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RESEARCH ARTICLE

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Manual interception of moving targets

II. On-line control of overlapping submovements

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Abstract We studied the kinematic characteristics of arm movements and their relation to a stimulus moving with a wide range of velocity and acceleration. The target traveled at constant acceleration, constant deceleration, or constant velocity for 0.5–2.0 s, until it arrived at a location where it was required to be intercepted. For fast moving targets, subjects produced single movements with symmetrical, bell-shaped velocity profiles. In contrast, for slowly moving targets, hand velocity profiles displayed multiple peaks, which suggests a control mechanism that produces a series of discrete submovements according to characteristics of target motion. To analyze how temporal and spatial aspects of these submovements are influenced by target motion, we decomposed the vertical hand velocity profiles into bell-shaped velocity pulses according to the minimum-jerk model. The number of submovements was roughly proportional to the movement time, resulting in a relatively constant submovement frequency (~2.5 Hz). On the other hand, the submovement onset asynchrony showed significantly more variability than the intersubmovement interval, indicating that the submovement onset was delayed more following a submovement with a longer duration. Examination of submovement amplitude and its relation to target motion revealed that the subjects achieved interception mainly by producing a series of submovements that would keep the displacement of the hand proportional to the first-order estimate of target position at the end of each submovement along the axis of hand movement. Finally, we did not find any evidence that information regarding target acceleration is properly utilized in the production of submovements.

Key words Reaching · Minimum jerk · Target acceleration · Human

Introduction

When we reach toward stationary objects without strict constraints on accuracy, arm movements of different amplitude and duration display an invariant bell-shaped velocity profile with an appropriate spatial and temporal scaling (Soechting and Lacquaniti 1981; Hollerbach and Flash 1982; Atkeson and Hollerbach 1985; Flash and Hogan 1985). On the other hand, when the location of the target changes suddenly during the movement, human subjects and monkeys can make corrective movements with a delay corresponding to visual reaction times, which suggests that they are capable of modifying their arm movements according to visual information at any time during the movement (Georgopoulos et al. 1981; Massey et al. 1986; Soechting and Lacquaniti 1983). Even for movements directed to stationary targets, corrective movements occur if precise reaching is required, and the velocity profiles of reaching movements deviate from a bell-shaped pattern (Milner and Ijaz 1990; Milner 1992). Similarly, a sequence of discrete movements are produced when human subjects and monkeys track a moving target (Miall et al. 1986, 1988, 1993).

For movements of a given amplitude, movement time increases logarithmically with accuracy, a relationship known as Fitts's law (Fitts 1954). Although alternative formulations other than the original logarithmic expres-

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sion have been proposed (Howarth et al. 1971; Schmidt et al. 1979; Kvalseth 1980; Meyer et al. 1982), the tradeoff between the durations and the spatial precision of movement has been observed under a variety of conditions (Kerr 1973; Flowers 1976; Langolf et al. 1976; Wade et al. 1978). Several models have been proposed that attribute such speed-accuracy trade-offs to the time needed for programming and execution of the corrective movements or submovements. In the deterministic iterative-corrections model (Crossman and Goodeve 1963; Keele 1968), an overall movement is composed of successive submovements, and each submovement travels a constant fraction of the remaining distance between the end-point of the previous submovement and the target. Since the movement is terminated when a submovement ends within the width of the target, this model accounts for the increase in movement time for smaller targets. More recently, Meyer et al. (1988) proposed an alternative model that accounts for the variability in the duration of the initial (or primary) submovement and the submovement end-point. In their stochastic optimized-submovement model (Meyer et al. 1988), an overall movement consists of primary and secondary submovements, the end-points of which follow a normal distribution because of a "neuromotor noise." This model also predicts a relationship between movement time and the target size that is qualitatively similar to Fitts's law.

Although these models were successful in describing some aspects of the movement such as movement duration, they did not deal with the movement kinematics directly. A bell-shaped velocity profile and its relative invariance with respect to temporal and spatial scaling has been explained by a model that postulates that a major objective of motor coordination is to minimize the rate of change of acceleration, or jerk (Hogan 1984; Flash and Hogan 1985). By superposing appropriately scaled submovements specified by this minimum-jerk model, Flash and Henis (1991) modeled accurately the modification of hand trajectory due to a sudden change in target location. They proposed that superposition of two submovements occurs without aborting or modifying the original trajectory of the first movement. The notion that complex trajectories are composed of overlapping submovements with invariant kinematic properties was applied in other types of movements, including handwriting (Morasso and Mussa-Ivaldi 1982) and reaching with high precision (Milner 1992). In addition, superposition of submovements were consistent with the data whether superposition was applied at the hand level or joint level, but trajectories obtained from the torque level superposition showed substantial deviation from the observed trajectories (Flash and Henis 1991).

We studied human arm movements directed to intercept a moving target at a fixed location (Port et al. 1997). The time that it took for the target to arrive at its location (target motion time) was randomly varied for each trial, in 0.3-s steps between 0.5 and 2.0 s. In addition, targets moved at constant acceleration, constant deceleration, or constant velocity. The effects of target acceleration and motion time on response times and different types of errors are described in the preceding paper (Port et al. 1997). We proposed that movement initiation is determined according to either of two alternative strategies, namely, reactive and predictive. According to the reactive strategy, the response time is composed of two components; a time for the target to travel a threshold distance and a constant processing time (Collewijn 1972; van Donkelaar et al. 1992). In contrast, according to the predictive strategy (or τ strategy; see Lee 1976; Lee and Reddish 1981), the movement is initiated when the first-order estimate of the time to target arrival, or τ, reaches a certain threshold. We showed that relatively high initial target velocity makes the predictive strategy unrealistic, thus forcing subjects to adopt the reactive strategy, and that only some subjects used the predictive strategy for slowly moving targets (Port et al. 1997).

In the present paper, we investigated how the movements are adjusted *in flight* for successful interception. Except for the shortest target motion time (0.5 s), the velocity profiles of arm movements displayed multiple peaks, indicating the presence of multiple submovements. Control of these submovements should be guided by information regarding target motion for successful interception. We examined several alternative mechanisms for such control, and the results were consistent with the hypothesis that the end-point of each submovement is linearly related to the target location estimated from the position and velocity of the target at the submovement onset.

Materials and methods

Experimental paradigms

All the details of the experimental paradigms and the method of data collection are described in the preceding paper (Port et al. 1997). Briefly, the subject started a given trial by capturing a disk (0.3 cm radius) presented at the bottom of a computer screen along the midline with a two-dimensional (2D) articulated manipulandum. After an unpredictable delay (1–3 s), a target (0.6 cm radius) appeared at either the left or right lower corner of the screen and began to travel along a 45° trajectory toward an interception zone directly above the start zone. In a given trial, the target motion time (i.e., time between the target onset and its arrival at the center of the interception zone) was randomly varied in 0.3-s steps from 0.5 to 2.0 s. In addition, three target acceleration types were used; in a given trial, constant acceleration, constant deceleration, or constant velocity was randomly selected. In each block, trials were repeated until the subject achieved an interception with a temporal error less than 100 ms in each combination of target motion time and acceleration type, and each of six subjects performed ten blocks. In the present study, we analyzed only these successful trials.

General

Standard statistical methods (repeated-measures ANOVA and *t*-test) were used to analyze the data. The Nelder-Meade simplex search method implemented in Matlab (Mathworks, Natick, Mass.) was used for nonlinear curve fittings.

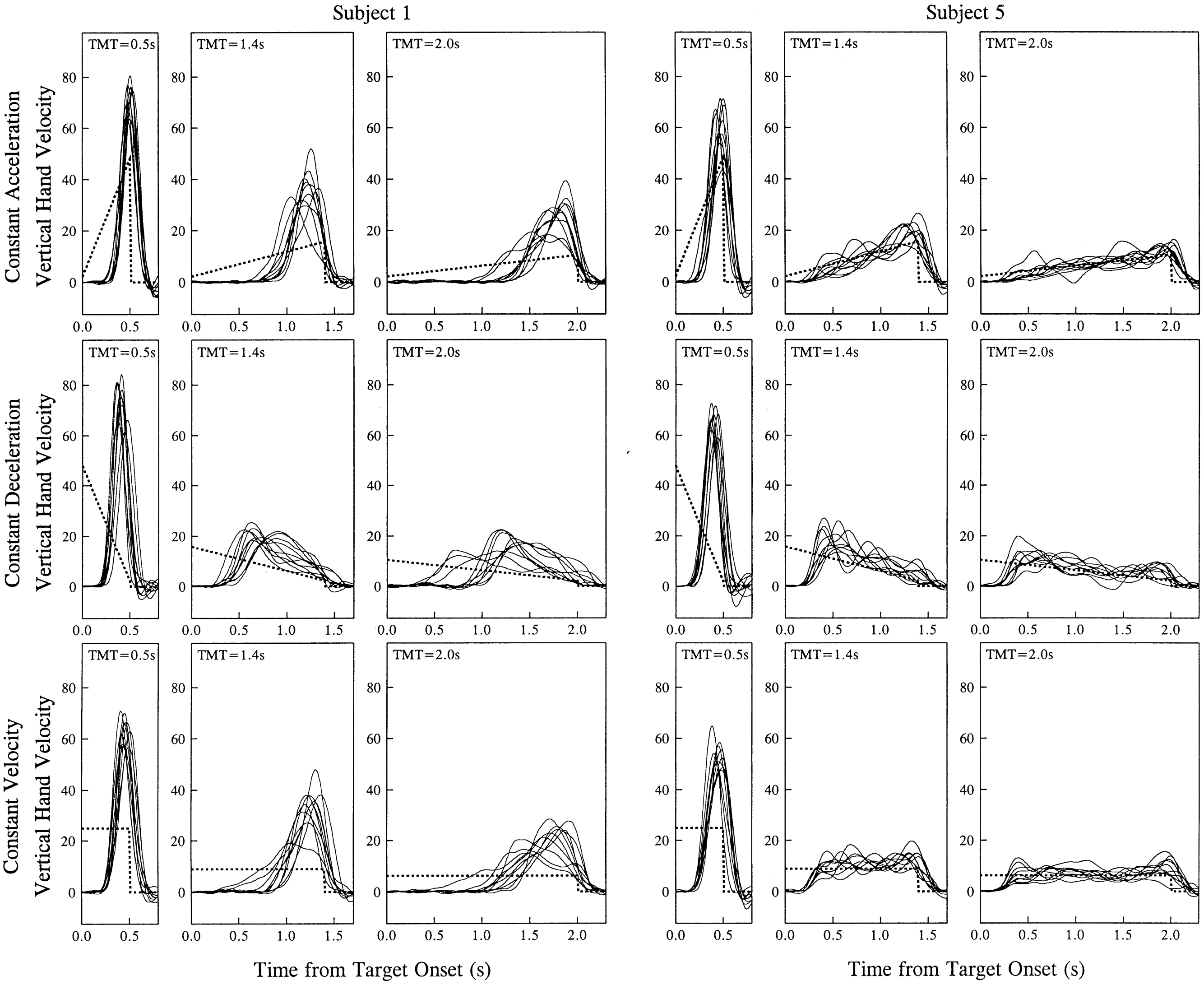

Fig. 1 Examples of hand velocity profiles during interceptive arm movements in two subjects. Only three of six target motion times (*TMT*) are shown here (TMT=0.5, 1.4, 2.0 s). *Top* Constant acceleration condition; *middle* constant deceleration condition; *bottom* constant velocity condition. In each condition, velocity profiles from ten successful trials are superimposed. Notice that the velocity profiles are more or less uniform in conditions where TMT=0.5 s, regardless of target acceleration; whereas, in those with longer TMT, velocity profiles are more variable and usually display multiple peaks

Decomposition of hand velocity profiles into minimum-jerk submovements

Only the vertical component of arm movement was analyzed in the present study, because the task required a vertical arm movement with a certain amplitude, and also because the actual trajectory was almost parallel to the y-axis. The goal of the following procedure was to decompose the velocity profile of the hand into the smallest number of submovements possible, using the velocity profile derived from the minimum-jerk model. Kinematics of single arm movements have been successfully described by the minimum-jerk model (Hogan 1984). This model assumes that movements of given amplitude and duration are generated in a way that minimizes the rate of change in acceleration (jerk). According to this model, hand velocity (v^J) is given by the following,

$$v^J(t;\, t_0, A, D) = 30\,(A/D)\,[\{(t-t_0)/D\}^2 - 2\,\{(t-t_0)/D\}^3 + \{(t-t_0)/D\}^4], \quad 0 \le t \le D, \tag{1}$$

where t_0 is movement onset, A is movement amplitude, and D is movement duration. We assumed that the velocity profiles of the interceptive arm movements (v^I) are linear superpositions of minimum-jerk velocity pulses with appropriate temporal and spatial scaling,

$$v^I(t) = \sum_{k=1}^{N_{sm}} v^J(t;\, t_0^k, A^k, D^k), \tag{2}$$

where N_{sm} is the number of submovements. We used a modified Powell's quadratically convergent method (Acton 1970) to find the three parameters (onset, amplitude, and duration) for each submovement that provide the best fit to the actual velocity profiles. Powell's (direction set) method is an algorithm to minimize a function of multiple variables in which the objective function is minimized successively along a set of conjugate directions. We used the least-square criterion, and the objective function to be minimized was,

$$O = \sum_{i=1}^{L} \left[v(t_i) - v^I(t_i) \right]^2 \tag{3}$$

where L is the number of data points collected every 10 ms between target onset and 300 ms after the target's arrival at destination, $v(t)$ is the actual vertical hand velocity profiles, and $v^I(t)$ is the sum of the minimum-jerk velocity pulses (Eq. 2).

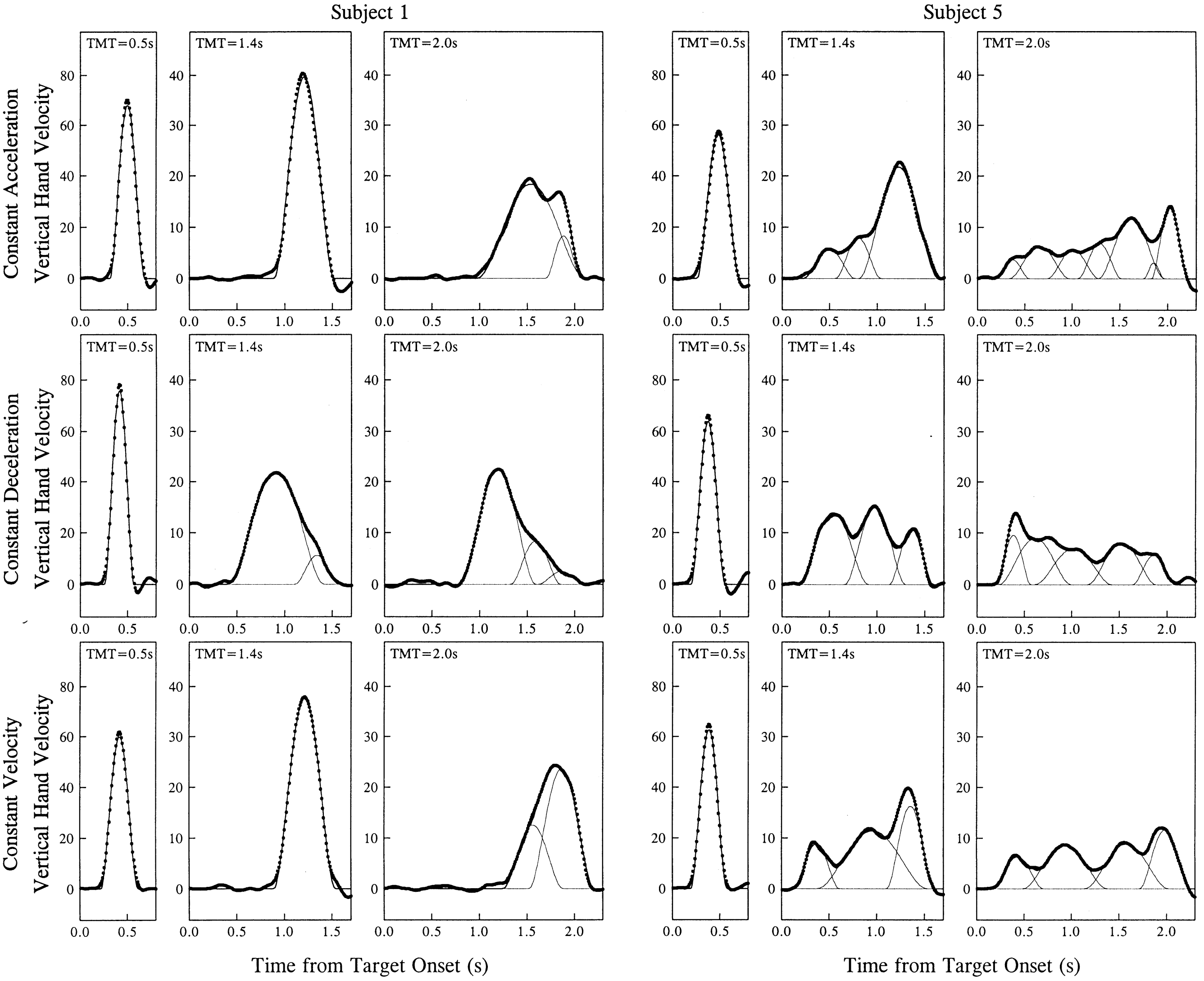

Fig. 2 Examples of decomposition of hand velocity profiles into minimum-jerk submovements. A single trial is randomly selected for illustration from each of the conditions shown in Fig. 1. The *dots* represent the original vertical hand velocity, obtained by smoothing and differentiating the vertical hand position. *Thin lines* and *thick lines* represent individual submovements given by the minimum-jerk model and their linear sum (superposition). *Thick lines* are most clearly visible in 0.5-s TMT and difficult to see in the other conditions, because they are too close to the original data

To avoid getting trapped in a local minimum during minimization of the objective function, it is important to start the search process with initial parameters close to the solution. Therefore, all the parameters of individual submovements were adjusted by hand to provide a reasonable fit to the data before the search algorithm was initiated. This was done using a computer program that displayed the minimum-jerk velocity pulses and their sum superimposed on the actual velocity profile for each trial, and allowed the user to adjust the parameters interactively. For initial parameters, only submovements with positive amplitude (upward moving) were included.[1] To find the smallest number of minimum-jerk submovements that can fit the data accurately, a single submovement was used initially, and the number of submovements (N_{sm} in Eq. 2) were gradually increased until R^2 between the model and the data reached 0.99.

Results

Effects of target motion on movement kinematics

Examples of vertical hand velocity profiles from two subjects are shown for three different target motion times in Fig. 1. In the conditions with the shortest target motion time (0.5 s, leftmost columns for each subject), the velocity profiles were bell-shaped and more or less symmetrical regardless of different target accelerations. In contrast, for longer target motion times, velocity profiles frequently displayed multiple peaks, suggesting the presence of multiple submovements. In addition, for longer target motion times, hand velocity profiles were affected by tar-

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[1] We included only positive submovements for initial parameters, although in some cases it was possible to achieve an equally good fit by replacing two successive positive submovements with a large positive and a concurrent small negative submovement. The latter was unrealistic, because it often included positive submovements with amplitude larger than the total amplitude required in the task

Table 1 Summary of submovement decomposition (*ISMI* intersubmovement interval)

Subject	ΣN_{sm}	N_{sm}		Amplitude (cm)		Duration (s)		Frequency (Hz)		ISMI (s)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	335	1.86	(0.75)	6.98	(4.43)	0.583	(0.268)	2.76	(0.68)	−0.288	(0.137)
2	456	2.10	(1.16)	5.14	(3.78)	0.574	(0.217)	2.50	(0.61)	−0.287	(0.219)
3	378	2.53	(1.04)	6.13	(4.44)	0.564	(0.196)	2.47	(0.61)	−0.259	(0.125)
4	531	2.95	(1.40)	4.39	(3.55)	0.571	(0.210)	2.45	(0.55)	−0.248	(0.205)
5	599	3.33	(1.57)	3.91	(3.17)	0.530	(0.200)	2.39	(0.55)	−0.237	(0.130)
6	563	3.13	(1.47)	4.15	(3.40)	0.558	(0.186)	2.34	(0.50)	−0.227	(0.158)
Total	2862	2.65	(1.37)	4.90	(3.87)	0.561	(0.205)	2.49	(0.60)	-0.252	(0.168)

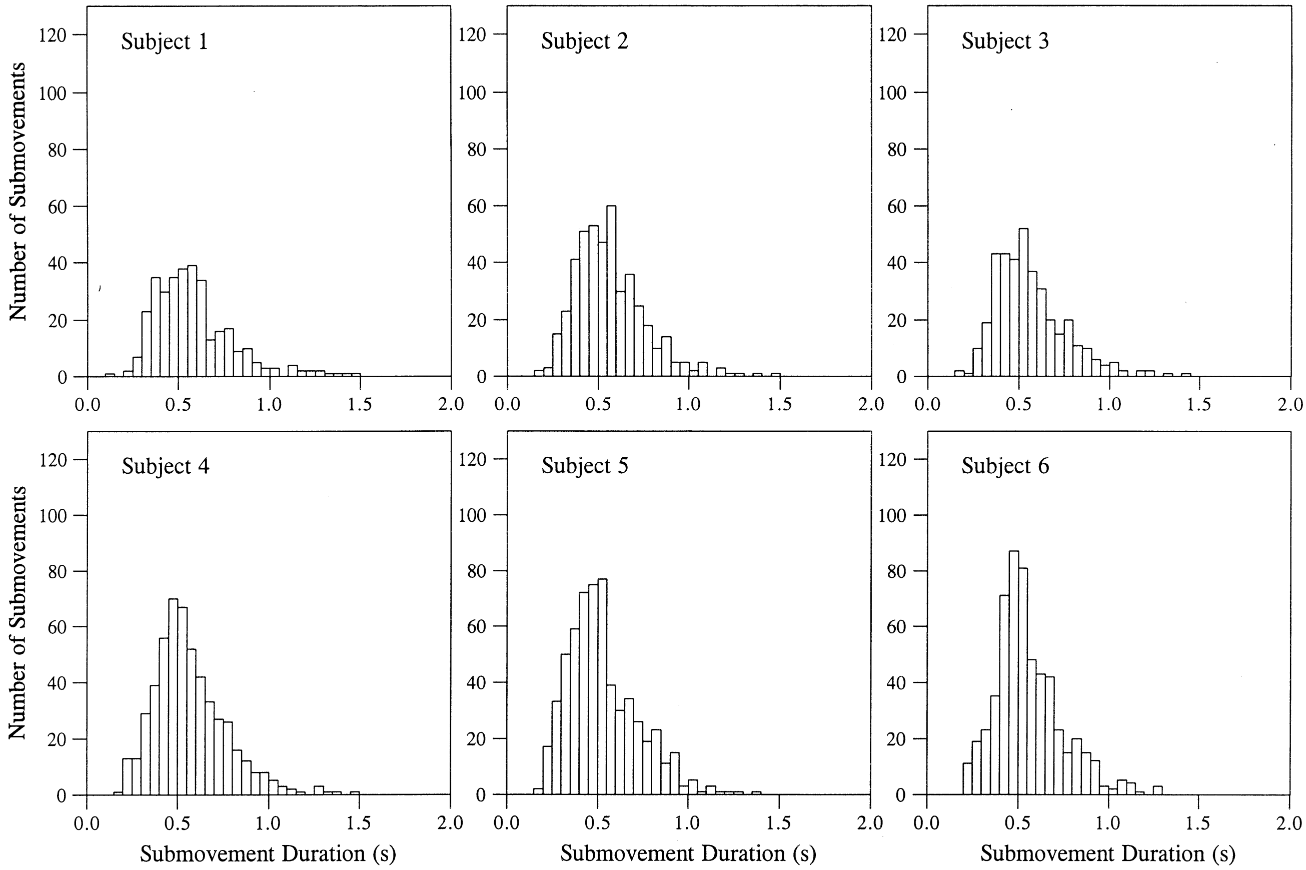

Fig. 3 Frequency histogram for the submovement duration for individual subjects

get acceleration. This tendency was more apparent in some subjects than in others. For example, in subject 5 (Fig. 1, right), the pattern of velocity profiles indicate that the subject might have tried to intercept the target by matching the vertical position or velocity of the hand with that of the target throughout most of the trial. Therefore, the peak velocity was reached earlier in the constant deceleration conditions (Fig. 1, middle row) than in the constant acceleration conditions (Fig. 1, top row). Although this association of target acceleration type and hand velocity profiles was not so obvious in some subjects, hand velocity profiles were affected by changes in the target velocity in all subjects in a similar manner.

Table 2 Subjects that showed significant effects of target characteristics on submovements (*TMT* target motion time, *TAT* target acceleration type)

	N_{sm}	Amplitude	Duration	Frequency	ISMI
TMT	2,4,5,6	2,4,5,6	2,5,6	–	1,2,5
TAT	–	–	6	6	4,5
TMT×TAT	–	5	–	–	–

Repeated-measures ANOVA, $P<0.05$

Decomposition of velocity profiles into submovements

To examine how multiple submovements are influenced by target motion, we decomposed the hand velocity profiles into the symmetrical bell-shaped submovements determined by the minimum-jerk model (see Materials and

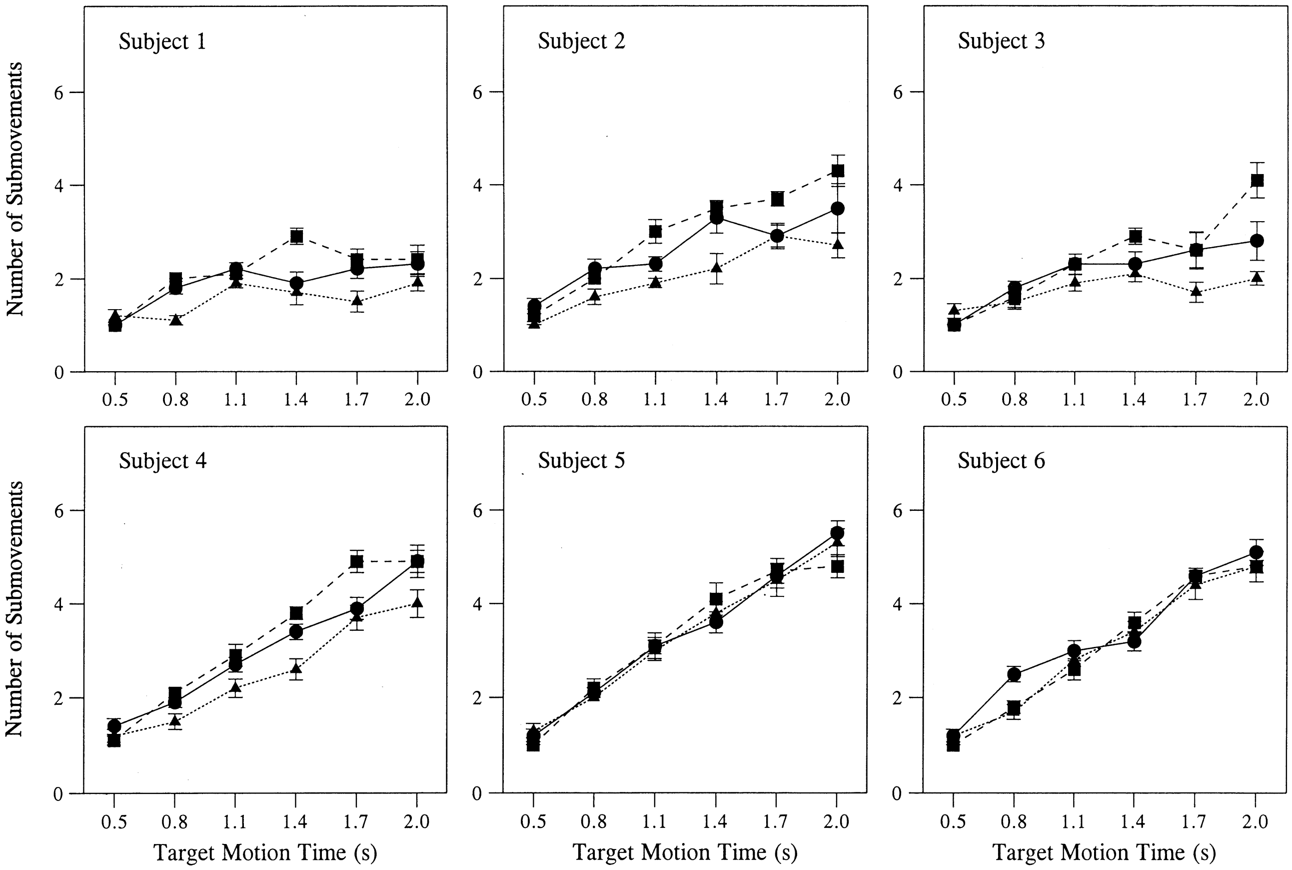

Fig. 4 Mean number of submovements per trial as a function of target acceleration type and target acceleration for individual subjects. *Error bars* indicate ±SEM (N=10)

methods). Some examples of such decomposition are shown in Fig. 2. In general, the hand velocity profiles could be fit by a relatively small number of submovements. The mean number of submovements per trial was 2.65 (Table 1), collapsed across all subjects, and the maximum number of submovements in a single trial was seven.

To examine whether the number of submovements was affected by amount of practice, mean number of submovements were calculated separately for individual blocks. In most subjects, there were no consistent effects of practice. We quantified the effects of practice with a linear regression between the number of submovements and the block number. Significant effect of block number was found only in subject 2 (P<0.05), in which the mean number of submovement increased from 2.1 to 2.9 between the first and the last blocks.

The mean number of submovements per trial varied significantly across subjects (repeated-measures ANOVA, F-test, P<0.01; Table 1). Since the amplitude of the desired movement is fixed, a larger number of submovements should result in a smaller submovement amplitude. As expected, the mean submovement amplitude also varied significantly across subjects (repeated-measures ANOVA, F-test, P<0.01), and the subjects with fewer submovements produced submovements with larger amplitude. On the other hand, submovement duration was relatively constant in all subjects and the differences were not statistically significant (repeated-measures ANOVA; Table 1, Fig. 3).

The effects of target motion time and target acceleration type on the number of submovements per trial, and submovement amplitude, duration, and frequency (number of submovements divided by the total movement time) were also examined for individual subjects. Among these variables, the number of submovements per trial was most frequently affected, and the submovement frequency was least frequently affected (Table 2). The number of submovements gradually increased with target motion time in all subjects (Fig. 4). The mean number of submovements per trial for 0.5-s target motion time collapsed across all acceleration types and subjects was 1.15, and there was a single submovement in 85% of the trials.

Control of submovement onset

In the preceding paper, we showed that some subjects had relatively constant response times regardless of target motion time and target acceleration, whereas others displayed larger variation in their response times in a manner consistent with the use of two alternative strategies (Port et al. 1997). Since the nature of the task requires the target motion time to be roughly equal to the sum of the

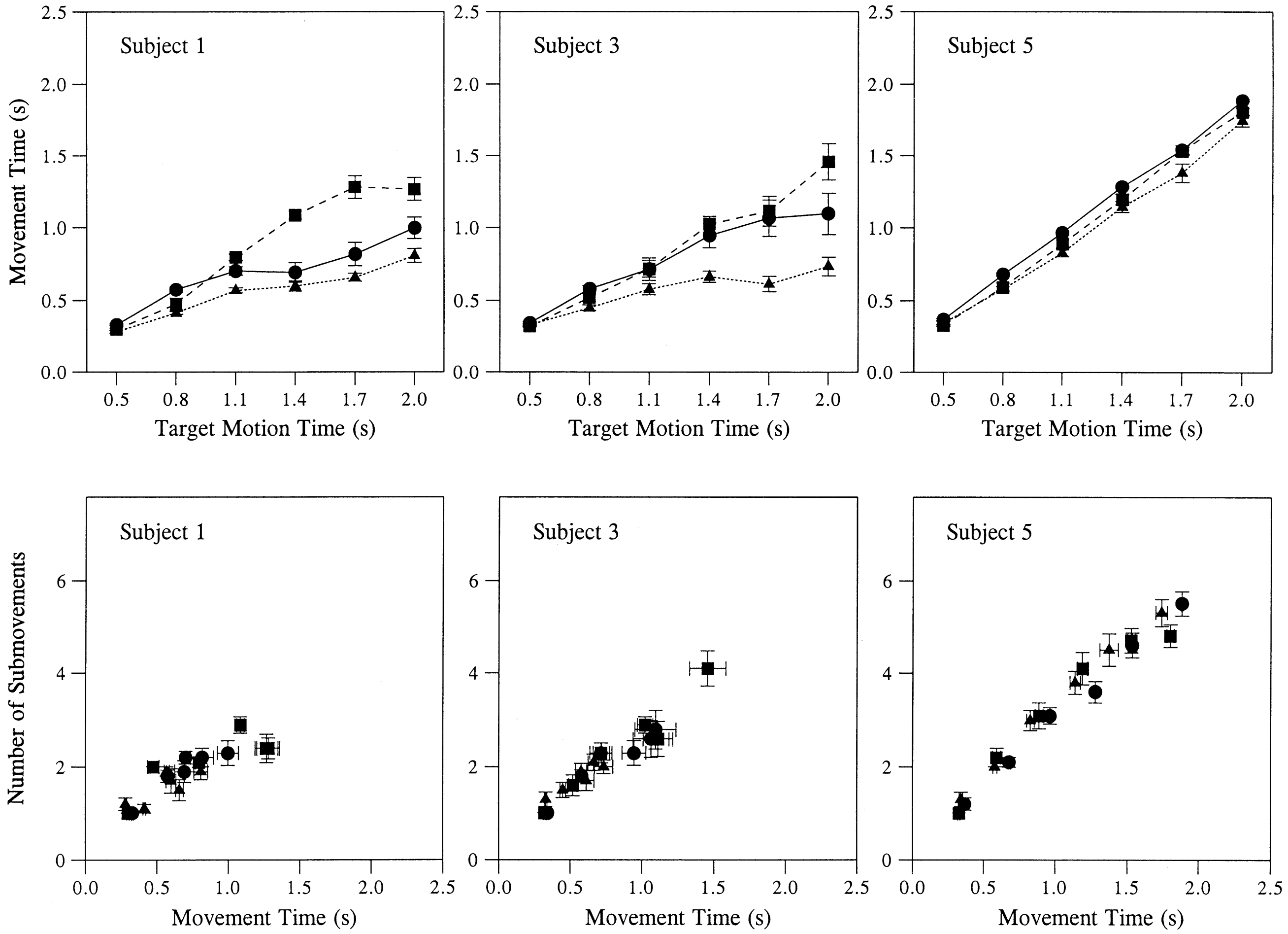

Fig. 5 *Top*: Mean movement time for individual subjects as a function of target motion time and target acceleration. Movement time is defined as the time between when the instantaneous vertical hand velocity exceeds 10% of the peak vertical hand velocity and when it returns below 10% of the peak velocity. *Circles* constant velocity; *triangles* constant acceleration; *rectangles* constant deceleration. *Error bars* indicate ±SEM (N=10). *Bottom*: Relationship between the total movement time and the number of submovements for individual subjects. These are the mean values computed for each combination of target motion time and target acceleration. *Error bars* indicate ±SEM (N=10)

response time and the movement time, the subjects with relatively constant response times (e.g., subject 5) showed greater variation in their movement times across different target motion times than the other subjects (e.g., subject 1), as shown in Fig. 5. The difference in the number of submovements among different subjects may be related to the difference in the movement times. Specifically, if submovements were generated at a constant rate in time, the number of submovements would be proportional to the movement time. Consistent with this hypothesis, the mean number of submovements in each combination of target motion time and target acceleration was roughly proportional to the mean movement time for the same condition (Fig. 5, bottom). The correlation coefficient between the number of submovements and the total movement time of the hand was 0.883, when computed for the total of 1080 successful trials in all subjects. Moreover, the submovement frequency, as defined as the number of submovements divided by the total movement time, was relatively constant in all subjects, and the differences were not statistically significant (repeated-measures ANOVA, Table 1).

If the sequence of submovements observed during the present task was controlled by a mechanism similar to an intermittent servo-controller (e.g., Craik 1947), one might expect that the interval between the onsets of two successive submovements, or submovement onset asynchrony (SMOA), would be more or less constant. The results were not consistent with such constancy of SMOA. Instead, SMOA varied systematically according to the duration of the preceding submovement (Fig. 6, top). These results were consistent with the hypothesis that, when several submovements are generated in parallel, there is a relatively constant overlap between two successive submovements. We defined intersubmovement interval (ISMI) as the onset of the following submovement minus the offset of the preceding submovement. As expected, the frequency histograms for the ISMI displayed a relatively narrow peak, and the mean ISMI was about –0.25 s (Fig. 6, bottom, Table 1). The ISMI was similar in all subjects, although small differences among different subjects were statistically significant (repeated-measures ANOVA, P<0.05; Table 1).

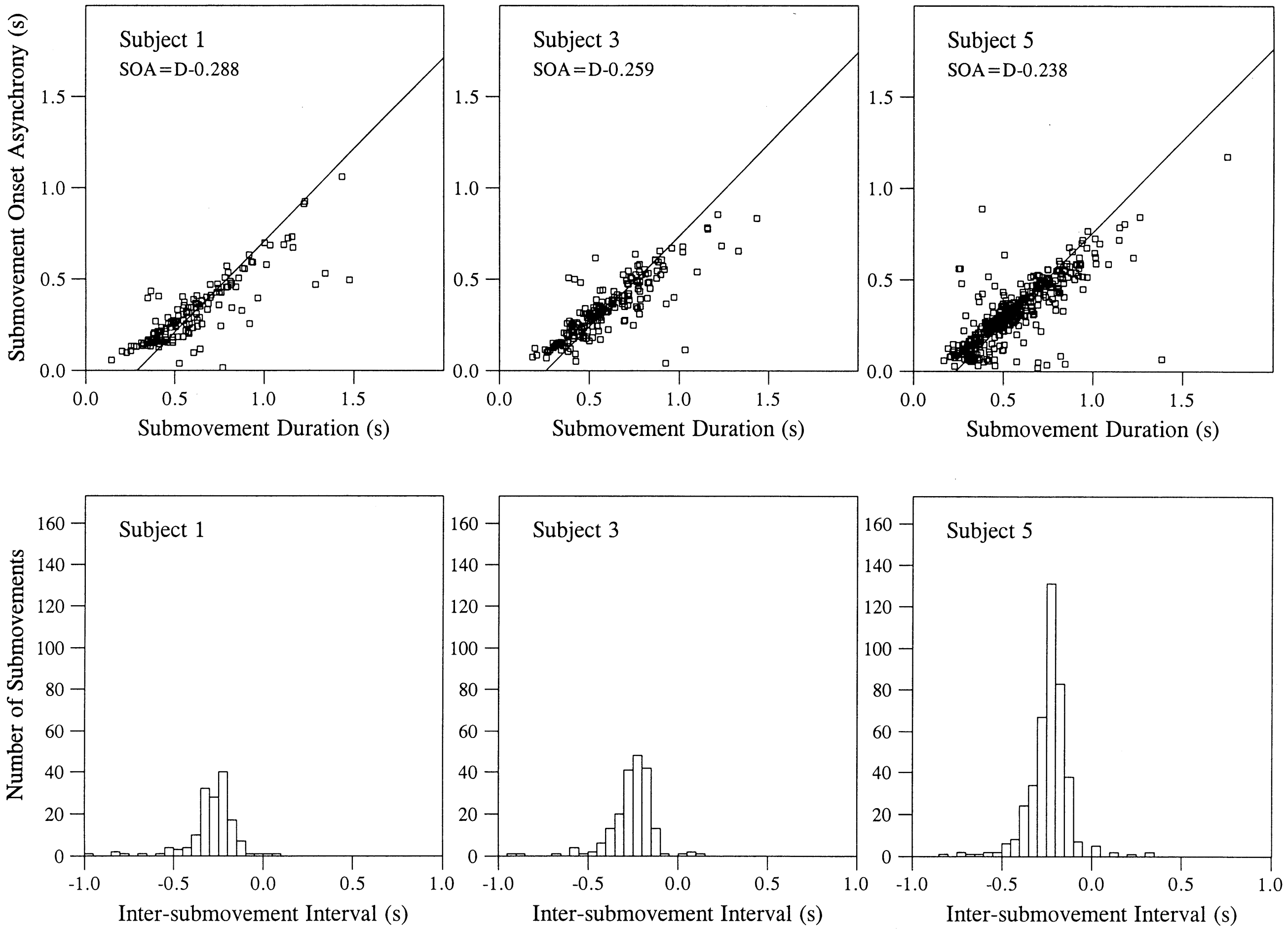

Fig. 6 *Top*: Relation between the duration of a submovement and the submovement onset asynchrony (*SOA*), which is defined as the time from the onset of the same submovement to the onset of the following submovement. *Solid line* represents a model that assumes a constant intersubmovement interval (ISMI) for each subject. *Bottom*: Frequency histogram for the ISMI, which is defined as the onset of a submovement minus the offset of the preceding submovement

Since both submovement duration and SMOA also have relatively narrow distributions (Figs. 3, 6), the relative constancy of the ISMI may be an inevitable outcome when these two variables were subtracted from each other. To evaluate this issue statistically, the submovement duration and the SMOA were randomly shuffled for the trials with multiple submovements. The frequency histogram for the ISMI was calculated for the reconstructed data set, and this procedure was repeated 1000 times to estimate confidence intervals. The results indicated that the narrow distribution of the ISMI observed in the data cannot be explained by those of the submovement duration and the SMOA (Fig. 7).

One possible mechanism of maintaining a constant ISMI might be related to target velocity, that is, relatively high target velocity might be a common cause for both submovements with longer duration and a large SMOA. For trials with more than one submovement, we found that there was a small but significant negative correlation between the target velocity and the submovement duration (r=–0.23, N=1782, P<0.001), and also between the target velocity at the onset of a submovement and the SMOA (r=–0.24, N=1782, P<0.001). However, these were substantially lower than the correlation between the submovement duration and the SMOA (r=0.64) and, therefore, unlikely to be an explanation for the relatively constant ISMI.

Control of submovement amplitude

To understand how amplitudes of successive submovements are determined, the following hypotheses were considered. In comparing these hypotheses, we used the cumulative submovement amplitude as a dependent variable, as it is more closely related to the desired location of the hand than the amplitude of individual submovements. In the first hypothesis, we considered the possibility that the desired hand location is determined by the time to target arrival at the destination. If the hand displacement from the destination and the time to target arrival are linearly coupled so that both become zero at the same time, the subject would perform the task successfully. One way to estimate time to target arrival is to use a distance-to-velocity ratio (target τ; Lee 1976), which provides a correct estimate for the time to target arrival

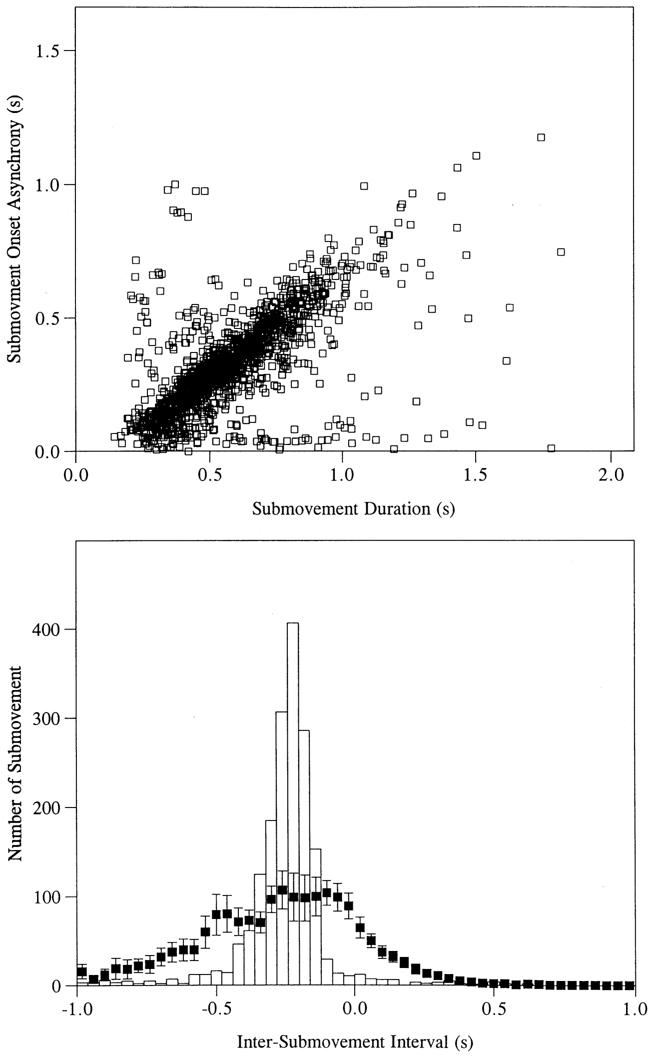

Fig. 7 *Top*: Relation between the duration of a submovement and its ISMI, collapsed for all subjects. The correlation coefficient between these two variables was 0.64 (N=1782). *Bottom*: Frequency histogram for the ISMI, which is defined as the onset of a submovement minus the offset of the preceding submovement. The *filled squares* and the *error bars* indicate the mean and the standard deviation for the same measure, computed by a bootstrap method (see text for details)

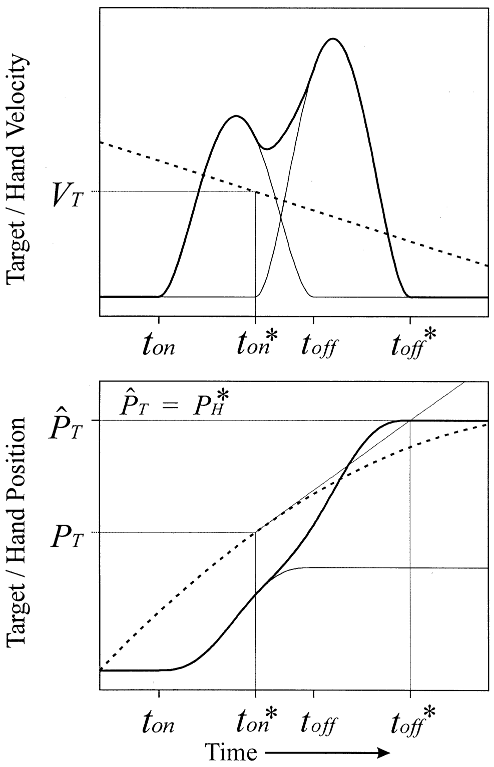

Fig. 8 *Top*: A schematic showing superposition of velocity profiles of two submovements (*solid line*) and a target (*dashed line*) moving with a constant deceleration. *Bottom*: Corresponding positions of the hand and the target. Target position ($\hat{P}_T$) at the offset of the second submovement (t_{off}^*) is estimated from the target position (P_T) and the target velocity (V_T, top graph) at the submovement onset (t_{on}^*). t_{on} and t_{off} indicate the onset and the offset of the first submovement. According to the position-control theory, the hand position at the end of the second submovement, P_H^*, is equal to the first-order estimate of the target position, $\hat{P}_T$

under constant velocity conditions. We refer to this possibility as the τ-control hypothesis. If one denotes the target position and velocity at the submovement onset as P_T and V_T, respectively, and target position at the destination as P_T^*, then, acording to the τ-control hypothesis, the cumulative submovement amplitude would be linearly related to the target τ, $(P_T^*-P_T)/V_T$.

The second hypothesis was that movement amplitude is determined by the estimated target position at the offset of each submovement. According to this hypothesis, the subject's strategy is to gradually eliminate the position error between the hand and the target with a series of discrete submovements so that the end-point of each submovement is linearly related to the estimated position of the target at the end of each submovement along the axis of the movement (y-axis).[2] It is assumed here that the system estimates future target position from the target position and velocity at the time of submovement onset (Fig. 8), as in the τ-control hypothesis. We refer to this possibility as the position-control hypothesis. If one denotes the vertical target position and velocity at the submovement onset as P_T and V_T, respectively, the duration of submovement as D_S, and the cumulative amplitude up to the preceding submovement along the y-axis as P_C, then, according to this hypothesis, the amplitude of the current submovement would be $[P_T+(D_S \times V_T)-P_C]$.

One problem with the position-control hypothesis is that the system has to determine the duration of the submovement in order to determine its amplitude. To avoid this problem, Miall et al. (1988) proposed that the system uses an average movement duration to estimate the position error. We refer to their proposal as the average-duration hypothesis. Similar to the position-control

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[2] In the present analysis, only the vertical components were considered, because the subjects made vertical movements, but the submovement amplitude in higher dimensions can be derived similarly if one uses vector expression for the same variables used in our analysis

Table 3 Parameters and R^2 in different models for determining submovement amplitude

Subject	τ-Control hypothesis				Position-control hypothesis				Average-duration hypothesis			
	a_1	a_2	a_3	R^2	a_1	a_2	a_3	R^2	a_1	a_2	a_3	R^2
1	−15.62	52.33	12.77	0.3784	3.01	−27.44	12.33	0.7526	0.78	2.95	12.60	0.3360
2	−11.75	42.40	12.65	0.4874	1.28	−5.30	12.43	0.7532	0.69	2.63	12.81	0.5574
3	−17.12	56.41	12.52	0.5091	1.95	−14.56	12.36	0.7726	0.86	1.75	12.62	0.4179
4	−13.50	47.84	12.49	0.6629	1.11	−3.05	12.59	0.8505	0.86	0.55	12.51	0.7326
5	−10.73	38.58	13.00	0.6589	1.07	−3.01	12.68	0.8501	0.92	−0.45	12.69	0.7571
6	−9.53	36.45	12.99	0.6594	0.84	0.84	12.88	0.8344	0.75	1.44	12.92	0.7124

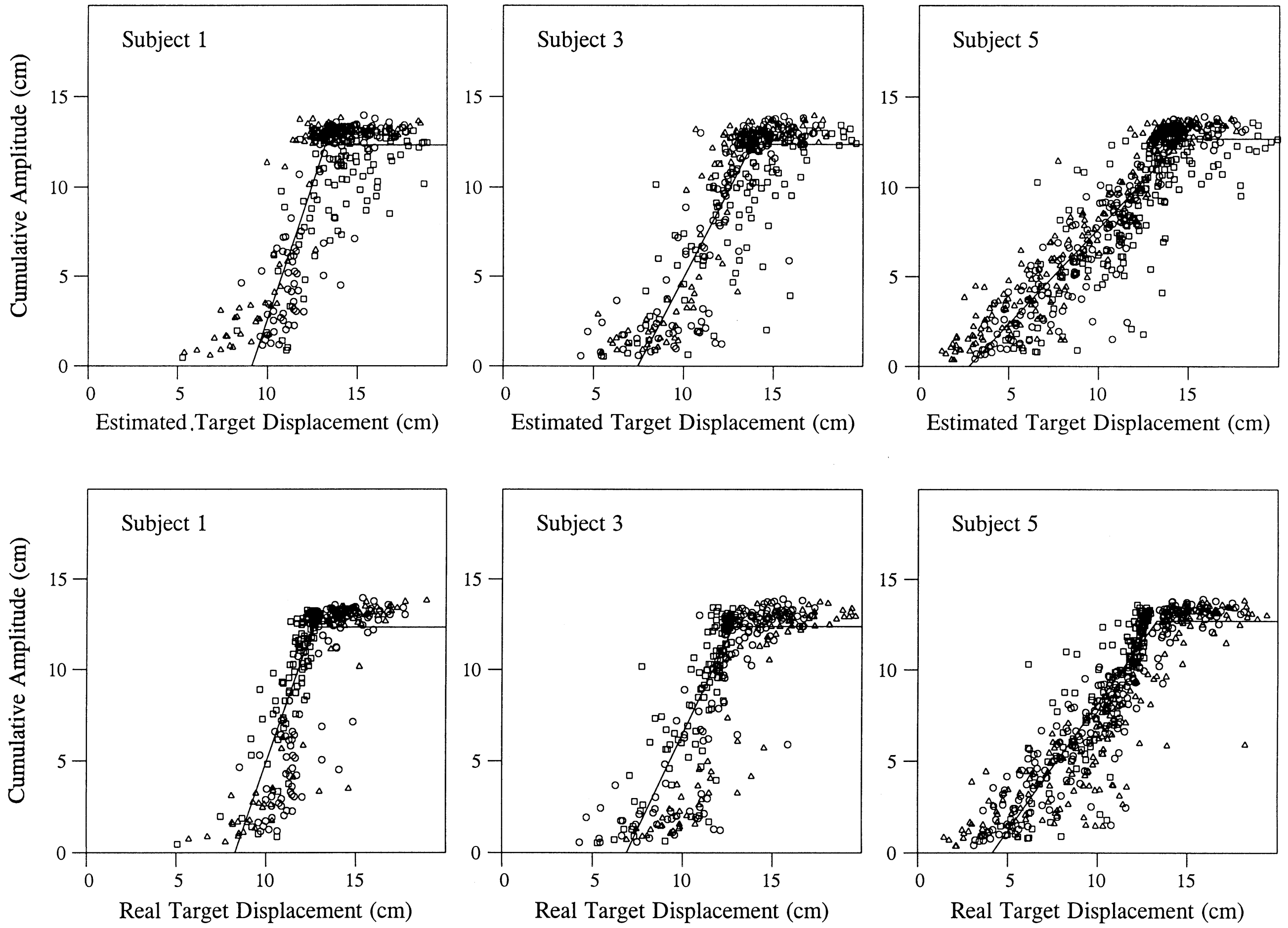

Fig. 9 *Top*: Relationship between cumulative movement amplitude and the first-order estimate of target displacement at the offset of submovements. Different symbols represent individual submovements in different target acceleration types (*circles* constant velocity; *triangles* constant acceleration; *rectangles* constant deceleration), and *solid line* represents the prediction from the position-control hypothesis. *Bottom*: Relationship between cumulative movement amplitude and real target displacement at the offset of submovements

hypothesis, the amplitude of the current submovement would be $[P_T+(D_m \times V_T)-P_C]$, where D_m is the average submovement duration in each subject.

To examine which of these three hypotheses best describes the data, the cumulative submovement amplitude was plotted as a function of either target τ or estimated target displacement for individual subjects. Target τ was log-transformed so that it would be normally distributed. Then, the following model was fit for each subject.

$$\text{Cumulative amplitude} = \max\,[\min\,(a_1 X + a_2, a_3), 0]$$

where X is either log (target τ) or estimated target displacement, and a_1–a_3 are the model parameters. Introduction of the third parameter a_3, corresponding to the maximum amplitude, was necessary to prevent the model from exceeding the amplitude limit in the task. The parameters obtained for each subject and the corresponding R^2 are summarized in Table 3. These results suggest that the position-control hypothesis explains best how the submovement amplitude is determined. The relationship between cumulative submovement amplitude and esti-

Table 4 Parameters and R^2 for the regression in Fig. 9 (bottom)

Subject	Slope	Intercept	R^2
1	2.84	–23.48	0.6500
2	1.57	–7.62	0.7179
3	2.08	–14.39	0.6777
4	1.28	–4.02	0.7626
5	1.39	–5.79	0.7393
6	1.09	–1.63	0.8231

mated target displacement along with the prediction from the model is shown in Fig. 9.

The remaining question is how the system determines submovement duration. One possibility is to use the mean velocity of a submovement as an intermediate variable. There was a relatively high positive correlation between the target velocity at the submovement onset and the mean velocity of submovements (r=0.77, N=2,862, across all subjects). Thus, mean velocity of a submovement may be first determined from the target velocity, and the submovement amplitude and duration may be subsequently determined. Another possibility is that the submovement duration is not precisely controlled in any way related to target motion, but varies randomly.

Effects of target acceleration on submovement control

If one assumes that the submovement amplitude is determined according to the position-control hypothesis described in the previous section, this provides an interesting opportunity to examine whether information regarding target acceleration is incorporated into this process. If target acceleration were taken fully into account, the submovement amplitude should be explained better by the real target position at the submovement offset than by the first-order estimate of target position, since the target acceleration was constant in all conditions. To examine such a possibility, a variant of the position-control hypothesis was examined, where the real target position was used instead of the first-order estimate of target position (Fig. 9, bottom). We found that this new model did not perform better than the original position-control hypothesis; in fact, there was a decrease of 0.07 in R^2 on average (Tables 3, 4). This suggests that information about the target acceleration was not fully utilized in determining the submovement amplitude.

Similar results were obtained when the correspondence between the model and the data for the position-control hypothesis was examined separately for different target accelerations. The errors between the model and the data could be due to the fact that the estimation of target position does not reflect target acceleration. However, these errors were not substantially reduced even when they were sorted according to target acceleration, although they were significantly affected by target acceleration in all subjects ($P<0.01$). These results indicate that submovements were affected by target acceleration in a systematic manner, but not enough to fully compensate for the effects of target acceleration.

Discussion

Individual differences in the control strategy

In performing the task employed in the present study, every subject showed some effects of target motion on the velocity profiles of the arm movement. It is evident both from the raw velocity profiles and from the relation between the cumulative submovement amplitude and the first-order estimate of target position that some subjects tried to intercept the target by matching the vertical position of the hand with that of the target. They achieved this goal not with a smooth velocity profile that followed that of the target, but with a series of discrete submovements. Other subjects who displayed shorter movement times and a smaller number of submovements showed weaker, but similar effects of target motion on their velocity profiles. Although it was not the goal of the present study to examine the effects of practice on the submovement control (e.g., Pratt and Abrams 1996), it is unlikely that these individual differences in the submovement control are due to different amounts of practice, because these different patterns of velocity profiles across different subjects (Fig. 1) were maintained consistently across different repetitions and also because, in all but one subject, there were no effects of practice on the mean number of submovements.

In the preceding paper, we showed that some subjects initiated their movements with relatively constant response times (e.g., subject 5). The results from the present paper indicated that these subjects adhered more strictly to the strategy of matching their hand position to the estimated target position in the dimension where movement is required. In contrast, the subjects who showed more variation in their response times according to target velocity also showed more variability in terms of the intermediate association between the hand and the target. One possibility is that these subjects were not capable of tracking the target (along the direction of hand movement) as faithfully as the other subjects, since they had shorter movement times. Since the number of submovements is probably limited by the movement time available, the reason that these subjects showed less consistent coupling between the hand and the target positions might be that they didn’t have enough time to generate more submovements. On the other hand, considering that the task did not explicitly require the subject to track the target continuously, a more likely possibility is that these subjects were more careful in terms of estimating target position and target velocity before initiating their movements, and thus acquired more accurate estimates about the time to target arrival at the destination. Therefore, they would have less need to continuously track the target for successful interception. In the present study, these two alternative possibilities could not be tested, because neither the response times nor the movement times were under direct experimental control. In order to distinguish between these possibilities, one needs to control the movement time and determine whether different subjects still show different degrees of coupling between the hand and the target.

Superposition of submovements

Several previous studies have provided support for the formation of complex trajectories by linearly superposing simple submovements with certain invariant characteristics (Morasso and Musa-Ivaldi 1982; Flash and Henis 1991; Milner 1992; Flanagan et al. 1993). The method of decomposition of velocity profiles used in the present study is similar to the one used by Flash and Henis (1991), who modeled the arm trajectory in the double-step paradigm with superposition of two minimum-jerk submovements. Most of the velocity profiles observed in the present study were more complicated than those in the double-step paradigm and therefore usually required more than two submovements. We adopted the minimum-jerk model mainly because of its mathematical simplicity, and the main results of the present study would not be affected by the exact mathematical function to describe individual submovements. For example, Milner (1992) performed a similar analysis to examine submovements found in the arm movements directed to small targets, requiring endpoint precision. The decomposition applied in that study was based on a prototypical velocity profile found in each subject, but it was still similar to the velocity profile determined by the minimum-jerk model. Flanagan et al. (1993) provided an alternative model based on the equilibrium-point hypothesis (Feldman 1986), with more emphasis on the biomechanical properties of the motor plant. They demonstrated that the central commands for shifting the equilibrium points associated with successive submovements may be applied sequentially without overlapping in time. However, in all of these cases, superposition occurs at the kinematic level, and the kinematics predicted by the equilibrium-point hypothesis were similar to those based on the minimum-jerk model (Flanagan et al. 1993).

Effects of target acceleration

In the preceding paper, we showed that there was a systematic bias in the pattern of constant temporal errors, i.e., the difference in time of arrival at the destination between the target and the hand. Positive constant temporal errors indicate that the hand arrived later than the target. If target acceleration were fully taken into account in determining the timing of interception, temporal errors would be similar in all target acceleration types. In contrast, we found that positive constant temporal errors were dominant in constant acceleration conditions, and negative constant temporal errors in constant deceleration conditions. These results suggest that subjects failed to fully compensate for the effects of target acceleration on their interceptive movements (Port et al. 1997). Similar conclusions were reached when the effects of target acceleration were examined on the submovement amplitude in the present study. When target acceleration was incorporated into the model to calculate real target position, it did not improve the fit between the target position and the cumulative submovement amplitude, which suggests that subjects were probably using the first-order estimate of target position in determining their submovement amplitude. Although there was still variability in the submovement amplitude that was not accounted for by the estimated target position, only a part of it was due to the target acceleration, and the remaining variability was probably due to a relatively inaccurate estimation of target position, imprecise mechanisms for producing a submovement with the desired amplitude, or both. Although the magnitude of target acceleration employed in the current study is above the perceptual threshold (Schmerler 1976; Werkhoven et al. 1992; Babler and Dannemiller 1993; Port et al. 1997), the results of the present study did not provide any evidence that subjects were able to fully compensate for target acceleration in their movements.

Constancy of intersubmovement interval and its significance

If one assumes that the generation of a submovement is constrained by the acquisition of adequate information regarding target motion (i.e., position and velocity), one would expect that the interval between the onsets of successive submovements, or SMOA, be relatively constant. Thus, it was somewhat surprising to find that the onset of a submovement had a relatively constant temporal relationship with the offset, instead of the onset, of the preceding submovement. On average, the onset of a submovement preceded the offset of the preceding submovement by 0.25 s. By comparing the distribution of this difference, or ISMI, with those produced by randomly permuting the association between the duration and the SMOA, we showed that a relatively constant ISMI was not due to the constraints in the distributions of the submovement duration and the SMOA.

A strong correlation between the duration of a submovement and SMOA (or constant ISMI) does not by itself indicate a direct causal relationship between these two variables; a third factor may influence both of these variables. One such factor might be target velocity, since a high target velocity may require submovements with larger amplitude and duration, and also make it more difficult to estimate future target location, thus delaying a preparation for the next submovement. Although there was a significant correlation between the target velocity and submovement duration, and also between the target velocity and the SMOA, it was substantially weaker than the correlation between the submovement duration and the SMOA. Thus, target velocity does not seem to be entirely responsible for a relatively constant ISMI. Alternatively, it might be the execution of a longer submovement itself that makes it more difficult to prepare the next submovement. One possibile reason for such direct causality might be related to information regarding the final hand position after completion of the preceding submovement. Availability of this information may be delayed according to the duration of the preceding submovement. Finally, it should be noted that the constancy of the ISMI we found in the present study is probably not a general principle that applies to all types of movements, since it has been already shown that, with sudden change in target location, an ongoing movement can be modified at any time during its execution (Georgopoulos et al. 1981; Soechting and Lacquaniti 1983; Massey et al. 1986).

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