Exp Brain Res (1997) 116:406–420

RESEARCH ARTICLE

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Manual interception of moving targets

I. Performance and movement initiation

Received: 5 July 1996 / Accepted: 4 March 1997

Abstract We investigated the capacities of human subjects to intercept moving targets in a two-dimensional (2D) space. Subjects were instructed to intercept moving targets on a computer screen using a cursor controlled by an articulated 2D manipulandum. A target was presented in 1 of 18 combinations of three acceleration types (constant acceleration, constant deceleration, and constant velocity) and six target motion times, from 0.5 to 2.0 s. First, subjects held the cursor in a start zone located at the bottom of the screen along the vertical meridian. After a pseudorandom hold period, the target appeared in the lower left or right corner of the screen and traveled at 45° toward an interception zone located on the vertical meridian 12.5 cm above the start zone. For a trial to be considered successful, the subject's cursor had to enter the interception zone within 100 ms of the target's arrival at the center of the interception zone and stay inside a slightly larger hold zone. Trials in which the cursor arrived more than 100 ms before the target were classified as "early errors," whereas trials in which the cursor arrived more than 100 ms after the target were classified as "late errors." Given the criteria above, the task proved to be difficult for the subjects. Only 41.3% (1080 out of 2614) of the movements were successful, whereas the remaining 58.7% were temporal (i.e., early or late) errors. A large majority of the early errors occurred in trials with decelerating targets, and their percentage tended to increase with longer target motion times. In contrast, late errors occurred in relation to all three target acceleration types, and their percentage tended to decrease with longer target motion times. Three models of movement initiation were investigated. First, the threshold-distance model, originally proposed for optokinetic eye movements to constant-velocity visual stimuli, maintains that response time is composed of two parts, a constant processing time and the time required for the stimulus to travel a threshold distance. This model only partially fit our data. Second, the threshold-τ model, originally proposed as a strategy for movement initiation, assumes that the subject uses the first-order estimate of time-to-contact (τ) to determine when to initiate the interception movement. Similar to the threshold distance model, the threshold-τ model only partially fit the data. Finally, a dual-strategy model was developed which allowed for the adoption of either of the two strategies for movement initiation; namely, a strategy based on the threshold-distance model ("reactive" strategy) and another based on the threshold-τ model ("predictive" strategy). This model provided a good fit to the data. In fact, individual subjects preferred to use one or the other strategy. This preference was allowed to be manifested at long target motion times, whereas shorter target motion times (i.e., 0.5 s and 0.8 s) forced the subjects to use only the reactive strategy.

Key words Target interception · Reaching · Acceleration · Coincidence timing · Human

Introduction

The ability to reach toward moving targets develops at a very young age (von Hofsten 1982). This ability devel-

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ops rapidly from birth, and by age 36 weeks infants can accurately intercept a moving object (von Hofsten 1979). Furthermore, infants seem to use a predictive strategy in which the initial movement is directed toward the interception point rather than tracking the moving object (von Hofsten 1980, 1983). Finally, infants are more likely to intercept faster, rather than more slowly moving targets (von Hofsten 1983). However, the quantitative aspects of the strategies used by infants or adults are little understood.

Two models have been offered to explain the initiation of the movement in intercepting moving targets; namely the threshold-distance and the threshold-τ model. The first of these was put forth by Collewijn (1972) to explain the optokinetic response time in the rabbit and might be applicable to the interception of moving targets by human subjects. This “threshold-distance model” is so named because it postulates that the stimulus must travel a certain visual angle before a motor response can be elicited. The model expresses the latency or response time as a function of two parameters, as follows:

$$\begin{aligned}&\text{Response time}\\&= \text{processing time} + \text{distance threshold time} \qquad (1)\end{aligned}$$

where processing time is a constant to account for delays in the nervous system, and distance threshold time is the time the stimulus takes to travel a certain distance. Since threshold time is a function of stimulus velocity, Eq. 1 can be rewritten as follows:

$$\begin{aligned}&\text{Response time} = \text{processing time}\\&+ \text{threshold distance}\left(\frac{1}{\text{target velocity}}\right) \qquad (2)\end{aligned}$$

This general model has also been shown to predict the response times of human smooth pursuit (Carl and Gellman 1987) and saccadic eye movements (Gellman and Carl 1991) to moving targets.

Van Donkelaar and colleagues (1992) applied the threshold distance model to analyze the initiation of manual interceptive movements toward targets moving with constant velocity. Two conditions were employed. In the first, the velocity of the target was predictable in a block of trials, whereas in the second condition the target velocity was randomized from trial to trial. They found that, as target velocity increased, response time decreased until it reached a plateau under both conditions. The model provided a good fit to the data and yielded a mean processing time of 195 ms and a mean threshold distance of target travel of 5.3 mm (see Eq. 2; values refer to the random condition). In the predictable condition, the first 60 ms of hand movement revealed that subjects were able to utilize target velocity information gained from previous exposure to a given target velocity to make systematic changes in initial hand velocity. However, in the random condition, subjects made movements with similar initial velocities across target velocities, which required on-line corrections to produce accurate interceptions. This study documented an effect of prior knowledge concerning target motion on the initiation of movement, but did not address the question of how the movement is controlled on-line to produce an accurate interception.

The second model of target interception incorporates the concept of the time-to-contact and τ (the tau margin) as proposed by Lee (1976). Under conditions of constant velocity, τ is a variable that could be computed by the brain to determine the time to contact with the object. The variable τ was originally defined under conditions of self motion in an optic flow field (Lee 1976), in which it was proven that τ is equal to the inverse of the rate of dilation of the retinal image. The general form of τ is as follows:

$$\tau = \frac{d}{\dot{d}} \qquad (3)$$

where d is the distance remaining from the organism to the object, and $\dot{d}$ is the time derivative of d (see also Lee and Young 1986). Although τ accurately specifies time-to-contact under constant velocity conditions, experiments indicate that it may also be used as an approximation of time-to-contact in interceptive actions under conditions of deceleration and acceleration (Lee 1976; Lee and Reddish 1981; Lee and Young 1986). For example, Lee and Reddish (1981) looked for a variable that gannets might use to decide when to initiate wing folding when diving into water. In addition to τ they examined several other variables, including the actual time to contact with the water, a height above the water, an approach velocity, or a time from the initiation of the dive. They found that the movement was initiated after a certain delay from the time τ reached a threshold. This study provided evidence that τ is a control variable used by the gannets to determine when to initiate a movement. In addition to τ being used as a variable in models for the initiation of movement, τ and the time derivative of τ, $\dot{\tau}$, have also been utilized in models of the on-line control of the decelerating phase of movements (Lee 1976; Zaal and Bootsma 1995).

In summary, two models have been proposed concerning the initiation of a movement toward a moving target. The threshold-distance model has been shown to model accurately the initiation of both oculomotor and reaching movements under conditions of constant velocity. The threshold-τ model has been applied successfully in modeling the initiation of a movement under conditions of constant acceleration.The present experiments examined performance and initiation of reaching movements of human subjects to intercept moving targets. The companion paper (Lee et al. 1997) presents an analysis of the on-line control of reaching to intercept moving targets. This work expands upon previous work (van Donkelaar et al. 1992) by examining the performance and initiation of reaching to targets moving under conditions of constant acceleration, constant deceleration, and constant velocity. The main objective is to apply the two above-mentioned models of movement initiation to our experimental paradigm. Preliminary results have been reported (Port et al. 1992).

Materials and methods

Subjects

Six healthy human volunteers (two women and four men, aged 22–36 years) from the University of Minnesota academic environment participated in these experiments. Two of the subjects (1 and 3) were among the authors of the present study (N.L.P., P.D.); the other subjects were naive to the task and the purpose of the experiment. All subjects were right-handed and used their right hand in the experiment. The experimental protocol was approved by the Institutional Review Board.

Apparatus

Subjects sat unrestrained in front of a two-dimensional (2D) articulated manipulandum (described previously by Georgopoulos et al. 1981), with the eyes approximately 57 cm from a 14-inch color monitor (Gateway 1024NI). The manipulandum was on a table which was approximately 10 cm above the subject's waist, and the position of the manipulandum where subjects started a trial (hold zone) was approximately 20 cm away from the subject's abdomen. By moving the manipulandum, subjects controlled the location of a position feedback cursor on the computer screen. The position of the manipulandum in *xy* coordinates was digitally sampled at a rate of 100 Hz and a spatial resolution of 0.125 mm. The gain was set to 1, so that movement of the feedback cursor had a one-to-one correspondence with that of the manipulandum. The monitor was adjusted for a screen resolution of 640 horizontal and 480 vertical pixels, with a refresh rate of 60 Hz. A personal computer was used for experimental control, visual presentation, and data collection.

Behavioral task

To begin a trial, the subject moved the feedback cursor (0.6-cm-radius ring) until it was superimposed on a "start zone" (0.3-cm radius) that was centered at the lower vertical meridian of the screen (Fig. 1). After the subject maintained this position for a random period of 1–3 s, a target (0.6-cm radius) appeared in the lower right or left corner of the screen. The target then traveled along a 45° path until it reached the vertical meridian of the screen, where it stopped at a location 12.5 cm directly above the center of the start zone. The subject was required to move the feedback cursor so as to intercept the target just as it reached its final position at the center of the interception zone. A trial was considered successful when the following conditions were met:

1. The subject was required to maintain the cursor around the start zone until 100 ms after target onset. This condition was imposed to prevent anticipatory movements to the target.
2. The subject had to move the manipulandum so that the feedback cursor would enter an invisible positional window (interception zone, 0.6-cm radius) centered on the final target location within 100 ms of the target's arrival at the meridian. Trials in which the cursor arrived more than 100 ms before the target were considered *early errors*, whereas those in which the cursor arrived more than 100 ms after the target were considered *late errors.*
3. After the cursor entered the interception zone, the subject was required to maintain the cursor within an invisible positional window (hold zone, 1.2-cm radius) for 0.5 s.

Trials were aborted when any of the above-listed conditions were not met. Subjects were notified of unsuccessful trials with a tone and of successful trials with a click. There were no constraints on the subject's direction of movement and no instructions or comments on when to initiate the movement.

Stimulus characteristics

For each trial, the characteristics of target motion were chosen randomly from 36 possible combinations of three types of target acceleration types × six target motion times × two starting positions (Fig. 2). Each target moved in a 45° path from the lower corner of the screen to the vertical meridian with one of six possible target motion times ranging from 0.5 to 2.0 s in 0.3-s increments (Table 1). Furthermore, the target moved with one of three possible acceleration types; namely constant acceleration, constant deceleration, or constant velocity. For any trial, then, the distance of the target from its initial position could be described by the standard equation of motion:

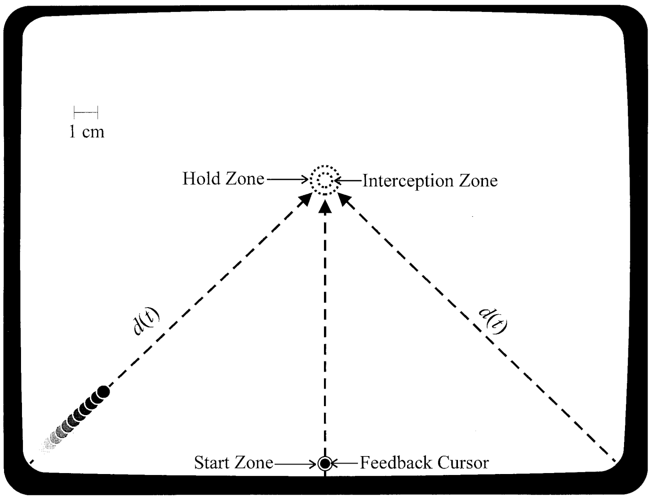

Fig. 1 Schematic diagram of the target-interception task [*d(t)* distance of target from starting point at time *t*]

$$d(t) = v_0 t + \frac{at^2}{2} \tag{4}$$

where $d(t)$ is the distance of the target from the starting point at time t, v_0 is the initial velocity, and a is the acceleration (Fig. 2). Equation 4 is the primary equation of motion that was used to calculate the target motion. Accelerating targets had a starting velocity of 3.0 cm/s and underwent an appropriate constant acceleration to achieve the desired motion time. Decelerating targets had velocity profiles that were mirror images of those of the accelerating targets and underwent constant deceleration to end with a velocity of 3.0 cm/s. Constant velocity targets traveled at the appropriate constant velocity to achieve the required motion time. Table 1 summarizes the 18 possible combinations of target acceleration types and motion times; the additional variable of target starting position (left or right lower corner) brought the total possible combinations to 36. The values in Table 1 were calculated with the following equations, which describe the relationship between the values in Eq. 4:

$$\text{A. Constant velocity:} \quad v_0 = \frac{\text{distance}}{\text{target motion time}}, \; a = 0 \tag{5}$$

$$\text{B. Accelerating targets:} \quad v_0 = 3.0,$$

$$a = \frac{2(\text{distance} - v_0 \times \text{target motion time})}{\text{target motion time}^2} \tag{6}$$

$$\text{C. Decelerating targets:} \quad v_0 = \frac{2 \times \text{distance}}{\text{target motion time}} - 3.0,$$

$$a = \frac{2(\text{distance} - v_0 \times \text{target motion time})}{\text{target motion time}^2} \tag{7}$$

where a is acceleration, v_0 is initial velocity and the distance the target traveled was fixed at 17.68 cm. Since the target is traveling at a 45° angle and the origin (0,0) of our coordinates is the center of the hold zone, the vertical and horizontal positions of the target at time t are as follows:

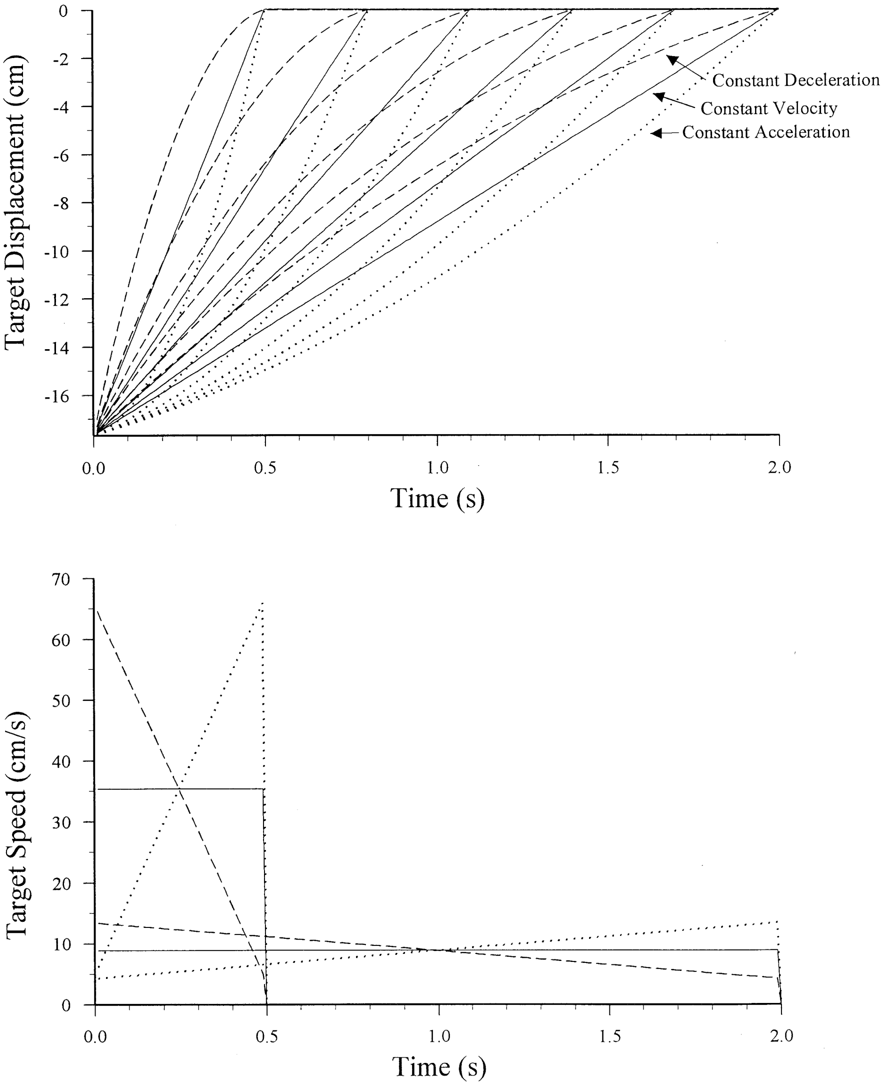

Fig. 2 *Top:* target displacement plotted against time for all target motion times (0.5–2.0 s in 0.3-s increments) and target acceleration types (constant acceleration, constant deceleration, and constant velocity). *Bottom:* target velocity plotted against time; for clarity, only two target motion times (0.5 s and 2.0 s) and all three target acceleration types (constant acceleration, constant deceleration, and constant velocity) are shown

Table 1 Stimulus characteristics

Target acceleration type	Target motion time (s)	$v_0\left(\frac{\mathrm{cm}}{\mathrm{s}}\right)$	$a\left(\frac{\mathrm{cm}}{\mathrm{s}^2}\right)$	Initial τ of the target (s)
Constant acceleration	0.5	3.00	129.41	5.89
	0.8	3.00	47.74	5.89
	1.1	3.00	23.76	5.89
	1.4	3.00	13.75	5.89
	1.7	3.00	8.70	5.89
	2.0	3.00	5.84	5.89
Constant deceleration	0.5	67.70	−129.41	0.26
	0.8	41.19	−47.74	0.43
	1.1	29.14	−23.76	0.61
	1.4	22.25	−13.75	0.79
	1.7	17.80	−8.70	0.99
	2.0	14.68	−5.84	1.20
Constant velocity	0.5	35.35	0.00	0.5
	0.8	22.09	0.00	0.8
	1.1	16.07	0.00	1.1
	1.4	12.63	0.00	1.4
	1.7	10.40	0.00	1.7
	2.0	8.84	0.00	2.0

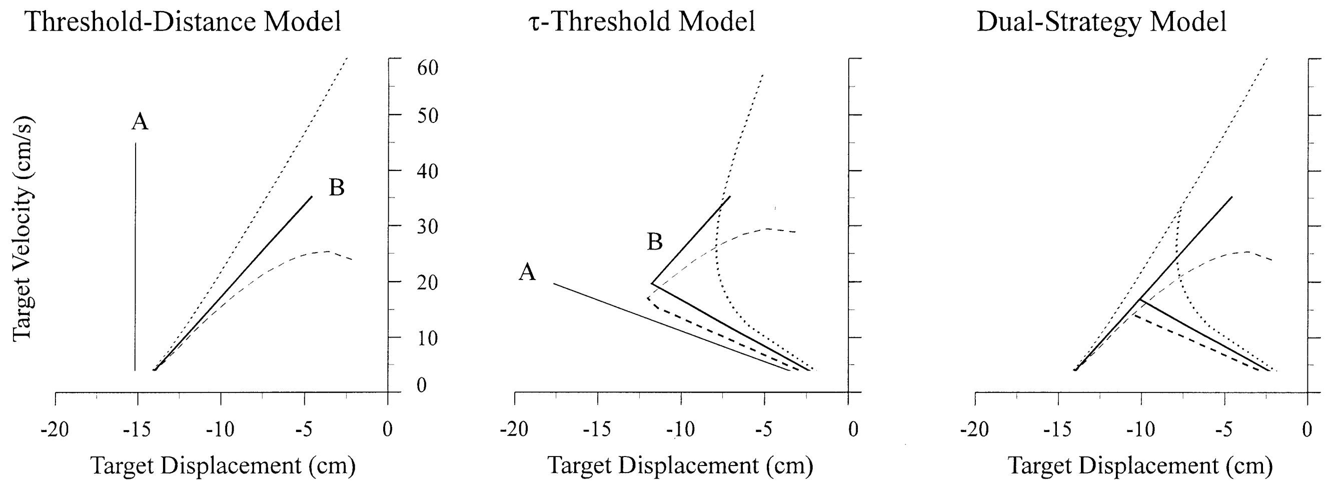

Fig. 3 Theoretical predictions in phase space of the three models examined. In each model the predicted response time is calculated from the equations described in Materials and methods (Eqs. 12 and 14 for the threshold-distance model and Eqs. 16 and 17 for the threshold-τ model). The predicted displacement of the target at the moment of hand movement initiation is plotted against the predicted target velocity. In both the threshold-distance model (*left*) and threshold-τ model (*center*), *line A* is the prediction of the model with zero processing time, and *line B* is the prediction of the model with a constant processing time. *Dotted, dashed, and solid lines* are for accelerating, decelerating, and constant velocity targets, respectively

$$y(t) = \frac{d(t)}{\sqrt{2}} \tag{8}$$

$$x(t)_{\mathrm{left}} = -12.5 + \frac{d(t)}{\sqrt{2}} \quad or \quad x(t)_{\mathrm{right}} = 12.5 - \frac{d(t)}{\sqrt{2}} \tag{9}$$

for targets from the left or right, respectively (Fig. 2).

Experimental design

Each experimental session comprised five repetitions of the set of 36 conditions, presented in a randomized block design. No nesting was employed. This randomization assured that there was no prior knowledge about the upcoming trial's target direction, acceleration type, and target motion time. Unsuccessful trials were randomized and repeated until correct performance was achieved. This was done to obtain an equal number of successful trials for all target conditions. Naive subjects were given one practice block immediately before the experimental session. The nonnaive subjects had approximately 20 blocks of practice.

Data analysis

General

Standard statistical analyses (Snedecor and Cochran 1989) were used, including analysis of variance (ANOVA). The 5% probability level was taken as the level of statistical significance for rejecting the null hypothesis. For the ANOVA of the percentage of early and late errors, when the sample size (n) was less than 50, 0% was counted as $1/(4n)$ and 100% was counted as $(n-¼)/n$, then the percentages were arcsine transformed. Nonlinear curve fitting was performed using the Nelder-Meade simplex search method (MATLAB version 4.2, 1994; The MathWorks, Natick, Mass.). The hand position was smoothed and differentiated using the finite impulse response (FIR) method (pass band 0–0.5 Hz; stop-band 13–50 Hz). For a given movement, response time was defined as the first time hand velocity reached 10% of its peak velocity.

Constant temporal error

The constant temporal error is the signed difference from the time at which the target arrived in the center of the interception zone until the cursor entered the interception zone. Negative and positive values mean that the cursor arrived before, or after, the target reached the center of the interception zone, respectively.

Threshold-distance model

In the threshold-distance model (Collewijn 1972), response time is the sum of a constant processing time and the time it takes for the target to travel a certain threshold distance (see Eq. 1). Under conditions of constant target velocity, both the constant processing time and the threshold distance can be determined by a linear regression of response time on the inverse of target velocity.

In the present study, targets traveled not only at a constant velocity, but also under conditions of constant acceleration or constant deceleration. To visualize the details of the threshold-distance model, we used phase plots in which the displacement of the target at the moment of hand movement initiation is plotted against the velocity of the target (Fig. 3, left). If the subject was using a threshold-distance strategy with zero processing time, a straight vertical line would be observed in the phase plot (line A in Fig. 3, left). However, if the subject is using the threshold-distance strategy with a constant processing time, a sloped line for constant velocity targets and two curves for the constant accelerating and decelerating targets would be observed (line B in Fig. 3, left). In order to solve for threshold time, Eq. 4 is rewritten in quadratic form:

$$\left(\frac{a \times \text{threshold time}^2}{2}\right) + (v_0 \times \text{threshold time}) - \text{threshold distance} = 0 \tag{10}$$

where a is target acceleration and v_0 is the initial target velocity of the target. Therefore, for a=0 (constant velocity targets):

$$\text{Threshold time} = \frac{\text{threshold distance}}{v_0} \tag{11}$$

and thus we obtain the same equation as the threshold-distance model (Eq. 2):

$$\text{Response time} = \text{processing time} + \text{threshold distance}\left(\frac{1}{\text{target velocity}}\right) \tag{12}$$

For $a \neq 0$ (constant acceleration and deceleration targets), by the quadratic equation:

$$\text{Threshold time} = \frac{-v_0 + \sqrt{v_0^2 + 2a \times \text{threshold distance}}}{a} \tag{13}$$

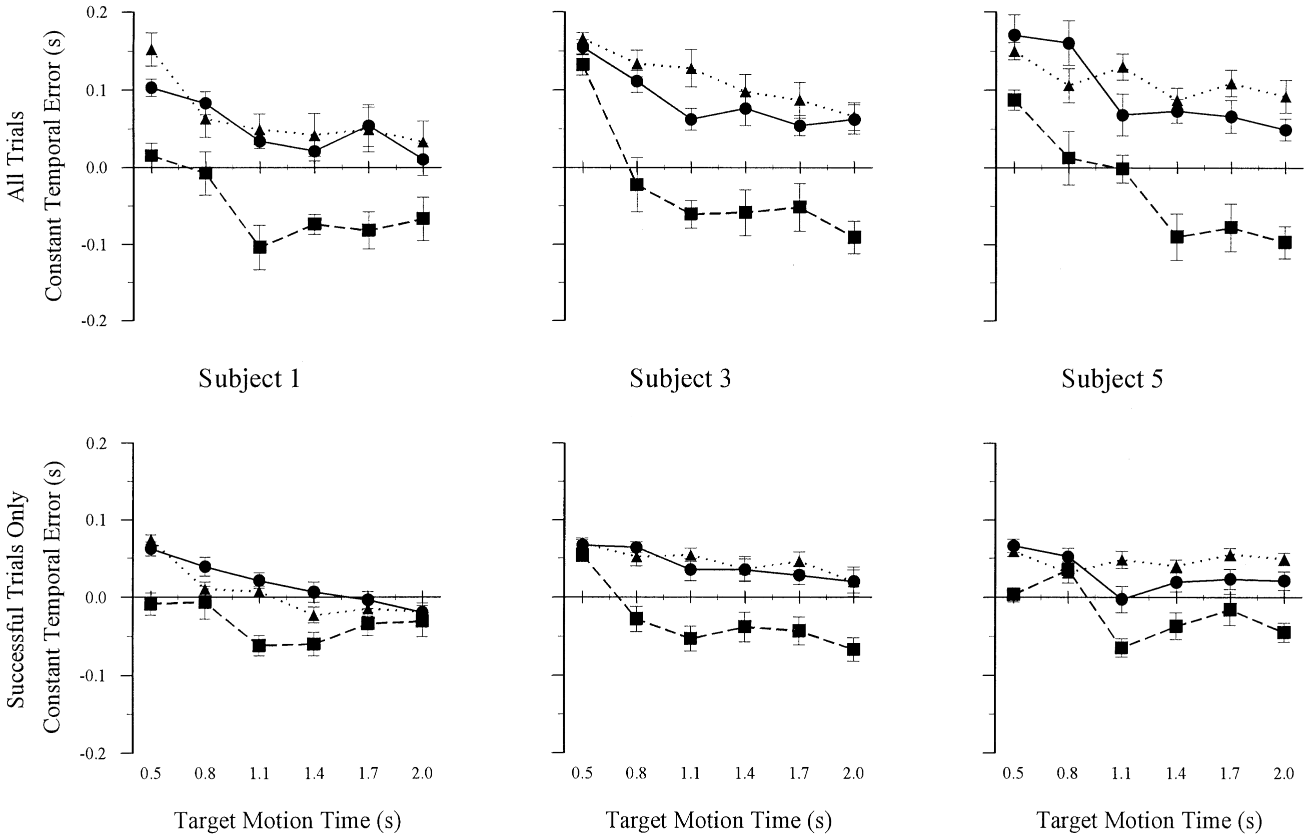

Fig. 4 *Top:* For each subject, mean (±SEM) constant temporal errors are plotted against target motion time for all trials. *Bottom:* Mean constant temporal errors computed for successful trials only. Positive temporal errors indicate that the hand arrived later than the target. *Triangles* and *dotted lines*, accelerating targets; *squares* and *dashed lines*, decelerating targets; *circles* and *solid lines*, constant-velocity targets

and in the threshold-distance model:

$$\text{Response time} \\ = \text{processing time} + \frac{-v_0 + \sqrt{v_0^2 + 2a \times \text{threshold distance}}}{a} \qquad (14)$$

The constant processing time and threshold distance are then determined using a nonlinear curve-fitting procedure and Eqs. 12 and 14.

Threshold-τ model

The τ of the target, which is a continuous variable changing with time, is defined as the distance of the target to the interception zone at time *t* divided by the velocity of the target at time *t* (see Eq. 3). In the threshold-τ model, a movement is initiated after a certain processing time from the moment at which the τ of the target decreases below a certain threshold. The initial τ of the target (i.e., τ at the time of target onset) is summarized in Table 1. Since the τ of target is the ratio of target position to target velocity, the threshold-τ model without a constant processing time would produce in the phase plots a straight line with a negative slope (line A, Fig. 3, center). The threshold-τ model with a constant processing time yields a straight line with a different slope for constant velocity targets, and curved lines for accelerating and decelerating targets (line B, Fig. 3, center). For targets that moved with a high initial velocity (e.g., decelerating target with 0.5 s motion time), the initial τ might already be less than the threshold τ. Under these circumstances, we assumed that the subjects would begin moving immediately after the constant processing time. It is this assumption that produces the sudden change in the prediction lines in the phase space (line B, Fig. 3, center). Otherwise, we assumed that the subjects waited until τ decreased below the threshold τ and then began moving after the constant processing delay. In this latter condition, response time is the sum of the processing time and the solution for threshold time in the following equation:

$$\tau = \frac{\text{target distance}}{\text{target velocity}} \\ = \frac{17.68 - \left(v_0 \times \text{threshold time} + \dfrac{a \times \text{threshold time}^2}{2}\right)}{v_0 + a \times \text{threshold time}} \qquad (15)$$

where 17.68 (cm) is the distance between the starting position of the target and the interception zone. Therefore, for a=0 (constant velocity targets),

$$\text{Response time} = \text{processing time} + \frac{17.68 - \tau v_0}{v_0}, \qquad (16)$$

and for $a \neq 0$ (accelerating and decelerating targets),

$$\text{Response time} \\ = \text{processing time} + \frac{-(a\tau + v_0) + \sqrt{(a\tau + v_0)^2 - 2a(v_0\tau - 17.68)}}{a} \qquad (17)$$

Dual-strategy model

The dual-strategy model is based on the assumption that on each trial the subject uses one of two alternative strategies, reactive or predictive, to decide when to initiate the movement. The threshold-distance model as described above is used to model the response time according to the reactive strategy. Similarly, the

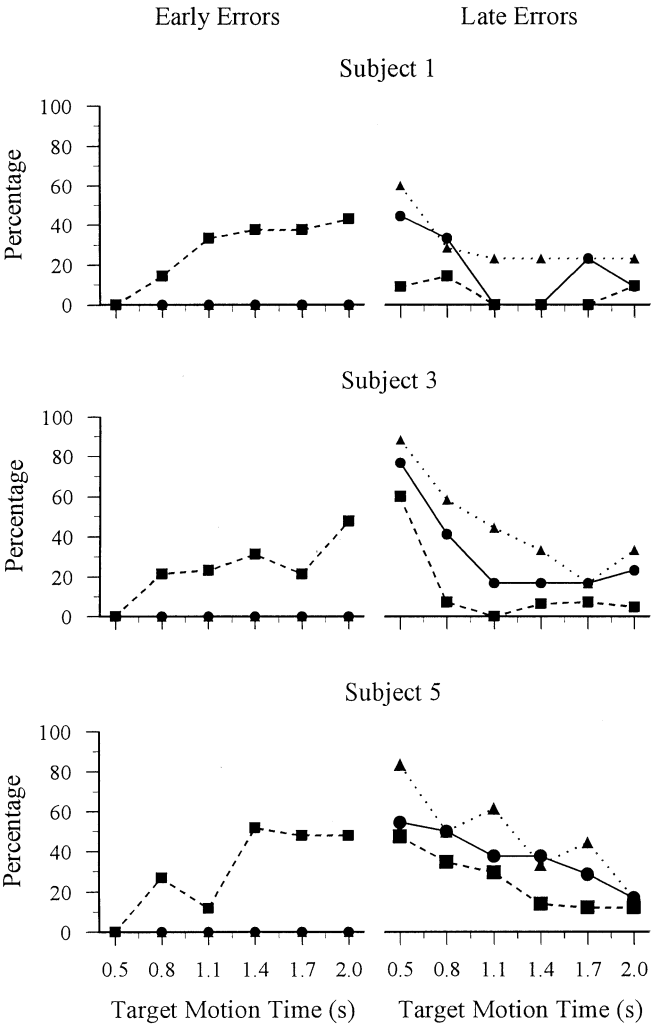

Fig. 5 The percentage of early and late arrival movements is plotted against target motion time for all three target acceleration types. Conventions are as in Fig. 4

threshold-τ model is used to model the response time according to the predictive strategy. It is further assumed that the predictive strategy is more time consuming to implement than the reactive strategy. Therefore, when the predictive strategy results in a smaller (faster) response time than the reactive strategy, the subject should respond according to the reactive strategy only. A single, constant processing-time term was determined for both models. During the curve-fitting procedure, a given trial was assigned to either the reactive or predictive strategy, depending on which strategy yielded a response time closer to the observed value. Therefore as a result of the curve fitting, in addition to getting estimates for the parameters of the model (i.e., a single processing time, a threshold distance, and a threshold τ) it was also determined which strategy was used in individual trials. The phase plot of Fig. 3 (right) demonstrates the position and velocity of the target at hand movement onset, as predicted by the dual-strategy model.

Results

Constant temporal errors

A total of 2614 movements were made by six subjects, of which 1080 of 2614 (41.3%) were considered successful (see Materials and methods). Analysis of the temporal errors revealed several systematic influences of the target motion parameters that were consistent across subjects. For all trials (Fig. 4, top) and for successful trials considered separately (Fig. 4, bottom), movements to decelerating targets tended to arrive at the target zone early with respect to the arrival of the target (negative temporal errors). In contrast, movements to accelerating and constant-velocity targets tended to arrive late (positive temporal errors). Regardless of acceleration type, movements arrived earlier for longer target motion times. An ANOVA revealed that for all subjects there were significant effects of target acceleration type ($P<0.001$) and target motion time ($P<0.001$). When all trials were considered, there was a significant interaction ($P<0.05$) for subjects 3, 4, and 6, and a marginal effect for subjects 2 and 5 ($P=0.052$ and 0.085, respectively). In the more restrictive case of only successful trials, there was a significant interaction for subjects 1 and 5 ($P<0.05$) and a marginal effect for subject 3 ($P=0.072$).

Table 2 Effects of the target on the percentage of early and late errors. The degrees of freedom are (1,2) for target acceleration type and (1,5) for target movement time

	Subject	Tail probability	
		Target acceleration type	Target motion time
Early arrival	1	0.000	0.283
	2	0.002	0.127
	3	0.000	0.109
	4	0.000	0.096
	5	0.000	0.207
	6	0.000	0.009
Late arrival	1	0.002	0.018
	2	0.006	0.003
	3	0.000	0.000
	4	0.029	0.062
	5	0.002	0.000
	6	0.000	0.000

Percentage of early and late errors

Inspection of the early and late errors revealed the difficulty of the task as well as the effects of both acceleration type and target motion time on the hand movement (Fig. 5). Overall, 7.8% and 50.9% of the movements were early and late errors, respectively, whereas the remaining 41.3% were successful trials. A large majority of early errors were produced in response to decelerating targets, and the percentage of early errors tended to increase with target motion time. There was a significant effect of acceleration type for all subjects (Table 2). However, there was a significant effect of target motion time for subject 6 only. Late errors occurred to all three target acceleration types, and the percentage of late errors tended to decrease with target motion time. These effects were significant in all subjects except sub-

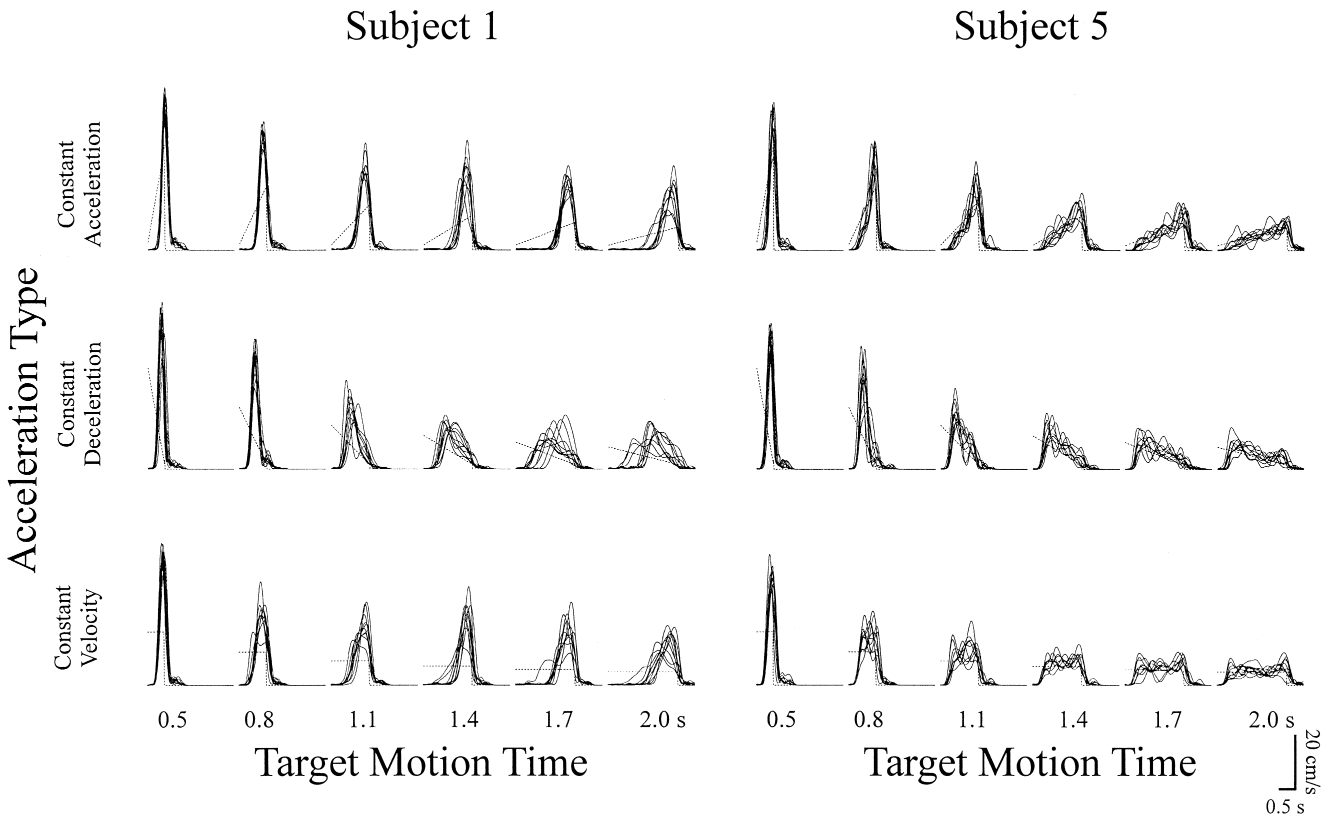

Fig. 6 For two subjects, individual hand velocity traces and target velocity are plotted against time for each target acceleration type and target motion time. *Solid lines* indicate hand velocity traces in individual trials and *dashed lines* are target velocity

ject 4, who showed a significant effect of acceleration type but only a marginal effect of target motion time (Table 2).

Initiation of interceptive movements

Systematic differences were found across subjects with regard to the initiation of hand movements. Examination of the individual movements revealed that some subjects (e.g., subject 1) varied systematically the time taken to initiate a movement, whereas others (e.g., subject 5) seemed to initiate the movement at a short, relatively constant interval after the target appeared (Fig. 6). An ANOVA was performed to assess the effects of subject, target motion time, and target acceleration type on response time. Significant main effects were found for subject, target acceleration type, and target motion time (P<0.0001), and for all two-way and three-way interactions (P<0.0001). These results, together with the clear differences in the profiles of hand velocity (Fig. 6), suggest that data from individual subjects should be analyzed separately.

The effect of the target characteristics on the initiation of hand movement becomes more evident when response time is plotted against target motion time for each of the target acceleration types. Figure 7 shows that some subjects varied the initiation of their response as a function of both target acceleration type and target motion time (i.e., subjects 1, 2, and 3), whereas other subjects (i.e., 5 and 6) showed relatively constant response times as a function of target motion time and only slight differences across the different target acceleration types. These influences of the target were analyzed by an ANOVA assessing the effects of target acceleration type and target motion time on response time. For subjects 1–5, significant effects were found for target acceleration type and target motion time plus the target acceleration type × motion time interaction (P<0.001). However, for subject 6 there was only a significant effect of target acceleration type (P<0.001).

Threshold-distance model

The threshold-distance model predicts that a subject will respond after some constant processing time *plus* the time it takes the target to travel a certain distance (Eq. 1). The phase plots show that the prediction lines capture the data for some subjects, but only partially so for other subjects (Fig. 8, top; see also Materials and methods; and Fig. 3, left). This and the following phase plots are useful in revealing the trends in the data qualitatively, but they are not suitable for comparing the goodness of the fit for different models, because the same distance can represent quite different lengths of time depending on the target velocity (the vertical axis). Table 3 summarizes

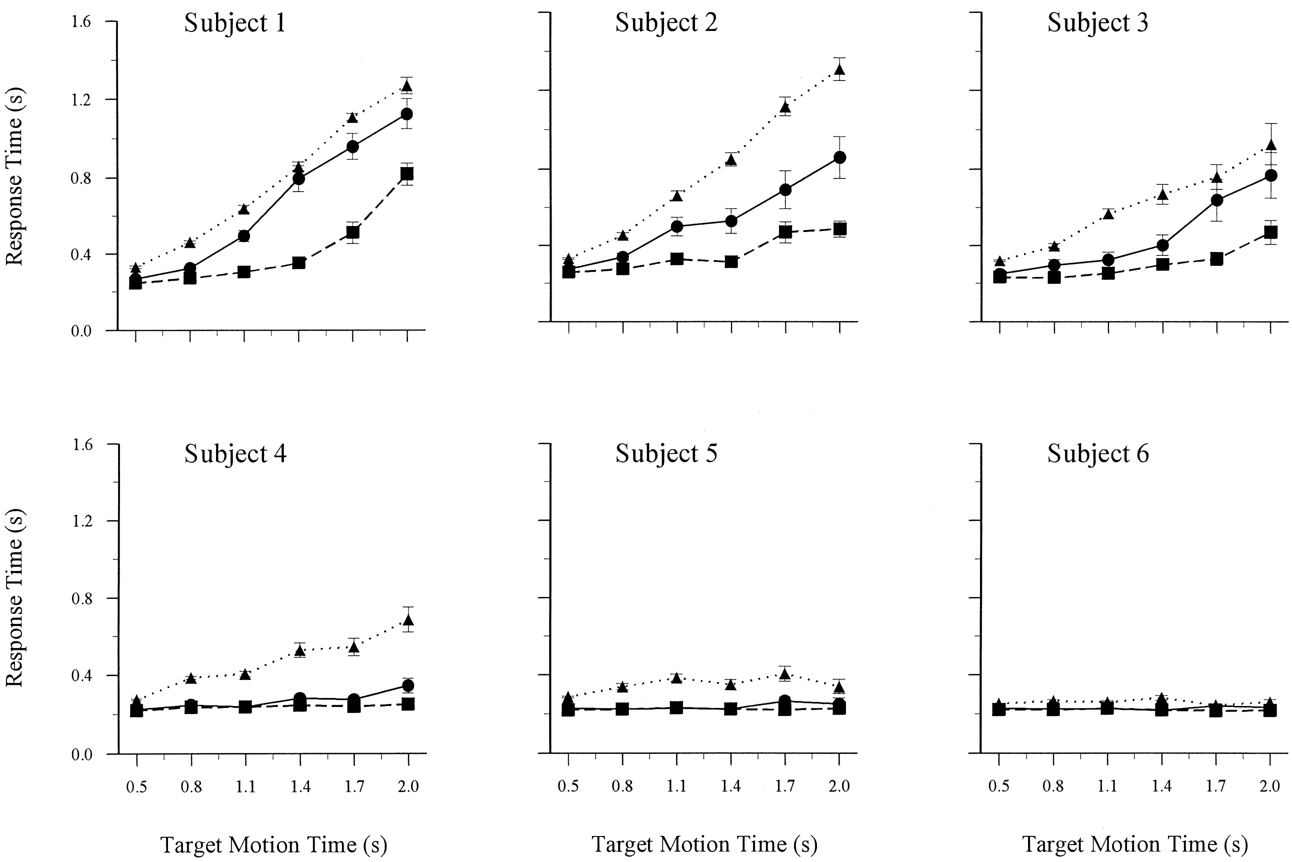

Fig. 7 Response time plotted against target motion time for each target acceleration type. Conventions are as in Fig. 4

the fit of the model and Fig. 8 (bottom) shows a plot of the predicted response time against the observed data. In general, the model fit the data only partially. Finally, for subject 1, the negative slope of the prediction lines reflects a negative processing time (the implication of this unexpected outcome is addressed in the Discussion).

Threshold-τ model

As Lee and Reddish (1981) have proposed, organisms might wait for τ to reach a certain threshold before initiating movement. The phase plots show that the prediction lines match the trend of the data for a few subjects (e.g., 1), but bear little resemblance to the data for other subjects (Fig. 9, top; see also Materials and methods; Fig. 3, center). The parameters of the model are summarized in Table 4, and Fig. 9 (bottom) plots the predicted response time against the observed data. In the present experiment, the τ-threshold model also only partially fit the data.

Dual-strategy model

Visual inspection of the phase plots for response times in individual subjects suggested that some subjects (e.g., 5) performed the task mostly based on the reactive strategy, whereas other subjects used both strategies (Fig. 10, top; see also Materials and methods; Fig. 3, right). In general, the dual-strategy model provided a better fit to the data than either the threshold-distance or threshold-τ models alone (Table 5). This is further demonstrated in Fig. 10 (bottom), where the predicted response time is plotted against the observed response time.

Assuming that the subjects performed the task using one of these alternative strategies, an important question is how the probability of selecting either strategy changes as a function of target acceleration type and motion time for each subject. To examine this issue, the number of trials in which the predictive strategy provided an estimate closer to the response time in any given trial were counted and divided by the total number of trials (Fig. 11). The frequency of choosing either strategy varied greatly among subjects. When the mean frequency of the predictive strategy was computed regardless of target parameters, subjects 1 and 6 showed the highest (0.291) and lowest (0.002) probability values, respectively. In addition, longer target motion times and the constant acceleration condition were associated with a higher frequency of occurrence of the predictive strategy. Thus it seems that some subjects (e.g., subjects 5 and 6) relied almost solely on the reactive strategy regardless of target velocity, whereas other subjects relied on the predictive strategy only for relatively low target velocity and switched to the reactive strategy with increasing target velocity.

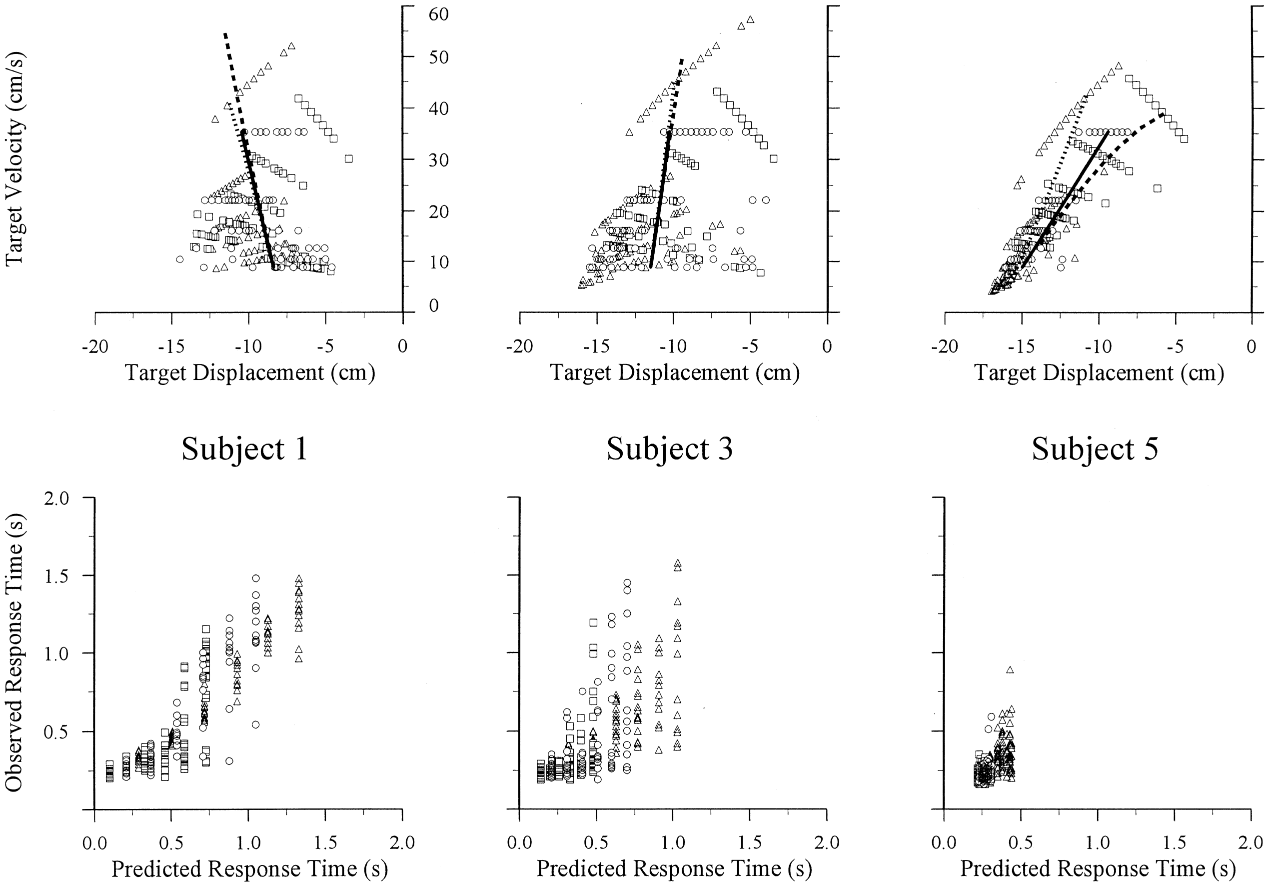

Fig. 8 *Top:* target displacement plotted against target velocity at the moment of hand movement initiation. The lines are the prediction of the threshold-distance model. *Dotted lines, dashed lines,* and *solid lines,* accelerating, decelerating, and constant-velocity targets, respectively. *Bottom:* the observed response time plotted against the response time predicted by the threshold-distance models

Table 3 Parameters and fit of the threshold-distance model

Subject	Constant processing time (s)	Threshold distance (cm)	R^2
1	−0.077	9.98	0.8115
2	0.035	7.16	0.6477
3	0.047	5.78	0.4516
4	0.133	2.33	0.4042
5	0.210	0.85	0.1423
6	0.216	0.14	0.1524

Lack of effect of practice and target direction

It is worth noting that there was no effect of target direction and trial repetition on either the response time or the constant temporal error (ANOVA, $P>0.5$). Furthermore there was no effect of repetition on either the percentage of early or late errors, except for subject 6, in which there was an effect of repetition on the percentage of late errors (ANOVA, $P=0.046$). However, in this case the effect was apparently due to variation among repetitions rather than a systematic change with practice.

Discussion

We investigated the capacities of human subjects to intercept moving visual targets in 2D space. Since the interception point was constant and the initial position of the hand was the same in all trials, the emphasis of the experiment was on the temporal aspects of the interception movement; namely on its initiation and on-line control. In this paper we dealt with the initiation of the interception movement. Specifically, we examined the question: How did subjects decide to start their movement? Two aspects of the experimental design were crucial for this decision. Firstly, the wide range of target motion types (constant acceleration, constant deceleration, and constant velocity) and target motion times (from 0.5 to 2.0 s) allowed freedom of choice in possible strategies to be adopted. And secondly, the demanding temporal accuracy of interception (±100 ms from target arrival) imparted serious constraints on the implementation of possible strategies. We discuss these various issues separately below.

Use of target acceleration in manual interception

The analysis of early and late errors indicates that subjects either did not have access to or were unable to fully

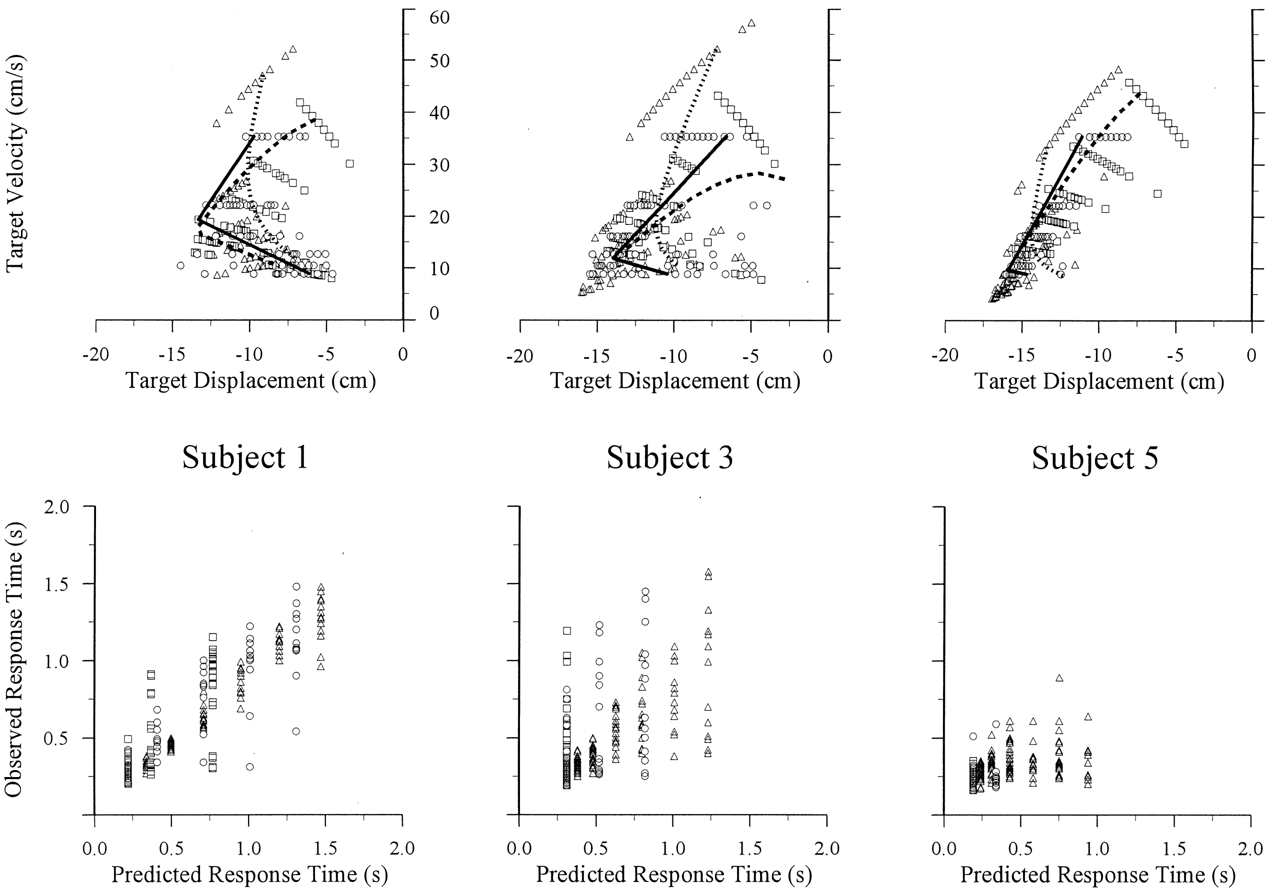

Fig. 9 *Top:* target displacement plotted against target velocity at the moment of hand movement initiation. The *lines* are the prediction from the τ-threshold model. Conventions as in Fig. 8. *Bottom:* the observed response time plotted against the response time predicted by the threshold-τ model

Table 4 Parameters and fit of the threshold-τ model

Subject	Constant processing time (s)	Threshold τ (s)	R^2
1	0.225	0.916	0.8284
2	0.340	1.358	0.6154
3	0.313	1.494	0.3868
4	0.208	1.814	0.4097
5	0.186	1.848	0.1122
6	0.229	5.410	0.0498

utilize information concerning the acceleration of target motion. This is supported by the finding that early errors occurred almost exclusively for decelerating targets (Fig. 5). In contrast, late errors occurred for all three target acceleration types, although accelerating targets produced the largest and decelerating targets the smallest percentage of late errors. Analysis of the constant timing errors yielded similar results (Fig. 4, top). For decelerating targets, the constant timing error tended to be negative (early hand arrival), whereas for accelerating and constant velocity targets the constant timing error tended to be positive (late hand arrival). Thus it seems that, if the target travels initially at high velocity but then decelerates, subjects are unable to compensate for this decrease in speed and arrive too early. However, if the target travels initially at low velocity and then accelerates, subjects are now unable to compensate for this increase in speed and arrive too late. This remains true even in the more restricted case of only successful trials (Fig. 4, bottom).

Although human subjects have been shown to be able to detect acceleration and deceleration, they may not be able to utilize such information in a motor task. Gottsdanker (1952, 1956) and Edwards (Gottsdanker and Edwards 1957) were among the first to study visual acceleration, and they concluded initially that, in sensorimotor tasks of tracking and interception, visual acceleration is acted on as if it were constant velocity. Subsequently, Gottsdanker et al. (1961) performed a purely perceptual experiment in which subjects had to discriminate between stimuli traveling with constant acceleration or constant velocity. They concluded that subjects were able to detect acceleration, but did so by comparing earlier velocity with later velocity rather than by directly sensing acceleration. This conclusion was further quantified by Schmerler (1976), who found that a change in velocity ratio of at least 2.9 for acceleration and 2.4 for deceleration was needed in order for subjects to be able to detect visual acceleration. Babler and Dannemiller (1993), in a somewhat different task from Schmerler (1976), found that an even smaller velocity ratio was required for threshold detection

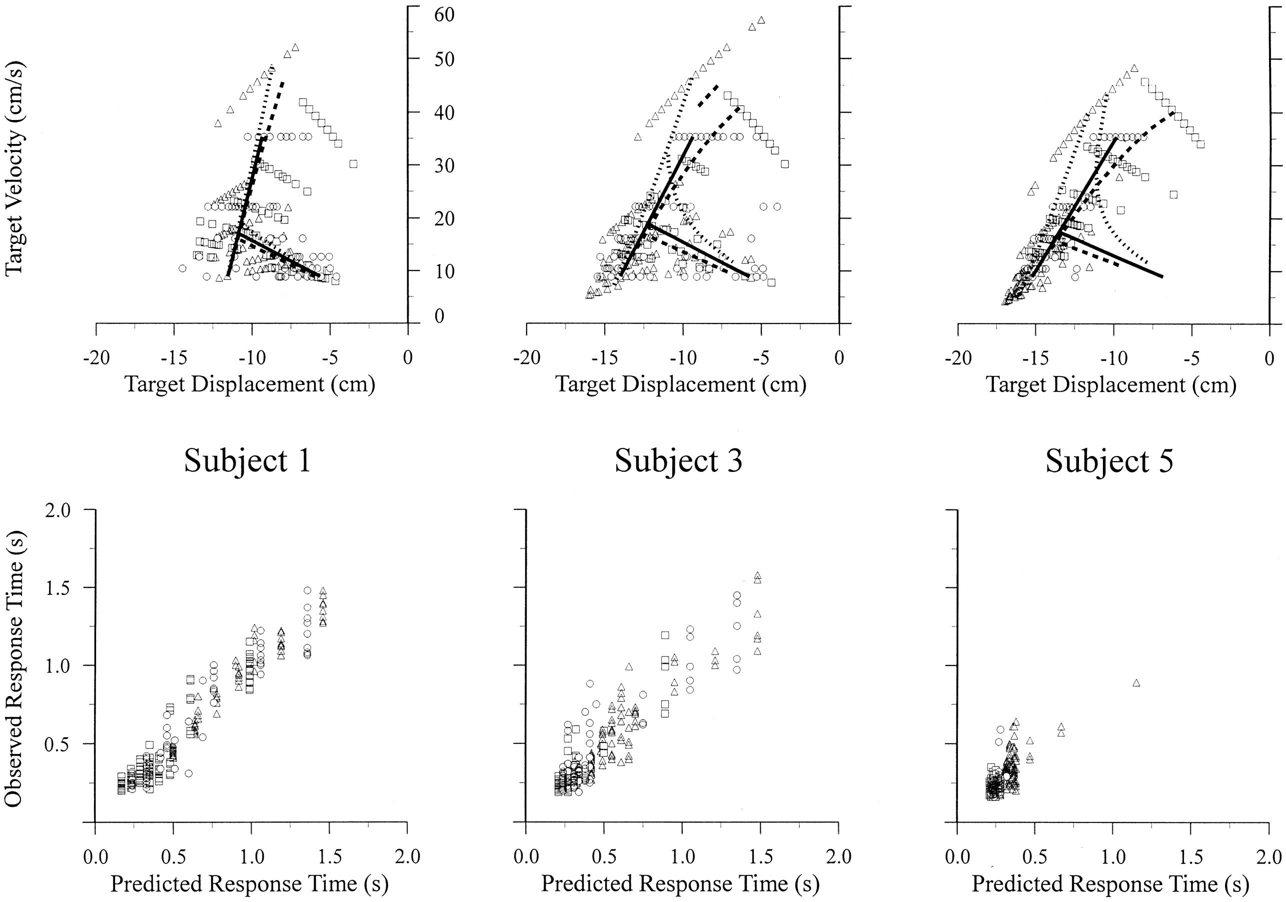

Fig. 10 *Top:* target displacement plotted against target velocity at the moment of hand movement initiation. The *lines* are the predictions from the dual-strategy model. Conventions as in Fig. 8. *Bottom:* the observed response time plotted against the response time predicted by the dual-strategy model

Table 5 Parameters and fit of the dual-strategy model

Subject	Constant processing time (s)	Threshold distance (cm)	Threshold τ (s)	R^2
1	0.084	5.39	0.721	0.9334
2	0.181	2.29	0.806	0.8866
3	0.176	2.11	0.825	0.8616
4	0.152	1.73	1.004	0.7810
5	0.204	0.64	0.980	0.7513
6	0.214	0.13	1.636	0.3223

of acceleration in a two-alternative forced-choice paradigm. In our experiment, the smallest ratio (4.89) was substantially larger than the amount determined by either Schmerler (1976) or Babler and Dannemiller (1993) to be necessary for perceptual detection. Thus, in the present experiments the acceleration and deceleration of the targets should have been detectable, but the motor system may not have been able to act upon this information.

Neurophysiological studies of visual acceleration

Neurophysiological studies examining visual acceleration have been conducted in the middle temporal (MT) extrastriate visual cortex, but it is not clear whether MT is involved in the visual perception of acceleration, much less in providing such information for reaching to intercept an accelerating target. Neurons in MT are known to play a role in visual motion perception and are tuned for the direction and speed of moving visual stimuli (for a review, see Maunsell and Newsome 1987). A small population of neurons in MT have also been shown to have small phasic responses to visual acceleration when the change of velocity is greater than approximately ten-fold (Movshon et al. 1990; Lisberger et al. 1995). However, it was concluded that these phasic responses were primarily the result of speed tuning and led these workers to conclude that MT neurons are not tuned with respect to acceleration; nor is there "a comprehensive representation of target acceleration in MT" (Movshon et al. 1990). However, it is still possible that another structure that receives velocity information from MT could differentiate responses of velocity-tuned MT neurons to obtain a representation of acceleration.

Effects of relative velocity

Recent experiments by Smeets and Brenner (1994, 1995) have demonstrated that relative velocity has an effect on

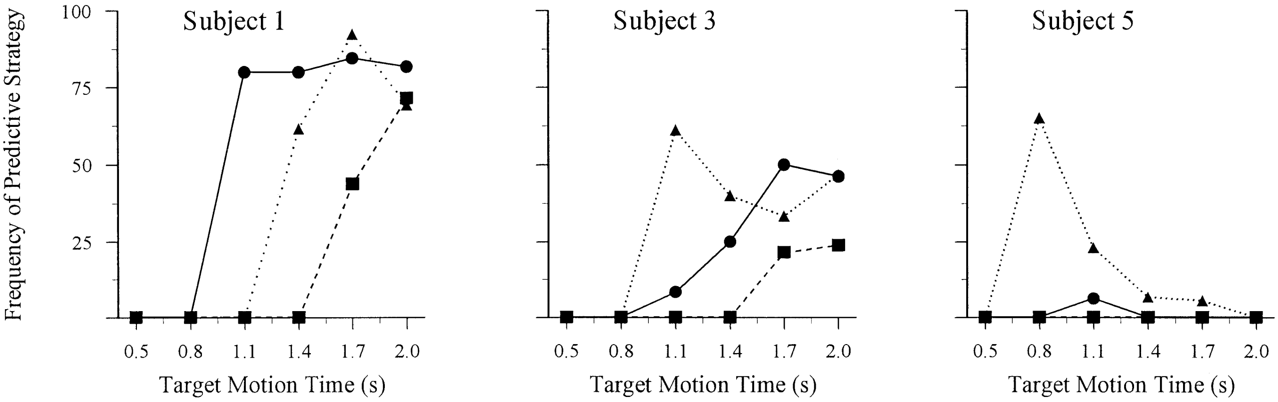

Fig. 11 The percentage of movements initiated based on the predictive strategy in the dual-strategy model plotted as a function of target motion time. Conventions as in Fig. 4

some aspects of movement. In what the authors referred to as a "hitting" interceptive experiment, subjects were asked to hit a target moving on a computer screen with an acrylic rod as quickly as possible (Smeets and Brenner 1995). To improve speed and accuracy, subjects were given feedback on their positional accuracy in hitting the target and their response speed and movement times. To investigate the effects of absolute and relative velocity on performance, Smeets and Brenner then manipulated the visual background such that it moved at different speeds and in a direction either identical to or opposite the direction of the target. Trials were presented in random order and static background trials were included. When the background moved opposite to the target, thus increasing the relative velocity of the target, subjects produced faster response times. The opposite effect was found when the background moved in the same direction of the target. There are several differences between the experiment by Smeets and Brenner (1995) and the current experiment, including the requirement to stop the hand on the target (in this case catch rather than hit the target) and the freedom to initiate a response at the subjects discretion. However, it is worth noting that the present experiment does not differentiate between absolute and relative motion. Had a moving background been presented in the current experiment, relative motion could very well have had an effect on the results.

Threshold-distance model

The general trend of the data is captured by the threshold-distance model, and in most subjects the overall fit of this model was superior to that of the τ-threshold model. However, the fit was not as strong as might have been expected, and some of the parameters produced by the threshold-distance model were difficult to interpret. To begin with, this model posits the existence of a constant positive processing time and a threshold distance the target must travel. In the present data, the constant processing time for some subjects was found to be negative and the threshold distance was found to be relatively large. The appearance of a negative processing time is contrary to the assertions of the model. For example, in subject 1, the model provided a processing time of –77 ms and a threshold distance of 9.98 cm. According to these values, the movement would be initiated 77 ms before the target traveled 9.98 cm. Furthermore, in the case of the decelerating targets with 0.5 s target motion time, the target would travel 9.98 cm in 177 ms, and thus the response time (RT=–77+177) should be 100 ms, which is less than the minimum response time possible and would not leave enough time for the brain to detect target motion. In the current experiment, then, the threshold-distance model was ruled out as the sole strategy for initiating the interception movement.

This result differs from that of van Donkelaar et al. (1992). However, there are substantial differences between their study and the current project. Firstly, both accelerating and decelerating targets were used in the present study, whereas van Donkelaar et al. (1992) used only constant-velocity targets. Secondly, in the present study, subjects were required to make a movement to a specific point in both space (the interception zone) and time (±100 ms from target arrival). These restrictions were absent in the study by van Donkelaar and colleagues. Thirdly, in the experiment by van Donkelaar et al. (1992), the target was stationary for a brief period of time before target motion cued the subject to intercept it. In the present study, the target appeared already in motion, as if it appeared from behind an occlusion. Finally, in the study of van Donkelaar et al. (1992), subjects were instructed to initiate their movements as rapidly as possible, whereas no instructions regarding the time of initiation were provided to subjects in the current study. These differences might explain the different findings of these two studies.

Threshold-τ model

Of the three models tested, the threshold-τ model provided the least explanatory description of our data, and this differs somewhat from the results obtained in the study by Lee and Reddish (1981) of the diving gannets and a study by Lacquaniti and Maiolo (1989a) of humans catching a ball. One difference between the design of the present study and that of Lee and Reddish (1981) is that the gannets were moving toward a stationary target (i.e., the water surface), whereas in the present study both the hand of the subject and the target were moving. This might account for some of the differences in the results. The present results also differ from those of Lacquaniti and Maioli (1989a, b), who studied the anticipatory electromyographic (EMG) activity of humans catching balls dropped from a point directly above their hands. They found that the onset of anticipatory EMG activity was roughly constant at about 100 ms with respect to the time of impact of the falling ball, regardless of the height from which the ball was dropped. They concluded that the onset of EMG activity was probably controlled in an on-line fashion based on an estimate of instantaneous time-to-contact of the ball. Although these results differ from those presented here, there are important differences in the methods employed. The present study investigated the initiation of a full arm movement to a moving target traveling under a variety of conditions, whereas, in the experiment by Lacquaniti and Maioli (1989a), the onset of anticipatory EMG activity to an impending collision of a ball accelerating at the rate of gravity was investigated. These differences in task conditions might be responsible for some of the different results obtained. In contrast to the findings of Lee and Reddish (1981) and Lacquaniti and Maioli (1989a), the present results suggest that the τ of the target might not be the only relevant control variable for movement initiation.

Dual-strategy model

Examination of response times using phase plots showed that the threshold-distance model does not fully explain the present data. In addition to providing a worse fit to the data than the dual-strategy model, the parameters produced by the threshold-distance model were difficult to interpret. This model provided unrealistic parameters, because it does not reflect the fact that some subjects used two alternative strategies. In fact, the parameters for the threshold-distance model, *when included as a part of the dual-strategy model* provided more realistic values. The processing times ranged between 84 and 214 ms, and the threshold distance ranged between 0.13 and 5.39 cm. The processing time as measured by van Donkelaar et al. (1992) was 195 ms and the threshold distance was 0.53 cm.

In a previous study of reaching toward moving targets (van Donkelaar et al. 1992), behavioral paradigms different from those of the present study were used, and this might explain some of the discrepancy in the parameters in the threshold-distance model between the two studies. For example, in the study of van Donkelaar et al. (1992), the subjects were instructed to intercept the target as soon as possible, regardless of its location, thus reducing the need for a predictive strategy. Thus, it is reasonable to assume that the subjects in the study by van Donkelaar et al. (1992) performed the task mostly according to a reactive strategy. In contrast, the subjects in the present study were required to intercept the target at a fixed location without explicit instruction regarding response speed. Nevertheless, estimates for the processing time were similar in both studies. The processing time in the dual-strategy model was 169 ms when averaged for six subjects in the present study, and this is comparable with195 ms from the interception task in the study by van Donkelaar et al. (1992). On the other hand, the dual-strategy model provided a mean threshold distance of 2.05 cm, substantially larger than the 0.53 cm distance reported in the study of van Donkelaar et al. (1992).

Reactive or predictive strategy?

The results of the present study suggest that the choice between reactive and predictive strategies in deciding when to initiate an interceptive movement depends on several factors, such as target velocity and individual differences. The experimental paradigm is also likely to play an important role. If the experiments are performed with more emphasis on the speed of the response rather than its accuracy, it is likely that subjects are biased toward adopting the reactive strategy. In this case, implementing a predictive strategy might be too time consuming since it would require an estimation of target displacement and velocity. On the other hand, if the experiments are designed to put more emphasis on the temporal accuracy of target interception, this might bias the subjects toward the predictive strategy. In the present experiments, there were relatively strict requirements for spatial and temporal accuracy in target interception, whereas there were no explicit instructions regarding the time to initiate a movement. Therefore, it might be expected that the subjects would perform the task using the predictive strategy exclusively. However, our results showed that only some subjects performed the task with both the reactive and predictive strategies and others relied entirely on the reactive strategy. These results may be related to the fact that, in the present experiments, a wide range of acceleration and initial target velocities were employed and presented randomly. The relatively long target motion times used in the present study (i.e., 2.0 s) were probably sufficient for any subject to initiate the movement according to the predictive strategy if it had been presented in isolation. On the other hand, the shortest target motion time (0.5 s) does not leave much time for the subject to estimate target velocity accurately before movement initiation. Therefore, adoption of the predictive strategy even for relatively long target motion times would depend on whether the subject is able to obtain enough information about the target velocity needed to decide between the two alternative strategies within the short response times required for the shortest target motion times.

Acknowledgements This research was supported by USPHS grant 1-PSMH48185-01, the Department of Veterans Affairs, and the American Legion Chair in Brain Sciences. We wish to thank David N. Lee for help in the experimental design and helpful discussions.

References

Babler TG, Dannemiller JL (1993) Role of image acceleration in judging landing of free falling projectiles. J Exp Psychol Hum Percept Perform 19:15–31

Carl JR, Gellman RS (1987) Human smooth pursuit: stimulus dependent responses. J Neurophysiol 57:1446–1463

Collewijn H (1972) Latency and gain of the rabbit's optokinetic reactions to small movements. Brain Res 36:59–70

Donkelaar P van, Lee RG, Gellman RS (1992) Control strategies in directing the hand to moving targets. Exp Brain Res 91: 151–161

Gellman RS, Carl JR (1991) Motion processing for saccadic eye movements in humans. Exp Brain Res 84:660–667

Georgopoulos AP, Kalaska JF, Massey JT (1981) Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty, and change in target location. J Neurophysiol 46:725–743

Gottsdanker RM (1952) The accuracy of prediction motion. J Exp Psychol 43:26–36

Gottsdanker RM (1956) The ability of human operators to detect acceleration of target motion. Psychol Bull 52:155–160

Gottsdanker RM, Edwards RV (1957) The prediction of collision. Am J Psychol 70:110–113

Gottsdanker RM, Frick JW, Lockard RB (1961) Identifying the acceleration of visual targets. Br J Psychol 52:31–42

Hofsten C von (1979) Development of visually directed reaching: the approach phase. J Hum Mov Studies 5:160–178

Hofsten C von (1980) Predictive reaching for moving objects by human infants. J Exp Child Psychol 30:369–382

Hofsten C von (1982) Eye-hand coordination in the newborn. Dev Psychol 18:450–461

Hofsten C von (1983) Catching skills in infancy. J Exp Psychol Hum Percept Perform 9:75–85

Lacquaniti F, Maioli C (1989a) The role of preparation in tuning anticipatory and reflex responses during catching. J Neurosci 9:134–148

Lacquaniti F, Maioli C (1989b) Adaptation to suppression of visual information during catching. J Neurosci 9:149–159

Lee D, Port NL, Georgopoulos AP (1997) Manual interception of moving targets. II. On-line control of overlapping submovements. Exp Brain Res 116:421–433

Lee DN (1976) A theory of visual control of braking based on the information about time-to-contact. Perception 5:437–459

Lee DN, Reddish PE (1981) Plummeting gannets: a paradigm of ecological optics. Nature 293:293–294

Lee DN, Young DS (1986) Gearing action to the environment. In: Heuer H, Fromm C (eds) Generation and modulation of action patterns. Springer, Berlin Heidelberg New York, pp 217–230

Lisberger SG, O'Keefe LP, Kahlon HW, Mahncke HW, Movshon JA (1995) Temporal dynamics in response of macaque MT cells during target acceleration. Soc Neurosci Abstr 25:664

Maunsell JH, Newsome WT (1987) Visual processing in monkey extrastriate cortex. Annu Rev Neurosci 10:363–401

Movshon JA, Lisberger SG, Krauzlis RJ (1990) Visual cortical signals supporting smooth pursuit eye movements. Cold Spring Harb Symp Quant Biol 55:707–716

Port N, Dassonville P, Lee DN, Georgopoulos AP (1992) Scaling of arm movements to moving targets. Soc Neurosci Abstr 19: 551

Schmerler J (1976) The visual perception of accelerated motion. Perception 5:167–185

Smeets JBJ, Brenner E (1994) The difference between the perception of absolute and relative motion: a reaction time study. Vision Res 34:191–195

Smeets, JBJ, Brenner E (1995) Perception and action are based on the same visual information: distinction between position and velocity. J Exp Psychol Hum Percept Perform 21:19–31

Snedecor GW, Cochran WG (1989) Statistical methods, 8th edn. The Iowa State University Press, Ames, Iowa

Zaal FTJM, Bootsma RJ (1995) The topology of limb deceleration in prehension tasks. J Mot Behav 27:193–207