then summed together from the modification time on, with the corresponding joint profiles (shoulder and elbow) of the first hand trajectory unit. Forward kinematics transformations were then used to derive the corresponding hand movements.

To test the feasibility of superposition at the torque level, the time-histories of the shoulder and elbow torques required to generate each hand trajectory unit were computed by applying the inverse-dynamics calculations (Brady et al., 1982) to the corresponding time-histories of joint positions, velocities, and accelerations. Since these calculations are also configuration dependent, again the second trajectory unit was assumed to start at the joint positions corresponding to spatial location B. Summing together the resulting shoulder and elbow torque profiles of the two trajectory units, forward dynamics and kinematics computations were then performed to obtain the hand movements resulting from the torque level superposition scheme.

In Figure 6, typical examples of the simulated trajectories and velocity profiles resulting from the joint level (dashed lines) and the torque level (alternating dots and dashes) superposition schemes are compared with the corresponding profiles resulting from the hand level superposition scheme (solid lines). Shown are the hand paths (left) and the x and y components of the velocity profiles (right). In spite of the nonlinear nature of the inverse-kinematics transformations, the trajectories obtained from the joint level superposition scheme were found to be quite similar to the ones obtained from the hand level superposition scheme and to the measured trajectories (not shown). However, the trajectories obtained from the torque level superposition scheme showed substantial deviations both from the ones obtained from the other two schemes and from the measured ones.

DISCUSSION

Our results provide evidence in support of the hypothesis that arm trajectory modification in the double target displacement paradigm may involve the vectorial summation of two independent trajectory plans. The first of these is the original unmodified (control) plan that specifies the motion between the initial hand position and the first target location. The second one is a time-shifted "control-like" trajectory plan that starts and ends at rest and has the same amplitude and kinematic form as a simple point-to-point movement between the first and second target locations. Furthermore, our results are consistent with the idea that an independent hand trajectory planning process is activated following the target switch, and that whenever the second motion plan is ready, it is continuously added to the initial unmodified one. For the longer ISIs, the initial response begins well before the second target is presented. The hand, therefore, starts moving toward the first target. As the ISI becomes shorter, however, the initial movement direction might already be affected by the second target presentation and thus might be in between the two targets ("movement averaging"). Here we have dealt only with movements initially directed toward the first target location. One possible explanation for the averaging phenomenon observed for short ISIs is that the superimposed trajectories AB and BC are activated almost at the same time. Alternatively, the initial superimposed trajectory might be directed toward an internally perceived initial target (Van Sonderen et al., 1988), rather than toward the actual target B. Further investigations are currently being conducted to determine which of

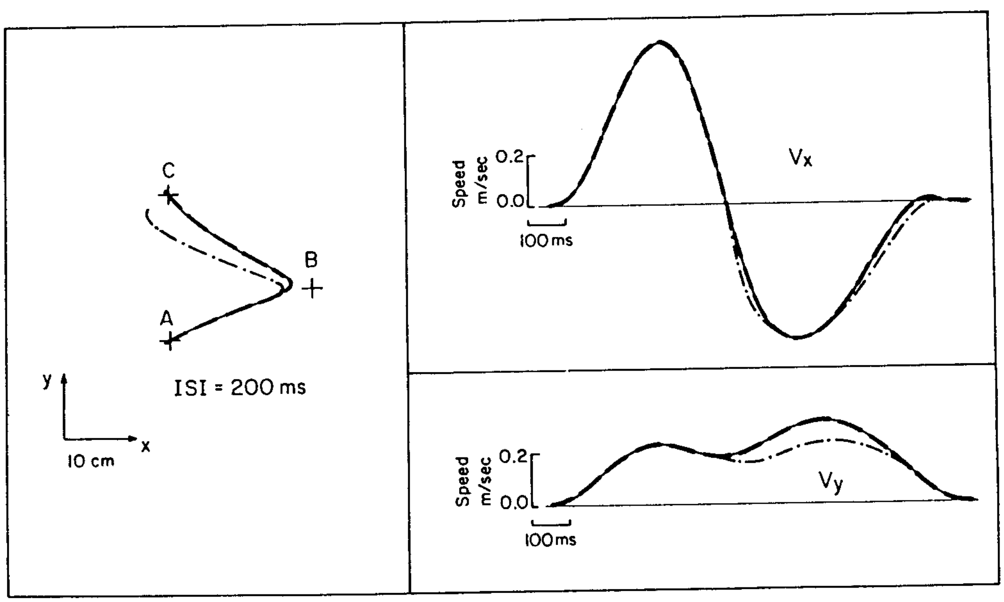


Figure 6. The level of superposition of the elemental hand trajectories. Simulated trajectories resulting from the superposition of the elemental hand trajectory plans at the hand (solid lines), joint (dashed lines), and torque (alternating dots and dashes) levels. Shown are the hand paths (left) and the x and y components of the velocity profiles (right).

these two explanations can better account for the combined effect of two successive stimuli on the initial movement direction.

Our results have demonstrated that the kinematic details of each modified movement might be dictated by the time delays between the initiation of the superimposed trajectory plans and by the units' durations. These results suggest that the observed kinematic variability of modified movements does not necessarily reflect differences in the strategies used to modify ongoing movements, but may result from the differences among the temporal and spatial parameters used to appropriately scale the underlying superimposed elemental movements.

The results have also shown that the superposition scheme is significantly better than the alternative abort–replan scheme in accounting for the kinematic data. In the superposition scheme, no information is required about the expected hand position at the modification time. This offers the possibility for parallel planning of trajectory primitives. The incremental changes in hand position, as specified by the two planning processes, could be continuously added to yield the combined trajectory plan. Since the elemental hand movements were shown to have the same kinematic form, as though derived from a common template, this finding provides further support for the idea that arm movements are internally represented in terms of hand motion through external space. Additional neurophysiological support for this view has been provided by recent studies that have shown that the spatial direction of hand motion is coded by the so-called "neuronal population vector," which represents a weighted sum of the firings of a population of motor cortical cells (Georgopoulos, Caminiti, Kalaska, & Massey, 1983; Georgopoulos, Schwartz, & Kettner, 1986). Aimed eye movements have also been postulated to be internally coded in terms of spatial coordinates (Robinson, 1975; Andersen, Essick, & Siegel, 1985) and to be modified on the basis of a similar superposition mechanism (Van Gisbergen, Opstal, & Roebroek, 1987). Such similarities between the internal representations of visual targets and aimed arm and eye movements may simplify visuomotor integration.

The spatial locations of visual targets (and/or target shifts) might be internally coded, and on the basis of this information the amplitude and direction of the intended movement might be derived. This information can then be used to internally code and trigger the generation of the elemental hand movement plans. At some level of the motor hierarchy the internally coded elemental movements must be summed together to yield the commands for lower levels of the motor hierarchy. Although it is not yet known whether and how desired hand motion plans are transformed into the corresponding joint rotations, we were interested in testing the hypothesis that the system may first transform each primitive into its corresponding joint rotations and then algebraically add the resulting joint level plans. Similarly, we also wished to test the feasibility of torque level superposition.

Our results have shown that although both the hand and the joint level superposition schemes did provide a good description of the observed behavior, the hand trajectories simulated on the basis of the torque level superposition scheme showed substantial deviations from the actual ones. Thus, we conclude that the basic hand motion plans are not summed at the torque or muscle levels. Regarding the joint level superposition, however, it should be noticed that the effects of the nonlinearities of hand to joint transformation, and vice versa, become greater when the distance between the first target location B and hand position at $t = t_s$ (the modification time) becomes larger. Hence, the good agreement between the measured and simulated motions resulting from the joint level superposition scheme might be a consequence of the fact that for the movements considered in our study, this distance was not large enough. Thus, in future work, further experimental conditions that may allow us to distinguish between the two alternative levels of superposition should be investigated.

How are the combined motion plans for the modified movement executed? As was recently suggested, explicit computation or derivation of joint torques is not necessary (Hogan, 1985; Flash, 1987). Since neurally activated muscles behave like tunable springs (Houk & Rymer, 1982), a limb's posture can be obtained when the joint torques produced by "spring-like" muscle groups are equal and opposite (Feldman, 1966; Bizzi, Polit, & Morasso, 1976). This implies that when an external force is applied, the limb is displaced by an amount that varies with both the external force and the muscle stiffness. When the external force is removed, the elastic forces of the muscles will restore the original equilibrium position. This led to the idea that movements result from a shift of the equilibrium point caused by a change in neural input. In particular, single-joint movements could be controlled by neural signals that specify a series of equilibrium positions for the limb (Bizzi, Accornero, Chapple, & Hogan, 1984; Feldman, 1986). Likewise, multijoint arm movements might be achieved by shifting the equilibrium point of the hand along the desired trajectory plans. The viscoelastic forces produced by the muscles will then automatically cause the arm to track the equilibrium point (Hogan, 1985; Flash, 1987). In the trajectory modification task, the combined hand trajectory plan could therefore be expressed in terms of an equilibrium trajectory, and then be executed via the mechanics of the neuromuscular system.

METHODS

Human two-joint planar horizontal arm movements, performed in the absence of visual feedback from the moving limb, were recorded using a transparent digitizing table. The table dimensions were 50.8 × 50.8 cm^2. The subject was seated in front of the table. Shoulder movement of the subjects was restrained by means of straps to the back of the chair, and the wrist was immobilized by bracing. All movements were confined to the horizontal plane, at the level of the subject's shoulder. The subject grasped a pen-like stylus which he/she moved towards the one lit target (Fig. 7a). No specific instructions were given to the subject with regard to movement speed, end-point accuracy, or the type of trajectory to be generated. Of the four participating subjects only one was aware of the tested hypotheses. The (x, y) coordinates of the pen tip, with respect to a coordinate system located at the shoulder, were measured at a rate of 100 samples per second with a spatial resolution of 0.025 mm. Velocities and accelerations were obtained by the Lagrange polynomial differentiation method. The data were gathered, stored, and analyzed by a PDP 11/73 computer. Further mathematical and graphical analysis was performed using an IBM-3801 mainframe computer, a Sun 3/50 workstation and a Symbolics 3670 Lisp-Machine.

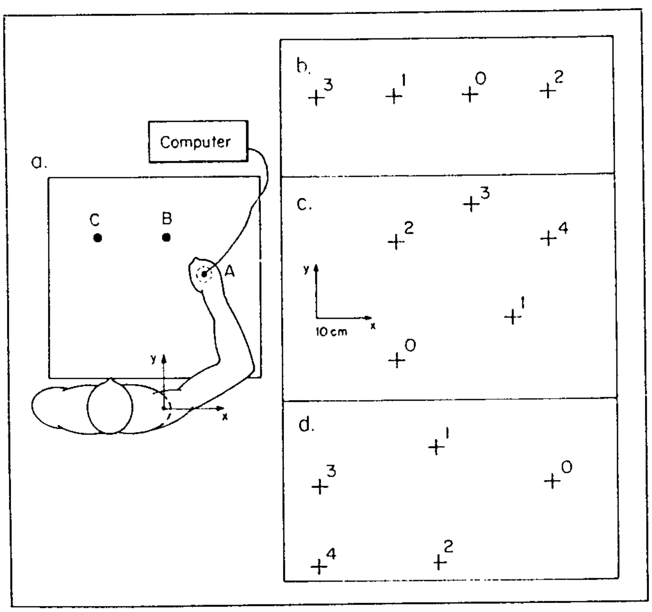


Figure 7. The experimental setup. (**a**) A schematic drawing of the seated subject and of the apparatus. Initially the target was at location *A*. It was then moved to location *B* and either remained lit (control trial) or was displaced again to location *C* (double displacement trial). (**b**) A one-dimensional target configuration. The (x, y) coordinates (in cm) of the initial hand location *A* (target 0) were (7.0, 47.5) with respect to the shoulder. The target sequences used were 01, 02 (control trials) and 012, 013, 021 (double displacement trials). (**c**) A two-dimensional target configuration. The (x, y) coordinates (in cm) of the initial hand location *A* (target 0) were (−6.7, 33.6) with respect to the shoulder. The target sequences were 01, 02 (control trials) and 012, 013, 023, 024 (double displacement trials). (**d**). Another two-dimensional target configuration. The (x, y) coordinates (in cm) of the initial hand location *A* (target 0) were (14.1, 44.2) with respect to the shoulder. The target sequences used were 01, 02 (control trials) and 012, 013, 021, 024 (double displacement trials).

Light emitting diodes installed underneath the table served as the visual targets. Target width was 1.0 cm. In these experiments, the hand is initially at rest at some specified location *A*. At time $t = 0$, a target located at one of two equally probable positions *B* is illuminated. It may remain lit (control condition, probability 0.4) or may shift again, following a specified *interstimulus interval* (ISI), to one of two equally probable locations *C* (probability 0.3 for each). In the three target configurations used (Fig. 7b–d) the target displacements *AB* and *BC* (ranging between 13.6 and 27.7 cm) were either in the same or opposite directions (Fig. 7b), or obliquely oriented with respect to each other (Figs. 7c and d). Eight different ISIs were used and were divided into four pairs (50 and 300 msec, 100 and 400 msec, 150 and 550 msec, and 200 and 700 msec). Each session consisted of three blocks of trials. Within each block, one of the three target configurations (Figs. 7b, c, and d) was used. All blocks were made up of four groups of trials and within each group one of the four ISI pairs was used. After each group of trials, the subject could relax for about 5 minutes before another group of trials employing a different ISI pair was presented. For the one-dimensional target configuration, each group consisted of 40 trials, i.e., 16 single-step (control) and 24 double-step target displacement trials. For the two-dimensional target configurations, each group consisted of 52 trials, i.e., 20 single-step and 32 double-step target displacement trials. Each subject was tested for all four ISI pairs and for all three target configurations.

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