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Interception of real and apparent motion targets: psychophysics in humans and monkeys

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Abstract Human subjects and monkeys intercepted real (RM) and apparent (AM) moving targets that traveled through a low contrast circular path. The subjects intercepted the targets at 6 o'clock by applying a net force pulse on a semi-isometric joystick which controlled a cursor on the screen. Eight target speeds (180–560°/s) were used. The starting points of the moving target were systematically placed around the circle in order to determine the effect of the target travel time and velocity on the decision to initiate the interception movement and on the interception accuracy. It was found that the probability of interception in the first revolution varied as a function of the target travel time, which followed an S-shaped psychometric curve. The minimum processing time (MPT) was defined as the target travel that corresponded to a 75% probability of interception in the first revolution on the psychometric curve. The MPT decreased slightly as a function of target speed and was larger in AM than RM. In addition, the interception accuracy increased when the target travel time was above the MPT, and the angular error was smaller in RM than in AM. Finally, the interception movement was initiated at different target locations and time-to-contacts, depending on the target speed and the motion condition. Interestingly, similar findings were observed in human subjects and monkeys. These results suggest that the neural mechanisms engaged in extracting the visual motion

information and in the implementation of the response are more efficient during RM than AM, and that such mechanisms need less processing time when the target is moving faster.

Keywords Target interception · Apparent motion · Target travel time · Humans subjects · Rhesus monkeys

Introduction

The interception of a moving target is a complex process that requires the analysis of visual motion information including target direction, velocity, position, and travel time (van Donkelaar et al. 1992; Manson and Carnahan 1999; Brouwer et al. 2002). In addition, a predictive strategy is involved to determine where and when the target is going to be at the end of the interception movement (Lee 1976; van Donkelaar et al. 1992; Port et al. 1997). In a previous article (Port et al. 1996) we studied the interception performance of human subjects using path-guided apparent motion targets. We found that the interception accuracy was degraded when compared to interceptions of real motion targets, and that the interception error increased as a function of target speed in both motion conditions. Nevertheless, in this previous work the target travel distance, velocity, and consequently the travel time varied, and a systematic study of the effect of target travel time on the interception performance was not attempted. Thus, in the present study we investigated the effect of the target travel time and velocity on the decision to initiate the interception movement and on the interception accuracy using real and path-guided apparent motion targets in human subjects and monkeys.

Materials and methods

Human subjects

Ten healthy human subjects (five women and five men, age range 24–34 years) participated in the experiments as paid volunteers. All

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subjects gave their informed consent before the commencement of the study. They had normal or corrected vision, and they were naive about the task and the purpose of the experiment. The experiments were approved by the appropriate local ethics committees.

Animals

Two male monkeys (*Macaca mulatta*, 4 and 7 kg body weight) were used. Animal care conformed to the principles outlined in the *Guide for Care and Use of Laboratory Animals* (National Institutes for Health publication number 85–23, revised 1985). The experiments were approved by the appropriate local ethics committees.

Visual display

A computer color monitor (Gateway 2000 model Crystalscan 1024) was used to display the visual stimuli. It was placed 57 cm in front of the subjects and ran at a 60-Hz refresh rate. The moving stimulus was a circle of 0.55 cm in diameter and traveled on a low contrast circular annulus of 5.78 cm outside diameter and 0.55 cm width (Fig. 1A). Eight angular velocities were used in the two conditions below: 180, 240, 300, 360, 420, 480, 540, and 560°/s. All the stimuli traveled CCW.

There were two visual motion conditions, namely a “real” and an “apparent” one (Fig. 1A). In the real motion condition (RM) the target was displayed every 16.7 ms. Although these stimuli were discrete, the interval of 16.7 ms is shorter than human visual persistence and, even at the fastest speed, the successive targets overlapped. This resulted in a smooth target motion, which was indistinguishable from a continuously moving target. In different trials, the stimulus started moving from any of 20 different points, distributed equidistantly on the circular path, every 18° (Fig. 1A).

In the apparent motion condition (AM), five stimuli were flashed successively for 16.7 ms, at the vertices of a regular pentagon. The interstimulus interval (ISI; the period between the onsets of consecutive stimuli) in this condition was 400, 300, 240, 200, 166.6, 150, 133.4, and 116.6 ms for the speed of 180, 240, 300, 360, 420, 480, 540, and 560°/s, respectively. Three different orientations of the pentagon were used. These orientations were such that no vertex was located on or around the interception zone at 6 o'clock ($270 \pm 18^\circ$, see below). The first stimulus was presented at any of the 15 possible visible points used in this condition (i.e., 5 vertices \times 3 orientations; Fig. 1A).

Apparatus and behavioral task

The monkeys were seated in a primate chair and human subjects were seated in a chair with the head restrained. The subjects operated a semi-isometric joystick (Measurement Systems, model 467-G824, Norwalk, Conn., USA) to intercept moving targets. This joystick was a vertical rod placed in front of the subject at midsagittal level and controlled a net force feedback cursor, which was displayed in the monitor as a circle of 0.55 cm in diameter. The x-y force exerted by the subject on the joystick was sampled every 5 ms. The feedback cursor was deflected constantly 1.5 cm to the left to simulate a bias force of 0.62 N and reflected, at any given moment, the net force, i.e., the vector sum of this simulated force and the force exerted by the subject on the joystick. At the beginning of the trial, the subject had to place the force feedback cursor within a gray circle of 1 cm diameter (“center window”) by exerting a force of 0.62 N in the rightward direction and keep it there for a variable delay period of time (1,000–3,000 ms), after which the target began to move. The subjects intercepted the moving target by applying a net force pulse on the joystick (minimum 1.75 N) such that the force feedback cursor intercepted the moving target at 6 o'clock (270°). After the interception, the screen was frozen and the position of the target and the feedback cursor at interception was shown for 200 ms. Monkeys received a liquid reward if the angle between the cursor and the target was less

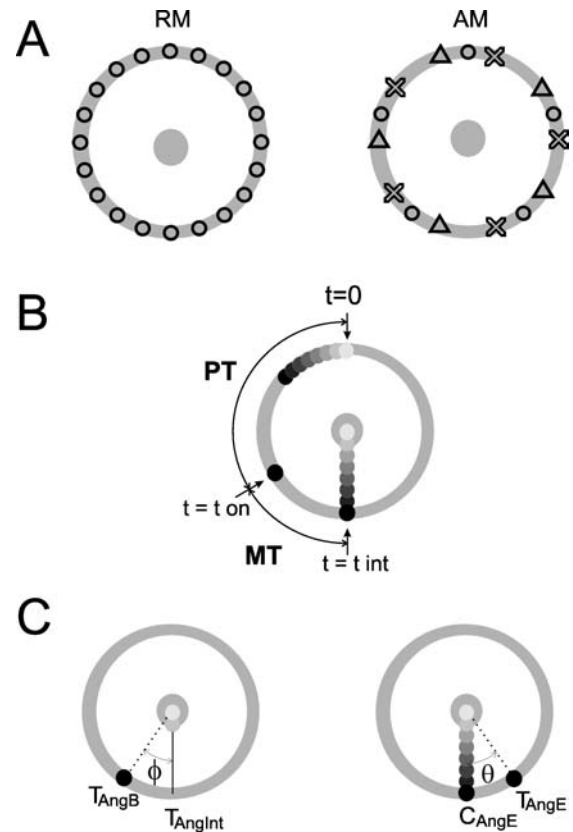


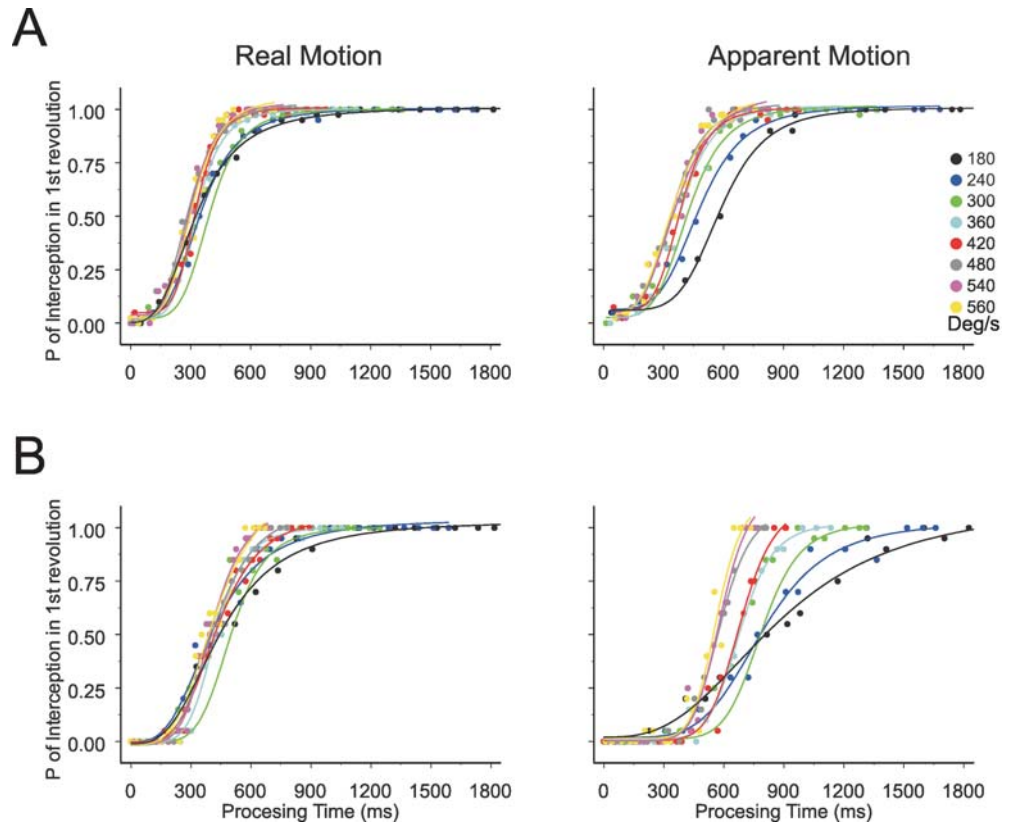
Fig. 1 A Interception task. *Left* Real motion condition (RM), the 20 starting points are illustrated. *Right* Apparent motion condition (AM), the five flashing targets at the vertices of a regular pentagon are depicted with different shapes for the three different orientations used and for a total of 15 starting points. **B** Behavioral times are defined: PT = processing time, from $t = 0$ (stimulus motion onset) to $t = t_{on}$ (movement onset), and MT = movement time, from $t = t_{on}$ to $t = t_{int}$ (end of interception). **C** Definition of angles ϕ and θ ; ϕ corresponds to the angle between the direction of the interception point (270° , TAngInt) and the direction of the target at the beginning of the movement (TAngB), and θ is the angle between the target (TAngE) and the feedback cursor (CAngE), when the cursor crossed middle of the low contrast path

than 18° . Human subjects heard a 1,000-Hz tone if the angle between the cursor and the target was less than 18° , indicating a correct trial, and a 3,000-Hz tone for incorrect trials.

Experimental design

All the possible combinations of target velocities, starting points, and motion conditions were interleaved and presented in a pseudorandom order in a block. Therefore, a block consisted of 160 trials in RM (8 speeds \times 20 starting points) and of 120 trials in AM (8 speeds \times 15 starting points). In the monkey experiments, four blocks were collected every day during the last month of training. We analyzed the last ten blocks collected during this period. Monkey 1 was trained in this task for 5 months and monkey 2 for 4 months before the last ten blocks were collected, and the percent correct trials was $>85\%$ in these blocks. In the human experiments, at least 80 practice trials were allowed, and the practice period was stopped when the subjects were comfortable with their performance. After the practice period, two blocks were recorded in each session. Two sessions were collected in different

Fig. 2A, B Psychometric functions for each target speed (color coded), representing the probability of interception in the first revolution against the processing time, for RM (*left*) and AM (*right*). **A** Psychometric curves of a male human subject. **B** Psychometric curves of monkey 2



days, for a total of four blocks and 1,120 trials for each human subject.

Statistical analyses

General

Standard statistical techniques were used for data analysis including analysis of variance (ANOVA; Snedecor and Cochran 1989). In general, for all the dependent variables we performed the following three ANOVAs. First, an ANOVA for human data where the target speed and motion condition were used as factors. Second, an ANOVA for monkey data where the target speed and motion condition were used as factors. Finally, we carried out an ANOVA comparing the human and monkey data in which the species (humans vs monkeys), target speed and motion condition were defined as factors. The level of statistical significance to reject the null hypothesis was $\alpha=0.05$. The SPSS statistical package (version 10; SPSS, Chicago, Ill., USA 1996) was used for the statistical analyses.

Logistic regression

The travel time of the target necessary for the decision to start the interception movement was defined as the “processing time.” Sigmoidal functions for each target speed were calculated in order to determine the minimum processing time. These curves were plotted as the probability of interception in the first revolution against the processing time (Fig. 2). A logistic regression was calculated for the data of each target velocity, in the form of:

$$y = \frac{(p_1 - p_4)}{1 + \left(\frac{x}{p_3}\right)^{p_2}} + p_4 \quad (1)$$

where p_1 and p_4 correspond to the minimum and maximum values of y , p_2 is the estimated slope, and p_3 correspond to the value of x at half of the maximum value of y . The percentage of variance explained (R^2) was greater than 80%.

Results

The processing time was the interval from the onset of the target motion to the onset of the movement (Fig. 1B). Using the data of different starting points, target speeds, and motion condition, we first computed the probability of interception in the first revolution and the mean processing time during those trials, and then performed a logistic regression for each combination of target speed and motion condition. The results showed that the sigmoidal curves in RM were shifted to the left with respect to AM in both humans (Fig. 2A) and monkeys (Fig. 2B). This indicates that subjects needed more stimulus travel time to initiate the interception during the first revolution in AM than in RM. In order to quantify this effect, we computed the minimum processing time (MPT), defined as the processing time that corresponded to a 75% probability of interception ($P=0.75$) in the first revolution in the logistic regression. An ANOVA was carried out for human subjects and monkeys separately, using MPT as the dependent variable and target speed and motion condition as factors. In human subjects, there was a significant main effect of target speed and motion condition on MPT (F test in ANOVA, $P<0.00001$ for both

Fig. 3 Minimum processing time (MPT) as a function of the target speed (mean \pm SEM). *Left* Human data. *Right* Monkey data. *Left* Human data. *Right* Monkey data. RM is continuous line and filled circles. AM is dashed line and open circles

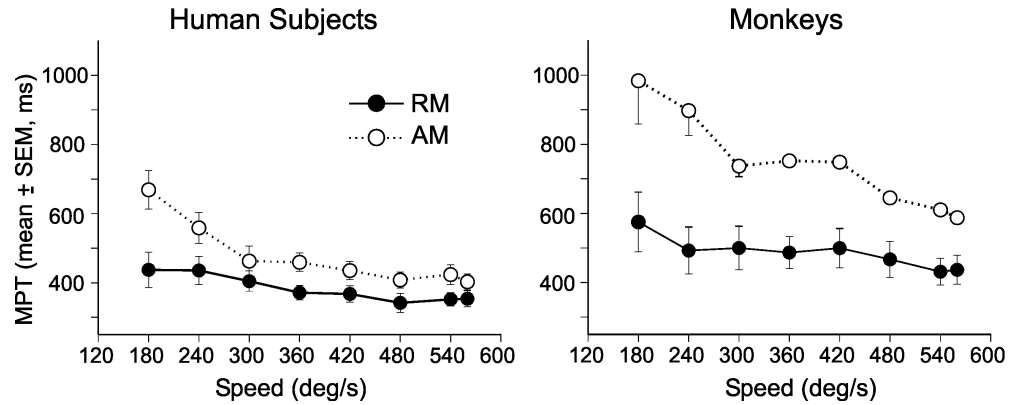
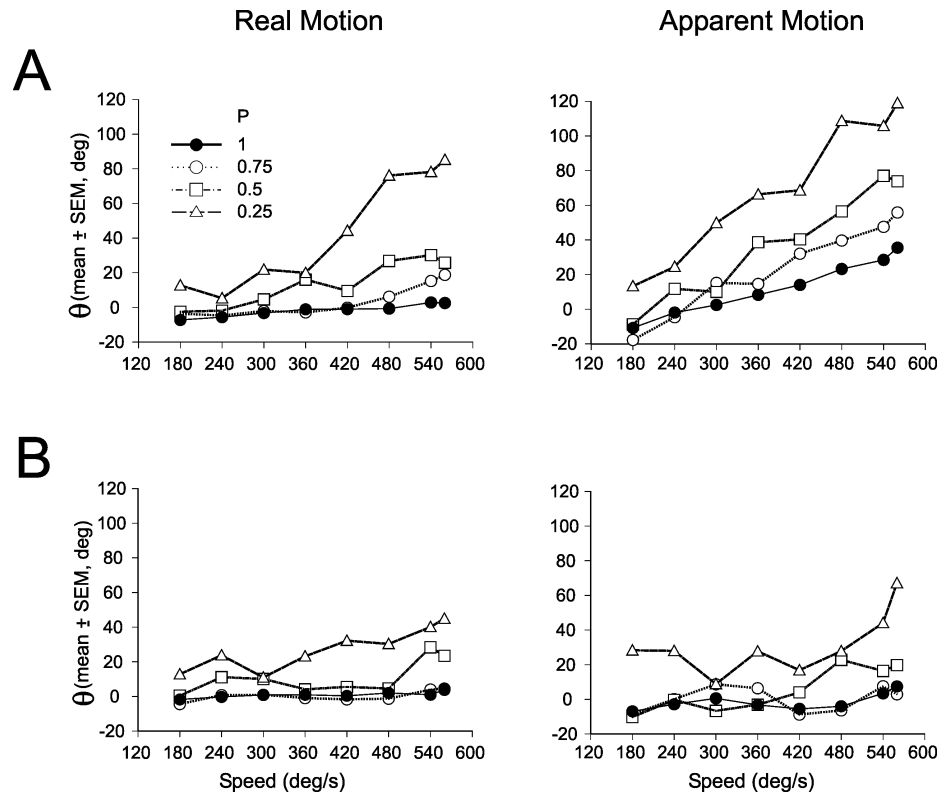


Fig. 4A, B Constant angle error, θ , as a function of the target speed for trials in which the probability of interception in the first revolution was between 0–0.25, 0.25–0.5, 0.5–0.75, and 0.75–1. *Left* RM. *Right* AM. **A** Human subject data. **B** Monkey data

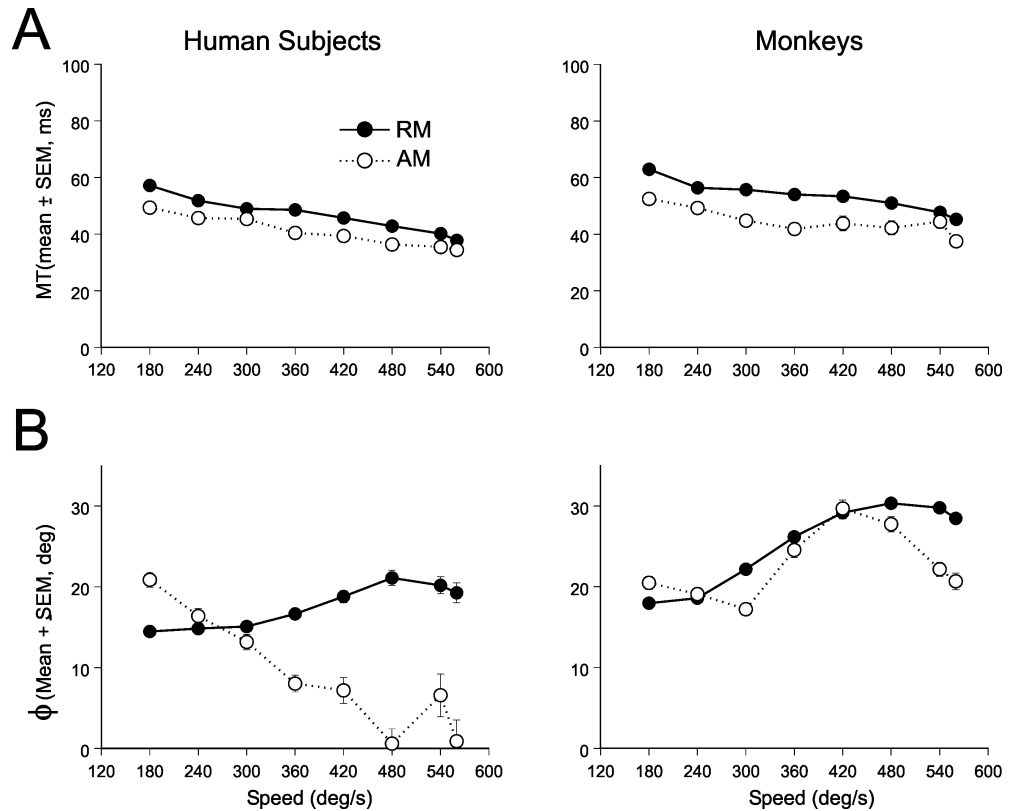


factors). This effect was also observed in monkeys ($P < 0.04$ and $P < 0.002$ for target speed and motion condition, respectively). The target speed \times motion condition interaction was not significant in either species. Furthermore, MPT was significantly longer in monkeys than in human subjects (F test on main effect of species, $P < 0.00001$; Fig. 3). Overall, MPT decreased as a function for the target speed and was larger in AM than in RM in both species (Fig. 3). The MPT in the slowest target speed (180 and 240°/s) of AM was very long in both human subjects and monkeys.

The primary measure of performance was the angular error in direction, defined as the signed angle, θ , between the target and the feedback cursor when the cursor crossed the middle of the low contrast path (Fig. 1C *right*). We

investigated how θ varied for different combinations of target speed and motion condition, and we determined the effect of the probability of interception in the first revolution on the interception accuracy. Figure 4 shows θ as a function of target speed for trials in which the probability of interception in the first revolution was between the following intervals: 0–0.25, 0.25–0.5, 0.5–0.75, and 0.75–1. An ANOVA was performed for human subjects and monkeys separately, using θ as the dependent variable and the probability intervals, target speed, and motion condition as factors. There was a significant effect of these factors and their two-way interactions on the angular error in both species ($P < 0.0001$ for all tests). Angle θ was larger in AM than in RM and increased with increasing target speed but decreased as the probability of

Fig. 5 **A** Movement time (MT) for different target speeds (mean \pm SEM). **B** Angle ϕ plotted as a function of the target speed (mean \pm SEM). Continuous line and filled circle correspond to RM. Dashed line and open circles denote AM. Left Human subject data. Right Monkey data. When the SEM is not visible is because it was smaller than the symbols used



interception in the first revolution increased (Figs. 4A and 4B for humans and monkeys, respectively). In fact, θ was closer to 0 at the probability interval 0.75–1. Since most of the interceptions occurred in this interval, these results suggest that, in general, subjects performed the task optimally. Finally, θ was significantly smaller in monkeys than in humans (F test on main effect of species, $P < 0.00001$). It is important to mention that when we analyzed the angle θ as a function of the processing time, regardless of the target speed, we found a decrease in the angle error variability as a function of the processing time. This effect was more evident in humans than in monkeys. However, the angle error was larger in AM than RM, even if it decreased as a function of the processing time in both motion conditions.

The movement time was defined as the period between the moment at which the force pulse was above the mean + 2SD of the force during the control period and the time at which the feedback cursor crossed the low contrast path (Fig. 1B). We performed an ANOVA using the movement time as the dependent variable, and target speed and motion condition as factors. The movement time showed a slight but significant decrease as a function of the target speed in humans and monkeys (Fig. 5A; $P < 0.0001$ in both cases). In addition, movement time was significantly larger in RM than in AM in humans ($P < 0.0001$; Fig. 5A left) and monkeys ($P < 0.0001$; Fig. 5A right). No significant effect on the motion condition \times target speed interaction was found in humans ($P < 0.362$) or monkeys ($P < 0.47$). Finally, the movement

time was longer in monkeys (F test on main effect of species, $P < 0.00001$).

The angle between the direction of the interception point (270°) and the direction of the target at the beginning of the movement, named ϕ (Fig. 1C left), was also analyzed. Target speed and motion condition as well as their interaction had significant effects on ϕ in humans and monkeys ($P < 0.0001$ for all F tests). In humans, ϕ was similar across target speeds during RM, but it decreased dramatically as a function of target speed in AM (Fig. 5B left). In monkeys, ϕ varied as a sigmoid function of target speed (Fig. 5B right).

Discussion

Five main results were obtained in the present study, namely: (1) the MPT decreased slightly as a function of target speed, (2) the MPT was larger in AM than RM, particularly for target speed below $420^\circ/\text{s}$, (3) the interception accuracy increased when the target travel time was above the MPT, (4) the angular error was smaller in RM than in AM, and (5) the interception movement was initiated at different target locations and time-to-contacts, depending on the target speed and the motion condition. The discussion below will focus on these points.

Human subjects were instructed (and monkeys trained) to intercept the target at 6 o'clock as accurately and as soon as possible. Thus, under these circumstances, the

decision to intercept a target depends on two main elements. One is the processing time that accounts for the period of visual motion information processing in the CNS, and the second is the correct use of this information to trigger the interception movement using a predictive strategy. Here we used different starting points in order to determine MPT. We found that the decision to intercept the target in the first revolution was probabilistic in nature, varying as a function of the processing time. In fact, we obtained S-shaped psychometric curves that were similar to the ones observed in classic detection and discrimination tasks of sensory stimuli, and, therefore, we defined the MPT as a threshold from these psychometric curves. Interestingly, the MPT decreased slightly as a function of target speed. It is plausible that, in the range of speeds tested, the neural mechanism engaged in extracting the visual motion information and the implementation of the response is more efficient when the target is moving faster. In this sense, it has been demonstrated not only that the capacity to intercept targets develops at a young age (~36 weeks) but also that infants are more accurate during the interception of faster rather than slower moving targets (von Hofsten 1980, 1983).

In a previous paper we demonstrated that the reaction time was larger for AM than RM targets (Port et al. 1996). However, the instructions to the subject in that experiment were only to intercept the targets as accurately as possible, and there were no constraints on their response time. The present study was explicitly designed to determine the MPT and we found again that the MPT was longer in AM than RM. This was particularly clear at the slowest target speeds (180 and 240°/s), whereas the MPT in AM was quite long. In separate psychophysical experiments performed in five human subjects, we observed that the detection threshold for apparent motion was 370.5°/s (ISI 194.3 ms; Merchant et al. unpublished observations). Thus, it is possible that at speeds above 370.5°/s the subjects were using the perceptual reconstruction of motion to intercept the target, and that could explain why the MPT was similar between RM and AM at these target speeds. On the contrary, below this threshold subjects might have used other target parameters such as the ISI to solve the interception problem, with more processing time requirements at the lowest target speeds above (Merchant et al. 2003a, b).

In AM the increase in MPT was not reflected in the interception accuracy. In fact, the angular error in AM was larger than in RM and increased considerably as a function of target speed, suggesting that the neural system engaged during AM interception needs more time to process the visual information, and is less efficient when it uses this information to trigger the interception movement. As we discuss below, this may be due to a lack of an accurate neural representation of target position during AM.

The interception performance may be affected by practice, since monkeys with months of training (4–6) were more accurate than human subjects with 1–2 days of practice. However, since monkeys not only were more

accurate than humans but also had larger movement times, it is possible that both species used different speed-accuracy trade-offs (see Plamondon and Alimi 1997 for a review). The monkeys executed the task on the basis of a liquid reward as a motivational drive. Since the reward was delivered using an accuracy rule (an angle of $<18^\circ$ between cursor and target), it is quite possible that the monkeys placed more emphasis on accuracy than on the speed of the movement. Conversely, human subjects were asked to be as accurate and as fast as possible, which may have produced a less accurate interception performance but with shorter movement times.

It has been shown that the movement time decreases as a function of the target speed in a variety of interception tasks (van Donkelaar et al. 1992; Brenner and Smeets 1996; Carnahan and McFadyen 1996). We found the same in the present study. In our task, the interception was restricted to a small angular window around 270° in the circular trajectory of the target. Therefore, the faster the target speed, the more temporal precision was needed to intercept the target. Thus, it is possible that the decrease in movement time in faster moving targets was related to the increment in the spatiotemporal accuracy required to intercept faster targets. In fact, this relation has been documented previously (Brouwer et al. 2000; Tressilian and Lonergan 2002). Similarly, it is possible that the decrease in movement time in AM with respect to RM was also due to an increase in the temporal precision demands in this motion condition. In AM the interception of the target was probably based on a perceptual “reconstruction” of the target trajectory that was more demanding in spatiotemporal terms than the actual motion in RM.

Three strategies have been postulated for the initiation of the interception movement: the threshold-distance model, which assumes that the movement is initiated when the target traveled a constant distance (van Donkelaar et al. 1992); the threshold- τ model, which suggests that the movement is triggered when first-order estimate of the time to arrival attain a particular threshold (Lee 1976); and the dual-model, which takes these two variables into consideration (Port et al. 1997). These strategies probably depend on task contingencies. The results of the present experiment suggest that the subjects were using a dual strategy, with a tendency to start the interception movements at a particular location in its trajectory and adjusting the movement time for the target speeds, but with some modifications on the target angle at the beginning of the movement (φ) depending on the target speed. This strategy was consistent across subjects and species, with the exception of AM in human subjects where the angle φ decreased as a function of target speed. This latter result suggests that in AM the subjects were unable to initiate the interception movement at the appropriate location, particularly at the higher target speed, which resulted in increasingly later interceptions as a function of target speed.

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