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RESEARCH ARTICLE

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Intercepting real and path-guided apparent motion targets

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Abstract Human subjects were instructed to intercept with a cursor real and apparent motion targets presented on a computer screen. Targets traveled counterclockwise (CCW) in a circle at one of five angular velocities (180, 300, 420, 480 and 540 deg/s), either smoothly (real motion) or in path-guided apparent motion. Subjects operated a computer mouse and were instructed to intercept targets at the 12 o'clock position; there were no constraints on when to initiate the response, which was a movement from the center of the screen towards and past 12 o'clock. We found the following: (a) for both motion conditions and all target velocities, subjects were late in intercepting the target, especially at higher target velocities; (b) for both motion conditions, the directional variability of the response increased as a linear function of the target velocity; (c) the directional variability of the response was systematically higher for the apparent than the real motion condition; there was no significant interaction between target velocity and target motion type; (d) the response time did not vary significantly with velocity, but was consistently longer for apparent than real motion targets; (e) the movement time was very similar for different target velocities; and (f) the moment of initiation of the interception movement was delayed appreciably at higher target velocities, relative to that dictated for perfect interception at a given target velocity. This delay was greater for the apparent motion target. These results demonstrated the following: (a) for both target motion conditions, interception was not fully predictive but lagged the target in spite of the constant target velocity and the unconstrained time allowed for initiating the interception movement; (b) subjects can intercept an apparent motion target but, compared with real motion, the performance is somewhat degraded overall; (c) the similarities in performance between the two target motion conditions, and the fact that target velocity influenced performance in a similar fashion, suggest that the motor system can access the visual information provided by the moving target; and (d) since movement time was similar for different target velocities, the strategy for interception relied on controlling the moment of initiation of the interception movement. This was successful for low target velocities but became unsuccessful at higher target velocities.

Key words Target interception · Apparent motion · Coincidence timing

Introduction

Apparent motion is a well-known perceptual phenomenon in which visual objects appear to be moving when physically they are a series of still frames. Most people experience this phenomenon, for example when viewing motion pictures and television. The original studies of apparent motion concentrated on two-dimensional linear motion (Exner 1875; Wertheimer 1912; Korte 1915). Much later, apparent motion studies progressed to two-dimensional curved trajectories (Shepard and Zare 1983), and biologically constrained three-dimensional curved trajectories (Shiffrar and Freyd 1990; Hecht and Proffitt 1991).

Exner (1875), followed by Wertheimer (1912), examined systematically the apparent motion effect. They studied the perception of linear motion produced when two small, spatially separated visual stimuli are flashed one after another with a given inter-stimulus interval (ISI). Korte (1915) showed that an increase in the ISI re-

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quires an increase in the spatial separation of the stimuli in order to preserve apparent motion. This relation was later shown to be a linear function (Corbin 1942; Shepard and Zare 1983).

Shepard and Zare (1983) found that if a low-contrast curved path was shown during the ISI between the location of two stimuli, the subject perceived the stimulus to follow the curved path rather than the shorter linear path. Furthermore they showed that the minimum ISI required to produce a smooth percept was no longer a linear function of the direct linear distance between the two targets, but rather a linear function of the length of the curved path. This phenomenon, called path-guided apparent motion, was used in the present study.

Apparent motion not only follows simple visual suggestions such as a faint path, but also follows biological constraints, for example the path of limb movements (Shiffrar and Freyd 1990). In such experiments, if the ISI is too short, biologically implausible linear motion can be perceived along the shortest path. However, if the ISI and spatial separation are within a given range, smooth three-dimensional, biologically plausible motion is perceived and not simply the shortest physical path. This finding indicates that the visual motion system takes into account prior knowledge of the physical and biological world when perceiving apparent motion. These results suggest that the perception of apparent motion involves higher-order cognitive functions.

Studies of hand movements intercepting moving visual targets have focused on the visual information extracted from the stimulus in order to perform the task successfully (Sharp and Whiting 1974; van Donkelaar et al. 1992; Tresilian 1994). Other studies have shown that human subjects can pursue with the eyes a motion percept that can be very different from the actual visual stimulus (Steinbach 1976). In this study we investigated the capacities of the human motor system to intercept real and path-guided apparent motion targets traveling in a circle. Preliminary results have been reported (Port et al. 1992).

Materials and methods

Subjects

Eight healthy human subjects (two women and six men, age range 23–36 years) from the University of Minnesota academic environment participated in the experiment as volunteers. They were naive about both the task and the purpose of the experiment. The experimental protocol was approved by the Institutional Review Board.

Apparatus

The experiment was conducted on a Silicon Graphics workstation (IRIS 4D/210 VGX). Subjects sat confortably, 57 cm away from a color 21-inch Mitsubishi monitor (HL6915SATK), and intercepted targets using a computer mouse that controlled a visible feedback cursor. The hand-held optical mouse and mouse pad were positioned horizontally in the subject's midsagittal plane. The computer monitor operated at 60 Hz. The mouse output was sampled at 60 Hz with a system clock precision of 10 ms.

Stimulus production

Real target motion

In this condition, the target (0.5 cm diameter) traveled in a circle 5 cm diameter subtending approximately a 5 deg visual angle. Targets traveled in one of five angular velocities: 180, 300, 420, 480 and 540 deg/s. Since stimuli were presented on the monitor at intervals of 16.7 ms, technically they were discrete stimuli as were the apparent motion targets. However, the time interval of 16.7 ms was shorter than human visual persistence. Furthermore, the distance that the real motion target moved every 16.7 ms was less than 4 mm for the fastest velocity. This is less than the diameter of the target, and therefore each successive target overlapped the previously displayed one. Thus these spatial-temporal values resulted in a discrete real motion target which was indistinguishable from a continuously moving target.

Apparent target motion

In this condition, the computer drew the same target but it was masked out of view in all but four locations, where it was displayed for two successive 16.7 ms frames. This produced very

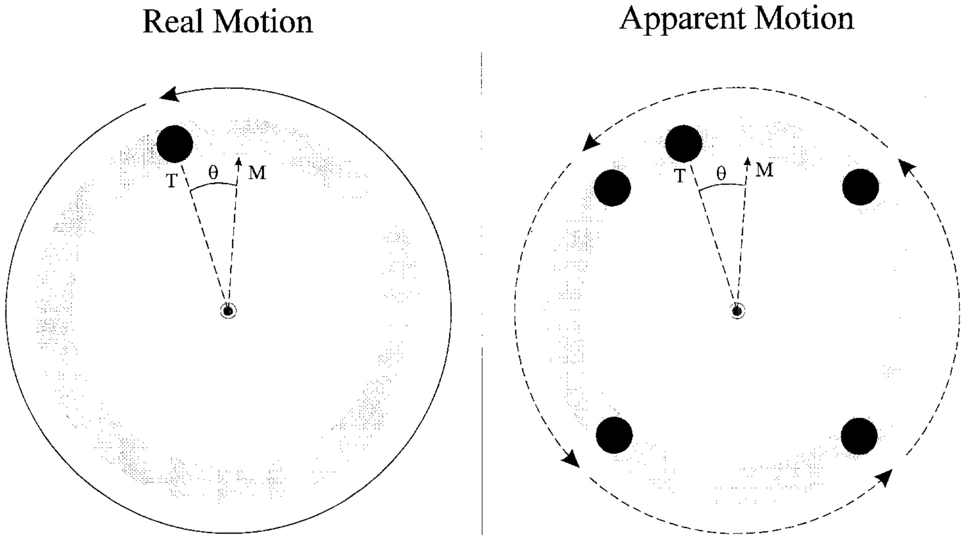


Fig. 1 Diagram of the task (see text). Subjects were instructed to intercept the moving target at 12 o'clock; the direction of one interception movement is also shown (*M*) together with the position of the target (*T*) when the interception movement crossed the target path (*gray annulus*). Angle θ is the angle between *M* and *T*

similar target velocities for both motion conditions. The four locations were equally spaced around the circle, one in each quadrant. The arc-length between any two successive locations was fixed at 3.9 cm. For each apparent motion trial the locations were randomized, and there was no combination with the target at 12 o'clock (±5 deg). Thus there were no trials in this condition in which the location of the target was in the interception zone. To produce a more convincing circular movement, the target traveled along a complete faint low-contrast circle during both conditions (Fig. 1). The ISIs for the apparent motion target were 500, 300, 214, 188 and 167 ms for the slowest to the fastest velocities respectively. These values were chosen so that a reasonably smooth motion would be perceived (Kolers 1972), at least at higher target velocities. All stimuli traveled counterclockwise (CCW) and began moving from the 3 o'clock position.

Behavioral task

Subjects were instructed to intercept the moving target at 12 o'clock (Fig. 1) using a hand-held optical mouse the position of which was displayed as a cursor (0.18 cm diameter) on the screen. At the beginning of the trial subjects placed the feedback cursor at the center of the display, within a circular positional window of 0.6 cm diameter. They were instructed to initiate their movement when they were ready to intercept. Interception movements were made from the center of the circle to the target as it crossed the 12 o'clock position. Although in the apparent motion condition the target crossed the 12 o'clock position only in a perceptual rather than a physical sense, subjects were similarly instructed to intercept the moving target at that position and move through the path of target motion without stopping at the target. After an interception, the screen was frozen and the true position of the target and feedback cursor at interception were shown. Thus in the apparent motion condition, the true position of the target at interception was shown at the end of the trial, although it was only visible at four locations during the trial. In addition, the difference in degrees between the target and feedback cursor was displayed on the screen after each trial.

Experimental design

Each block of ten trials consisted of the two target motion types at five velocities. Trials were randomized within each block, and blocks were repeated 10 times (giving a total of 100 trials per subject). Three practice blocks immediately preceded the 10 recorded blocks.

Data analysis

General. Standard statistical analyses (Snedecor and Cochran 1989; Winer 1971) were used to analyze the data, including repeated measures analysis of variance (ANOVA); the 5% probability level of the F-test (two-tailed) was taken as the level of statistical significance for rejecting the null hypothesis.

In certain cases post-hoc t-tests were performed to test the statistical significance of pairwise comparisons between the two conditions at each of the five target velocities. Since five simultaneous comparisons were performed in these cases, the nominal probability level of $\alpha=0.05$ was adjusted according to the Bonferroni inequality (Snedecor and Cochran 1989) to $\alpha'=0.05/5\approx0.01$, so that $P<0.01$ was considered statistically significant.

Constant error in direction

The primary measure of performance was the error in direction, defined as the signed angle, θ, between the direction of the target and the direction of the feedback cursor relative to the starting position, when the cursor crossed the path of the target (Fig. 1); a positive sign indicated that the target was CCW relative to the feedback cursor at the interception point. Thus a positive angle indicated that the feedback cursor crossed the circle after the target had passed that position, and that, therefore, the interception was late; conversely a negative angle indicated that the interception was early.

Variable error in direction

This was defined as the standard deviation of angle θ above. The variable error was calculated for each subject-velocity combination using the 10 repetitions available for each such combination. Since the repetitions were used for these calculations, the ANOVA for the variable error was performed using the subjects, motion type and target velocity as factors, without repetitions.

Timing error in interception

This was defined as the time difference between the moment at which the cursor intercepted the circular target path and the moment that the moving target had passed (or was to pass) from that point. This measure is the time equivalent of the constant error:

$$\text{Timing error} = \theta/\text{Target velocity} \qquad (1)$$

A positive temporal error means that the cursor arrived at the interception after the target had passed through it, and vice versa for a negative value.

Response time

The response time was the period of time that elapsed from the onset of target motion until the subject moved the feedback cursor out of the center window (see above).

Target motion during the response time

Since there were no constraints as to when the subject initiated the interception movement, it was considered interesting to know how many cycles of target motion passed before that moment. For that purpose the number of target cycles during the response time was calculated as follows:

$$\text{Number of target cycles} = [\text{Response time}\times\text{Target velocity}]/360 \qquad (2)$$

Movement time

The movement time was the time elapsed from the exit of the feedback cursor from the center window until it reached the interception point on the circle.

Actual and ideal target angles at movement initiation (Fig. 2)

Two target angles were calculated. One, ϕ, was between the direction of the interception point (at 12 o'clock) and the direction of the target at the movement of initiation of the interception movement (actual angle). The other angle, δ, was between the interception point and the direction at which the target should have been at the moment of the initiation of the movement, if this movement were to intercept the moving target accurately (ideal angle). Given a particular movement time and a particular target velocity, these two angles provide different information concerning the moment of initiation of the interception movement.

Missing data

Altogether, 800 values (8 subjects×5 velocities×2 motion conditions×10 repetitions) were available for each of the variables ana-

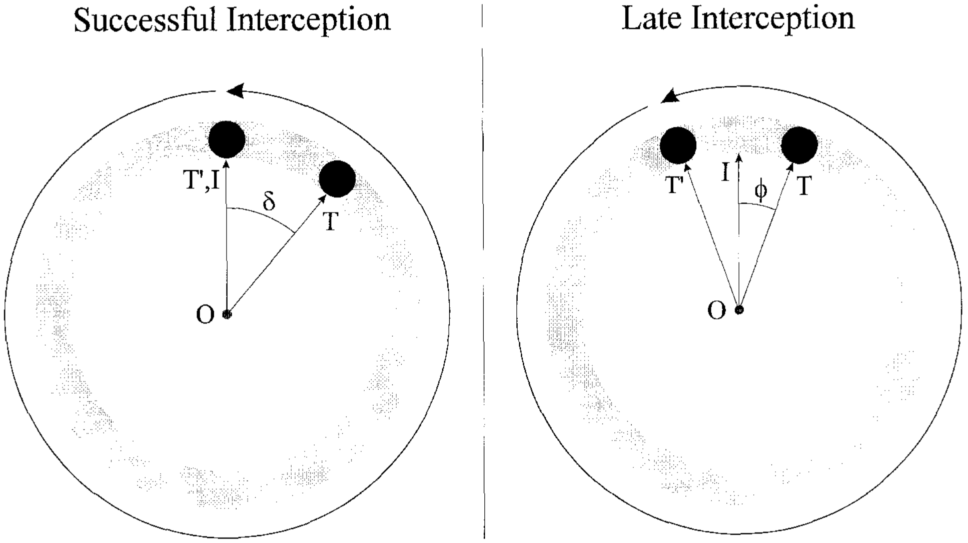


Fig. 2 Ideal (δ) and actual (ϕ) angles (see text) between target position (*T*) at movement onset and the 12 o'clock interception point (*I*) for successful and late interception. In successful interception, the target *T'* is at the same position as *I*. In late interception, *T'* is past *I*

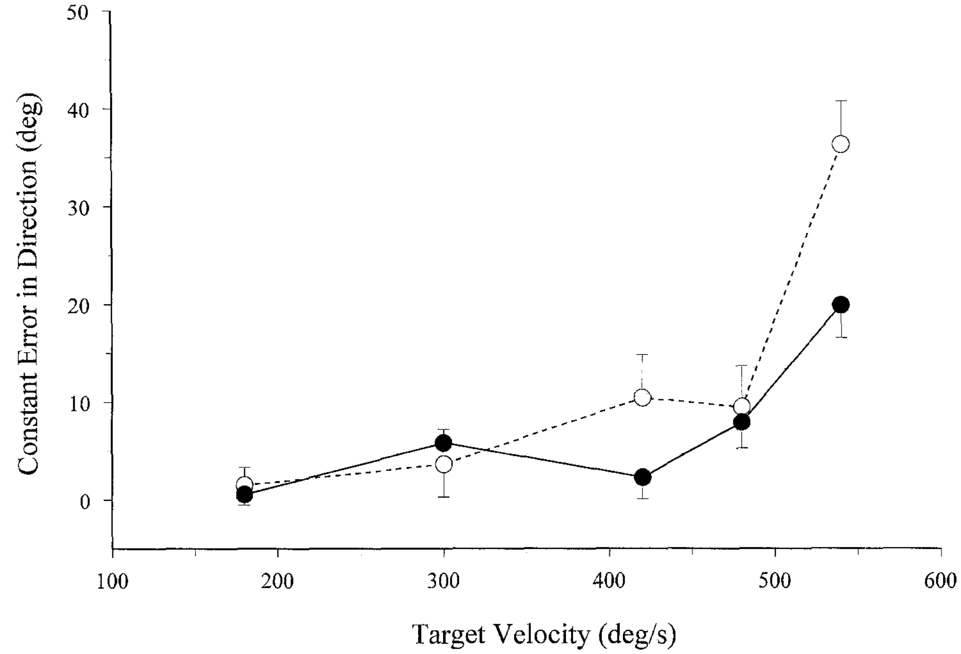


Fig. 3 Constant error in direction plotted against target velocity. *Continuous line* and *filled circles* are for the real motion condition. *Dashed line* and *open circles* are for the apparent motion condition. *Vertical bars* represent the standard error of the mean (SEM). (Only one side of the SEM is shown to avoid overlap between conditions.) For real motion, *n*=77, 78, 79, 80, 80 trials for the five target velocities (from slowest to fastest); for the apparent motion condition, *n*=80, 79, 78, 77, 76 trials

lyzed. Of these values, 16 could not be used due to errors in data collection. To perform the repeated measures ANOVA, these missing values were estimated as follows. By design, 10 repetitions were presented for each velocity×motion type combination. When a value was missing, fewer than 10 numbers were available for that combination; the missing number was given a value selected randomly from a normal distribution with the mean and variance of this sample.

Results

Constant error in direction (Fig. 3)

Constant errors tended to be positive, which means that subjects were late in intercepting the target; this was true for all target velocities and both target motion conditions. The ANOVA showed that the main effect of velocity was statistically significant ($P<0.00005$), but not the motion type effect or the velocity×motion type interaction. The constant error increased slightly with target velocity for the first four velocities and then rose sharply at the highest velocity, especially in the apparent motion condition. This last difference was statistically significant (t-test, $P<0.005$).

Timing error in interception (Fig. 4)

Timing errors were similar in both target motion conditions and all velocities except for the highest velocity, in which this error increased substantially, especially in the apparent motion condition. In the ANOVA, only the target velocity effect was statistically significant ($P=0.002$).

Fig. 4 Constant timing error in interception plotted against target velocity. Conventions are as in Fig. 3. (Only one side of the SEM is shown to avoid overlap between conditions)

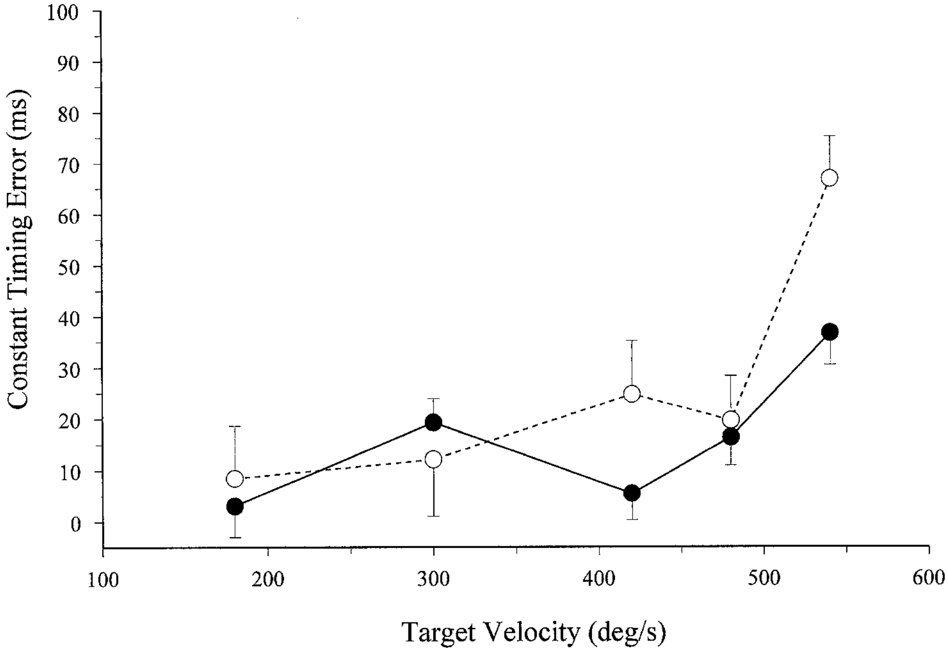
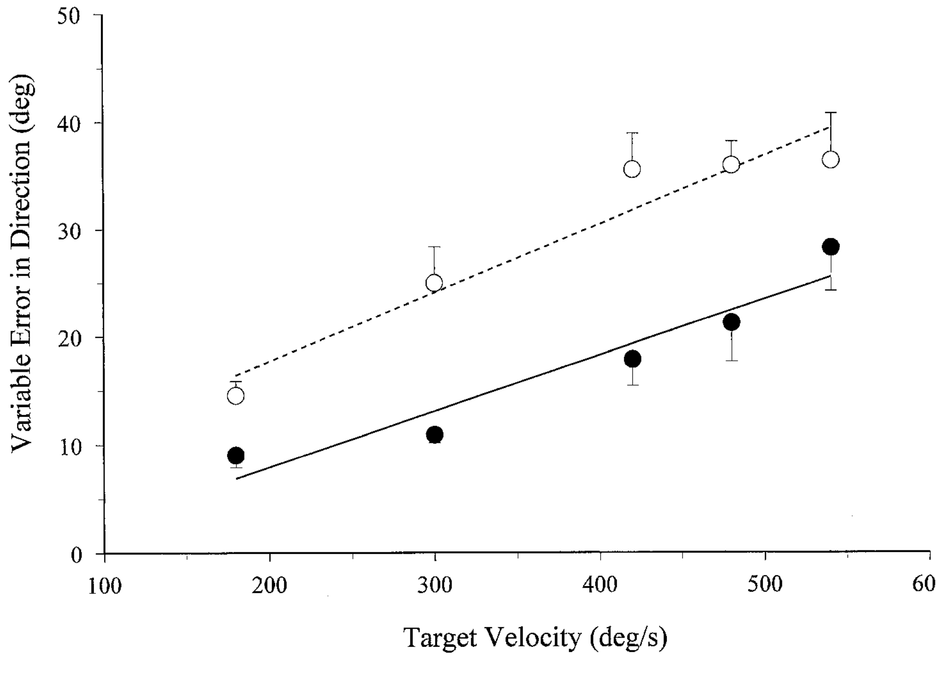


Fig. 5 Variable error in direction plotted against target velocity. Conventions are as in Fig. 3. n=8 subjects per point plotted. (Only one side of the SEM is shown to avoid overlap between conditions)



Variable error in direction (Fig. 5)

The variable error increased as a linear function of target velocity for both target motion conditions, and was systematically higher for the apparent motion condition. The ANOVA showed that the main effects of velocity and motion type were statistically significant ($P<0.00005$ for both cases) but not the velocity×motion type interaction.

Orthogonal polynomial contrasts indicated that the increase in the variable error with target velocity was linear (t-test, $P<0.00005$). The following linear regression equations were obtained:

Real target motion:

$$\text{Variable error} = -2.49+0.052 \text{ target velocity} \quad (r^2=0.92) \tag{3}$$

Apparent target motion:

$$\text{Variable error} = 4.89+0.064 \text{ target velocity} \quad (r^2=0.92) \tag{4}$$

Response time

Subjects took several seconds before initiating the response (data not shown). It should be noted that subjects were not instructed on, nor were there any constraints on their response times. The average response time for apparent motion targets was 1.8 s longer than the response

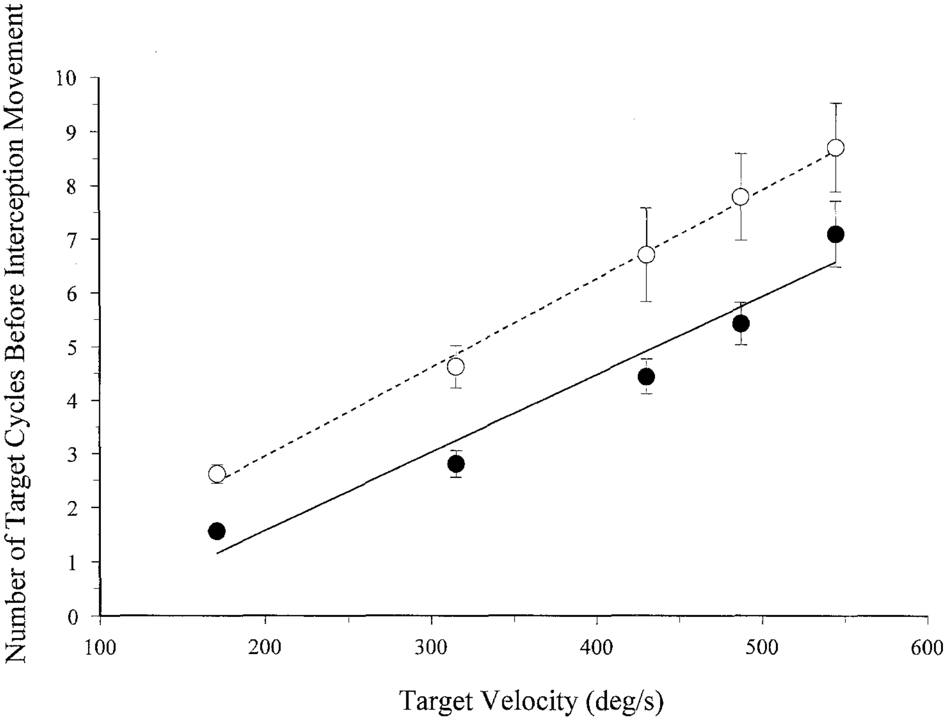


Fig. 6 Average number of target cycles before the interception movement plotted against target velocity. Conventions are as in Fig. 3

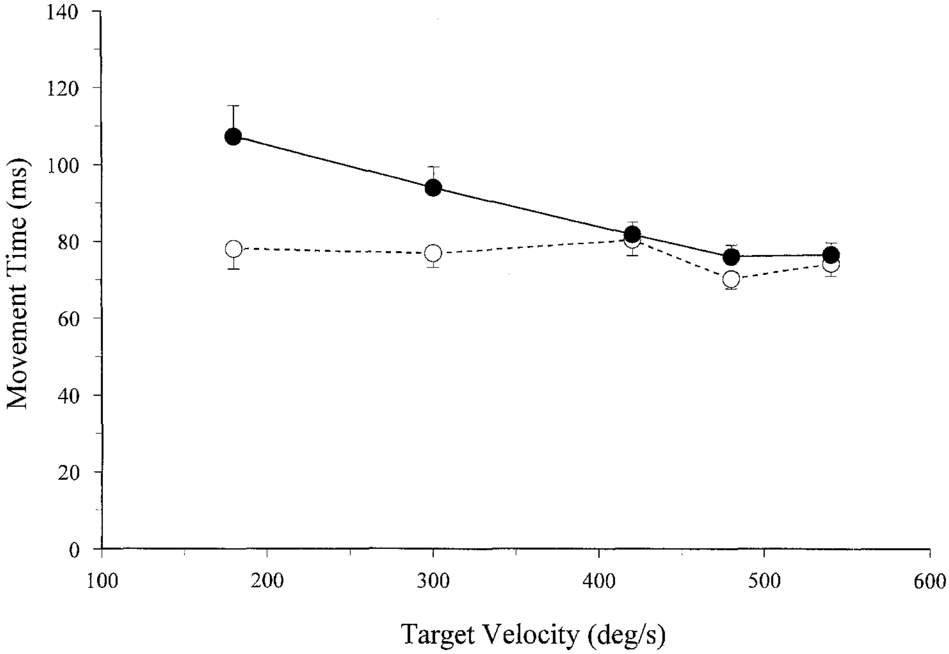


Fig. 7 Average movement time plotted against target velocity. Conventions are as in Fig. 3. (Only one side of the SEM is shown to avoid overlap between conditions)

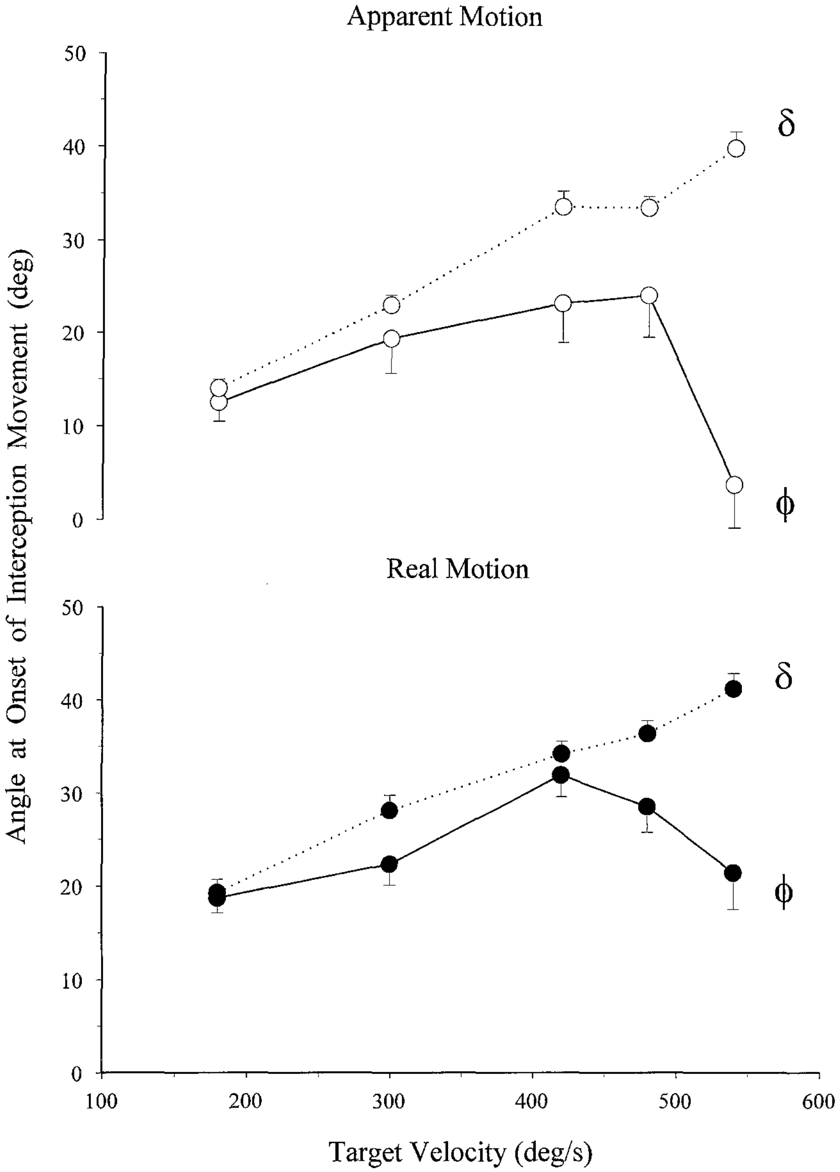
time for real motion targets (5.6 vs 3.8 s for apparent and real motion targets, respectively). The ANOVA showed that the main effect of motion type was statistically significant (P<0.00005), but not the target velocity effect or the velocity×motion type interaction.

Target motion during the response time (Fig. 6)

The information above conveyed by the response time can be translated into the number of cycles traveled by the target during that time. This number increased with stimulus velocity and was overall higher in the apparent motion condition (5.66 vs 3.95 cycles in the apparent and real motion conditions, respectively). The ANOVA showed highly significant effects of motion type (P<0.00005) and target velocity (P<0.00005) but the velocity×motion type interaction was not significant.

The number of cycles traveled by the target increased as a linear function of the target velocity. The following regression equations were obtained:

Fig. 8 Average ideal (δ) and actual (ϕ) angles (see Fig. 2) plotted against target velocity. (Only one side of the SEM is shown to avoid overlap between conditions)



Real target motion:
Cycles = −1.28+0.0142 target velocity (r^2=0.95) (5)

Apparent target motion:
Cycles = −0.36+0.0165 target velocity (r^2=0.99) (6)

Movement time (Fig. 7)

Subjects made rapid movements by which they attempted to intercept the moving target without stopping. The movement time was overall longer in the real motion condition, in which it decreased with target velocity. The ANOVA showed that the main effect of velocity was statistically significant (P=0.0005), as well as those of motion type (P=0.0002) and velocity×motion type interaction (P=0.0198). Only the difference between the two conditions at the lowest target velocity was statistically significant (t-test, P<0.005).

Actual and ideal target angles at movement initiation (Fig. 8)

The ideal target angle, δ, at movement initiation increased as a linear function of the target velocity for both target motion conditions. The actual target angle, ϕ, decreased sharply at higher target velocities. This decrease in ϕ, relative to δ, was statistically significant at the highest target velocity for both apparent (t-test, P<0.001) and real target motion conditions (t-test, P<0.001).

Discussion

The goal of these experiments was to assess the ability of human subjects to intercept moving targets under real and apparent motion conditions, and thus to identify similarities and differences in motor performance when the information to the motor system comes from real target motion or from perceptually reconstructed motion of a sequence of stationary targets. There were four major findings of our study: (a) subjects performed similarly in these two conditions in that they were consistently late in intercepting real and apparent motion targets with a similar magnitude of average constant error; (b) motor performance was more variable when intercepting apparent than real motion targets at all target velocities; (c) response times were appreciably longer when intercepting apparent than real motion targets at all target velocities; and (d) the timing of initiation of the intercepting movement was delayed at higher target velocities, relative to that dictated for perfect interception at a given target velocity.

Behavioral task

The task was designed in a way that facilitated the performance of the subjects by reducing several constraints. Firstly, the spatial trajectory of the interception movement was always the same, so that there was no uncertainty in selecting a movement. In addition, the movement did not have to stop at the target but just intercept its path. Therefore, the emphasis was on the temporal aspects of the movement, namely the moment of its initiation and its velocity. Secondly, ample time was allowed for the subjects to initiate the interception movement, since there were no temporal constraints on the response time. Finally, knowledge of results was provided at the end of every trial. Therefore, the results obtained reflect best performance under optimal conditions.

Constant error in direction

The average interception errors were small (within 10 deg, with the possible highest value of 180 deg; Fig. 3) and very similar in the two motion type conditions for the first four target velocities, up to 480 deg/s; however, they rose sharply at the highest velocity of 540 deg/s, especially in the apparent motion condition. These findings indicate that the arm motor system has similar and good access to information provided by real and apparent motion targets, except at the highest velocity tested.

Timing of interception

Subjects were consistently late in intercepting real and apparent motion targets, especially at higher target velocities. However, even for the low velocities the interception was late on the average (Fig. 4). The similarity of performance under both target motion conditions indicates that the arm motor system has similar access to information regarding real and apparent moving targets.

The late interception is somewhat surprising, especially for real motion targets, since there were no constraints in taking time to prepare for the interception movement and since targets moved at constant velocity. In tracking tasks, subjects can track a moving visual stimulus with zero lag, which suggests a successful, predictive motor control strategy (Poulton 1981). However, it seems that such a predictive model, although successful for tracking, is not effective for intercepting a moving target. There are major differences between these two task conditions, the most important one being that in the tracking task there is a continuous tracking error available to the subject which can be used for adjusting the tracking velocity so as to minimize that error; such a signal was only intermittently available in the interception task, at the end of the trial, and that information was apparently not sufficient to produce an accurate, predictive performance in subsequent trials.

Variable error in direction

The variable error provided an excellent measure that differentiated the two target motion conditions as well as the velocity of target motion: it was consistently higher in the apparent motion condition and increased linearly with target velocity (Fig. 4). Increase in variability can be interpreted as decrease in information (Fisher 1925); therefore, these findings indicate that information decreased, and, therefore, the interception performance was degraded, under conditions of apparent and higher target velocity. The effect of the apparent motion condition is not surprising, for the information provided by the target was, by definition, less in this than in the real motion condition. The loss of information with increasing target velocity is less obvious to explain, but it is in accord with better tracking performance at low than high target velocities in tracking tasks (Poulton 1981). However, what is important is the lack of interaction between the motion type and target velocity conditions. Although the slope in the apparent motion condition was 1.3× that of the real motion condition (see Results), the interaction between target motion type and velocity did not reach statistical significance. This finding indicates that the sources causing degradation of performance are independent and additive with respect to motion type and target velocity.

Response time and target motion during the response time

Subjects were instructed to initiate the interception movement when they were ready, and, indeed, they began moving several seconds after the target motion started. An obvious explanation for this waiting is that they thus acquired sufficient information concerning target motion to initiate the interception movement at the appropriate time and with the required velocity. One aspect of target motion possibly used was the total path traveled by the target during the response time. Interestingly, this measure provided an excellent predictor of the motion type as well as the target velocity (Fig. 6): it was consistently higher in the apparent motion condition and increased linearly with target speed. Although the slope in the apparent motion condition was 1.17× that in the real motion condition (see Results), the interaction term was not statistically significant, which suggests that the two slopes did not differ significantly.

It is important to note that even with this increased sampling time of the target motion, the interception performance was still degraded in the apparent motion condition and with increasing target velocities, as shown by the increase of the variable error in direction (Fig. 5; see preceding section). These findings imply (a) that performance would have been much worse under the conditions above *if the response time allowed had been fixed* at some low value, and (b) that even these longer times of sampling target motion were not sufficient to offset the loss of information. In fact, the increase in the response time can be conceptualized as yielding a gain of information, in an attempt to counteract the loss of information resulting from perceptual (i.e., stimulus coding) and perceptual-motor (i.e., using the stimulus information to generate a movement) processes. These results indicate that this attempt is only partially successful and that, overall, information is lost.

Movement time and initiation of the interception movement

The movement time did not vary as a function of target velocity for apparent motion targets and it was similar for apparent and real motion targets at the highest velocity. By keeping the movement time almost constant, the subjects reduced the complexity of the task to that of initiating the intercepting movement at the right moment. This strategy was also observed in other interception tasks (Schmidt 1969; Tyldesley and Whiting 1975). This indicates that for these velocities the control strategy for interception relied on the timing of initiation of the interception movement. In fact, this summarizes the control problem of the task; namely, given a particular target angular velocity, *when* to start and *how fast* to make the interception movement. Since we know the movement time and the target velocity, we can compute the timing of the initiation of the interception movement. There are two aspects of this analysis. First, we can find out the target position at which the movement *should have been initiated* for successful interception (Fig. 2, left panel). The average δ is plotted in Fig. 8 (dotted curves); as expected from the different target velocities, δ increases with target velocity. The second aspect of this analysis regards the target angle ϕ at which the interception movement was *actually* initiated. Since the target was consistently intercepted late, $\phi < \delta$. Figure 8 plots average ϕ against target velocity (continuous curves). Even if ϕ is consistently lower that δ, it becomes sharply lower at higher target velocities. The target velocity (540 deg/s) at which ϕ becomes appreciably smaller than δ indicates that the system has passed its limits of selecting the right moment for initiation of the interception movement dictated by the particular target velocity.

Neural correlates of target interception

Visual target motion is encoded and analyzed in several visual cortical areas, especially in the “dorsal” stream of areas in the visual cortex (Merigan and Maunsell 1993). Cells responding to rotatory target motion have been described in the posterior parietal cortex (Sakata et al. 1986) and the medial superior temporal (MST) area (Saito et al. 1986; Tanaka and Saito 1989; Sakata et al. 1994). However, no studies have been done on the neural coding of path-guided apparent rotatory motion.

A different question concerns the way in which the motor system gains access to information from the moving target for producing the interception movement. Anatomical pathways could involve cortico-cortical connections (Caminiti et al. 1995), subcortical loops through the cerebellum, or both. This problem remains to be investigated.

The results of recent neurophysiological studies of interception of a target moving along a linear path (Port et al. 1994; Kruse et al. 1994, 1995) indicate that the motor cortex is involved with processing the temporal characteristics of the interception movement. Obviously, other brain areas are involved in interception tasks of the kind discussed above and that employed in the present study. These areas are likely to include the visual cortical areas involved in analyzing target motion as well as associated subcortical visuomotor structures. The neural mechanisms underlying the various stages involved in target interception as well as the specific contribution of each one of these areas under different task conditions remain to be elucidated.

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