ORIGINAL ARTICLE

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# Development of interception of moving targets by chimpanzees (*Pan troglodytes*) in an automated task

**Abstract** The experiments investigated how two adult captive chimpanzees learned to navigate in an automated interception task. They had to capture a visual target that moved predictably on a touch monitor. The aim of the study was to determine the learning stages that led to an efficient strategy of intercepting the target. The chimpanzees had prior training in moving a finger on a touch monitor and were exposed to the interception task without any explicit training. With a finger the subject could move a small "ball" at any speed on the screen toward a visual target that moved at a fixed speed either back and forth in a linear path or around the edge of the screen in a rectangular pattern. Initial ball and target locations varied from trial to trial. The subjects received a small fruit reinforcement when they hit the target with the ball. The speed of target movement was increased across training stages up to 38 cm/s. Learning progressed from merely chasing the target to intercepting the target by moving the ball to a point on the screen that coincided with arrival of the target at that point. Performance improvement consisted of reduction in redundancy of the movement path and reduction in the time to target interception. Analysis of the finger's movement path showed that the subjects anticipated the target's movement even before it began to move. Thus, the subjects learned to use the target's initial resting location at trial onset as a predictive signal for where the target would later be when it began moving. During probe trials, where the target unpredictably remained stationary throughout the trial, the subjects first moved the ball in anticipation of expected target movement and then cor-rected the movement to steer the ball to the resting target. Anticipatory ball movement in probe trials with novel ball and target locations (tested for one subject) showed generalized interception beyond the trained ball and target locations. The experiments illustrate in a laboratory setting the development of a highly complex and adaptive motor performance that resembles navigational skills seen in natural settings where predators intercept the path of moving prey.

**Electronic Supplementary Material** Supplementary material is available for this article if you access the article at http://dx.doi.org/10.1007/s10071-003-0175-x. A link in the frame on the left on that page takes you directly to the supplementary material.

**Keywords** Interception · Anticipatory control · Hunting · Navigation · *Pan troglodytes*

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## Introduction

Interception tasks with human subjects generally consist of presenting the subject with a moving target that has to be caught or intercepted. In some tasks the subjects are to catch a ball thrown to them from different directions, while in other tasks the subjects are presented with a visual target that moves on a computer monitor and has to be intercepted, for example, by the subject steering a cursor controlled by a mouse or a joystick into the target as it moves (e.g., Brenner and Smeets 1996; Dubrowski and Carnahan 2001; Kossoko and Bootsma 1998). In general, interception tasks are used to address issues related to dynamics of motor control, in particular anticipatory control. When consistent movement characteristics of the target begin to control behavior, so that the subject intercepts the moving target in its path, the subject is commonly said to "predict" or "anticipate" the future location of the target (e.g., Dorfman 1977).

Although a considerable body of literature exists regarding interception tasks with human subjects (e.g., Brenner and Smeets 1996; Williams 1988) very little lab-

oratory research on interception is found with animal subjects. This is surprising given that interception skills are seen so readily when animals, especially primates, hunt and forage in natural or semi-natural environments (e.g., Boesch and Boesch-Achermann 2000; Call 2000; Dyer 1998; Goodall 1986; Menzel 1978; Teleki 1973). The present research was, in fact, inspired by a casual observation of spontaneous social behavior in a troupe of captive chimpanzees at Primate Research Institute, Kyoto University, Japan. The chimpanzees spend most of the day outside in a large open enclosure with towers, ropes, trees, and a stream of water. One day it was observed that a fight broke out between a newly introduced adult female and several of the other chimpanzees. The female ran away from the fight but was chased by several of the resident chimpanzees around the perimeter of the enclosure. Another female, who had previously been observed to befriend the new chimpanzee, did not take part in the chase but instead observed it from a distance. Suddenly she ran diagonally across the enclosure at a high speed aiming for a spot near a tower where the chased female would soon arrive. The moment the two chimpanzees met the chased chimpanzee was embraced by the other female, which resulted in an instant breakup of the chase. Seen from a distance, the interception of the chased subject's path was impressive for its precision and timing. We wondered what it would take to establish a laboratory model of such performance. The present research thus sought to determine whether captive chimpanzees can learn to intercept a moving target in a laboratory situation and, if so, what developmental stages they go through in acquiring the task.

Regarding interception tasks for primates, Brooks et al. (1978) trained four monkeys (*Macaca fascicularis*) to track a moving target on a cathode ray display by moving a handle horizontally that in turn produced horizontal movement of a vertical cursor. The monkeys learned to move the cursor to the target by chasing it but apparently never showed any evidence of intercepting the cursor movement. A similar method used by Newsom et al. (1976) and Jaeger (1980) yielded similar results. Rumbaugh et al. (1989) described a chase task for two rhesus monkeys (*M. mulatta*), in which the subjects moved a cursor to a target on a computer monitor using a joystick. The direction of target movement was randomly determined and thus not predictable at trial start. The subjects chased the target and apparently became more efficient at doing so after several thousand trials. In a study of motor cortical activity in rhesus monkeys, Port et al. (2001) described an interception task in which two monkeys had to move a handle forward within a time limit to make a cursor intercept a target that moved in a predictable linear path toward a fixed but invisible interception point. Washburn and Rumbaugh (1992) conducted experiments in which rhesus monkeys moved a joystick-controlled cursor toward a moving target. In some conditions the target moved in a circular path around the monitor, and subjects demonstrated evidence of predicting the target's movement by placing the cursor ahead of the target. In a later experiment also using the joystick task with rhesus monkeys (Filion et al. 1996), the target

moved in a predictable linear path and then disappeared "under" a large circle only to emerge on the other side in continuation of the path. The subjects apparently learned to bring the cursor to a location near the point where the target emerged and thereby showed some evidence of target interception. The experiments by Washburn and Rumbaugh (1992) and Filion et al. (1996) show that predictive movements can be obtained under some experimental conditions. However, these authors did not provide any detailed data regarding acquisition of this performance or control conditions to determine whether anticipation of the target's movement can occur before the target moves or when the target moves from novel locations. Interception tasks have apparently not been described using chimpanzees as subjects.

Development of anticipatory movement in animal subjects is of theoretical interest from the perspective of stimulus control of behavior because to intersect a moving target's path the subject must move the cursor toward a point where there is *no* stimulus. With chasing, the subject merely follows the moving target. In contrast, with interception the subject anticipates where the target will later be and then steers the cursor toward that location before the target arrives there. Dorfman (1977) described effector anticipation as the motor component of moving the cursor at the right speed, in the right direction, and terminating the movement at the right location. Thus, the performance of successfully intercepting a moving target is complex and dynamic.

Our task was based on the previous experience of two chimpanzee subjects who had learned to move a finger from one point to another in a smooth, continuous movement over the surface of a touch-sensitive monitor (Iversen and Matsuzawa 1996, 1997, 2001a, 2001b). In the present experiment, two small visual objects, a ball and a target, were presented on a monitor. The overall task design was very simple. The target moved in a predictable trajectory, for example, clockwise around the edge of the monitor. Using a finger, the subject had to move the ball to the target by dragging it over the monitor surface. When the ball hit the target the subject received reinforcement.

The purpose of the experiments was to examine what sort of navigational strategies the chimpanzees would develop in an automated task in which the subject simply had to transport an object to a target that moved continuously at a fixed speed and in a predictable path.

## Methods

### Subjects

Two adult, female chimpanzees (Ai age 18 years, Pendesa age 17 years) participated in the experiment. Both subjects had considerable prior laboratory experience (e.g., Fujita and Matsuzawa 1990; Kawai and Matsuzawa 2000; Matsuzawa 1985a, 1985b, 2001; Tomonaga and Matsuzawa 1992). In particular, both subjects had used a touch monitor in automated drawing tasks (Iversen and Matsuzawa 1996, 1997, 2001a) and in an automated finger-maze task (Iversen and Matsuzawa 2001b). The subjects were not

food deprived and received 100–200 daily training trials in the present experiment. The chimpanzees lived in a group of 11 chimpanzees in an outdoor enclosure with an attached indoor residence (Ochiai and Matsuzawa 1997).

### Apparatus

From the outdoor enclosure, the subjects entered an experimental booth (150×180×200 cm), which was equipped with a Mitsubishi FHC Vex color-display 21-inch monitor on one wall. A Micro-touch transparent touch screen (for capacitance detection) was integrated with the monitor surface to enable automatic recording of the touch location. Bits of fruit were delivered automatically as reinforcement into a tray under the monitor; delivery was accompanied by a 0.5-s beeping sound. An Epson (PC-386 ES) personal computer was used for programming using the QuickBASIC language. The screen window was 640×400 pixels, and with the monitor used, 100 pixels equaled 5.83 cm. The experiment was fully automated.

### Previous experience

Both subjects had been trained to sweep a finger over the surface of the touch monitor in a controlled manner. In a drawing task (e.g., Iversen and Matsuzawa 1996), sweeping the finger over the monitor surface between two points left a fingertip-wide trace of blue "electronic ink" exactly when and where the finger touched, and the subjects were thereby drawing on the monitor. Thus, the subjects had learned to aim the finger at one small stimulus on the monitor and then to move the finger across the monitor, without lifting it, to another small stimulus. In a fingermaze task (Iversen and Matsuzawa 2001b), the subjects moved one object toward a target while avoiding various obstacles that formed a maze; this movement did not leave a trace on the monitor. Thus, the subjects had considerable experience in placing the finger at one visual object and then moving the finger across the monitor surface to another object.

### General procedure

On each trial in a session, the screen presented just a ball and a target. The ball was a blue disk, 30 pixels in diameter, and the target was either a closed white square (15×15 pixels) or a red triangle (base 15 pixels, height 13 pixels). The stimuli appeared on a black monitor surface. Electronic supplementary material (ESM) S1 shows an image of a subject interacting with the stimuli on the monitor. The target either moved continuously at a fixed speed when the subject moved the ball or remained stationary, depending on the procedure (see below). The subject could move the ball freely on the monitor at any speed, and the ball's movement followed the finger's movement precisely and instantaneously. The finger movement over the monitor's surface had to be continuous. Thus, the subject could not lift the finger and place it at a new location and bring the ball with it. The ball stopped moving when the subject stopped moving the finger, and if the subject lifted the finger from the monitor the ball remained at its current location. Ball movement was in reality a series of small jumps consisting of deleting the ball at its previous location and then presenting it at the new location a few pixels away from the previous location; however, the nearly instantaneous deletion and presentation of the ball generated a visual impression of continuous movement. When the target moved, it progressed in jumps of 15 pixels, which was sufficient for a visual impression of continuous movement at the movement speeds used in this task. The target began to move shortly after the subject began to move the ball thus allowing for determination of the finger's initial movement path before the target moved. (The target began to move exactly when the subject had generated ten movement points, which usually took about 50 ms; a movement point was defined as a detected finger location at least 3 pixels from the previously detected location). The subject received reinforcement when the ball hit the target. Hitting the target was defined as bringing the center of the ball within an invisible circle (40 pixels in diameter) around the center of the target. If the periphery of the ball hit an outer edge of the screen the ball stopped, and the subject had to dislodge it by moving it away from the edge; however, such edge collisions occurred only a few times in the first few sessions. Trials were separated by a 1-s intertrial interval.

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## Experiment 1

The purpose of the experiment was to establish the basic interception task. Each session featured a series of trials in which each trial presented the ball and the target in different constellations (e.g., ball in one corner of the screen and target in another corner); the target remained stationary until the subject began to move the ball. There were no timing constraints involved in solving the task. Because the target moved at a fixed speed, the chimpanzees could simply chase the target with the ball and eventually catch up with it by increasing the speed of finger movement. However, given the natural propensity for intercepting moving objects often seen during hunting and foraging among a variety of species, we predicted that the subjects probably would develop the more advanced performance of intercepting the target. After repeatedly experiencing the target's fixed movement trajectory the subjects might be able to come under anticipatory control of the target's movement and thus move the ball such that it intercepts rather than follows the target. The strategy of the experiment was to wait for such performance to develop. Once the subjects intercepted the target we tested whether they used cues from the target's initial movement on a given trial to guide their behavior or whether they had learned the general movement of the target. The test consisted of presenting probe trials where the target remained stationary throughout the trial. If the subjects used local movement cues then they would move the ball straight to the target because it was not moving on probe trials. Conversely, if they had learned that the target always moved in the same pattern then they would at first move the ball as if the target would also move. Hence, they would move the ball toward the future rendezvous point toward which they normally moved it, even though the target remained stationary on probe trials.
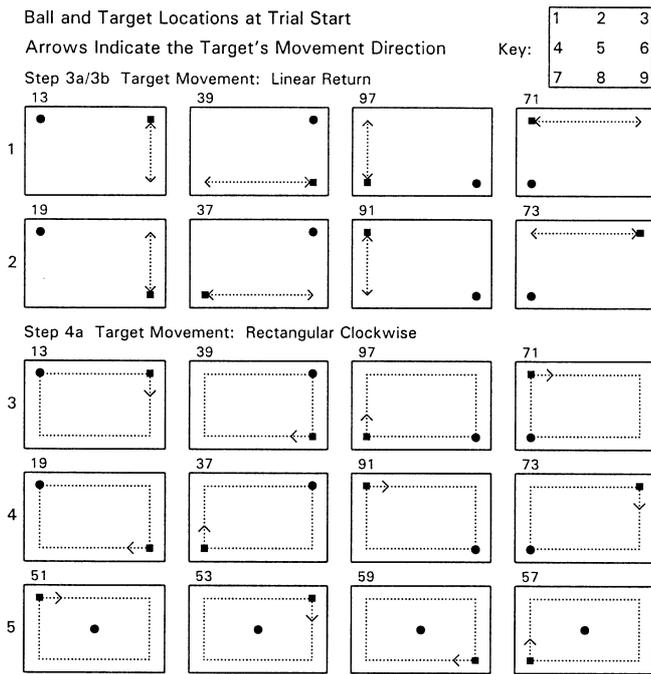
### Method

#### *Subjects*

Because of unequal availability for the research, Pendesa was the main subject and had more procedures and test conditions than did Ai, who served mainly to replicate parts of the experiment. Therefore, the procedural details are given separately for the two subjects.

*Pendesa*. The following training steps were used.
*Step 1*. Baseline of ball movement with a stationary target (5 sessions, each of 24 trials). When a trial began, the

Ball and Target Locations at Trial Start

Arrows Indicate the Target's Movement Direction      Key:

Step 3a/3b  Target Movement:  Linear Return

Step 4a  Target Movement:  Rectangular Clockwise

**Fig. 1** Configurations of ball and target locations for training steps 3a/3b and step 4a. Each *frame* represents the perimeter of the screen area and illustrates what the screen looked like at trial start showing the ball (*circle*) and the target (*square*). The subject moved the ball with a finger. In training steps 3a/3b, the target moved back and forth (at a fixed speed) along a linear path. In training step 4a, the target moved around the edge of the screen in a clockwise rectangular pattern. For each step, the frames show all the possible trial configurations. Step 3a had all eight configurations in rows 1 and 2, and step 3b had only the four configurations in row 1. Step 4a had all 12 configurations in rows 3–5. The *numerals* above each frame identify the trial type. The first numeral indicates ball location and the second indicates target location. The ball and the target could each occupy one of nine locations as indicated by the key in the *upper right corner*

screen showed the ball and the target (white square) in one of eight constellations; the ball appeared (by random selection) in one of the four corners of the screen, and the target appeared in one of the three remaining corners. The target was stationary on all trials. The subject had to move the ball to the target by placing a finger on it and then dragging it over the monitor to the target; the ball visually followed the finger movement.

*Step 2.* Preliminary assessment of chasing a moving target (10 sessions, each of 24 trials). To determine an appropriate movement speed of the target and to test the programs developed for the experiment, Pendesa had preliminary sessions in which the target (white square) moved at a fixed speed as long as Pendesa moved the ball at any speed. On a given trial the target moved in an unpredictable direction (left, right, up, down, or along diagonals) from its position at trial start. Once the target began to move it moved in a predictable linear path toward an opposing edge of the screen, and if it reached that edge before being hit by the ball, it moved back again, and so on. The target's movement speed was increased gradually over sessions from 70 to 310 pixels/s (the latter is equal to

18 cm/s). Because of program development, data were not collected consistently from this phase and are not presented.

*Step 3a.* Training with predictable linear target movement (15 sessions, each of 24 trials). The target's movement speed was set at 350 pixels/s (20 cm/s) for all sessions. The ball and target appeared at trial start in one of eight constellations, as shown in rows 1 and 2 in Fig. 1 (the target's movement direction is indicated by arrows). Trial types are coded with respect to ball and target locations, respectively, as indicated on the key in Fig. 1 and shown above each frame. To make target movement predictable, the target always moved in a linear path 50 pixels from the edge of the screen. The target moved back and forth along this linear path until hit by the ball.

*Step 3b.* Further training with predictable linear target movement (3, sessions each of 32 trials). The task was nearly the same as in step 3a except that it was simplified so that ball and target appeared at trial start only in one of the four constellations shown in row 1 in Fig. 1. The target's movement speed was 350 pixels/s (20 cm/s), and the target moved as in step 3a.

*Step 3c.* Testing with non-moving target probes (5 sessions, each of 32 trials). To determine if the subject's initial movement of the ball was guided by anticipation of target movement, probe trials froze the target in its initial position. Four probe trials were inserted within a session of regular trials, which were as in step 3b; probe types were balanced across the four initial ball/target locations shown in row 1 in Fig. 1. Reinforcement was given on both regular trials and probe trials when the ball hit the target.

*Step 4a.* Training with predictable clockwise target movement (15 sessions, each of 36 trials). The target always moved in a clockwise rectangular pattern 50 pixels from the periphery of the screen. When the target reached the end of one linear segment it turned 90° and continued on the next segment, and so on, thus forming a rectangular movement path; the target kept moving on this path around the edge of the screen until the subject hit it with the ball. At trial start the target appeared in one of the four screen corners, and the ball appeared in one of two of the three remaining corners or at the center of the screen, resulting in 12 trial types, as shown in rows 3–5 in Fig. 1. Notice that the target did not appear in a location such that it would move directly toward the ball's initial location. The target's movement speed was increased from 350 to 650 pixels/s (the latter is equal to 38 cm/s) during the first 10 sessions and then kept at 650 pixels/s.

*Step 4b.* Testing with non-moving target probes (4 sessions, each of 36 trials). The task was as in step 4a, except that each test session had 4 probe trials during which the target did not move; the remaining trials were as in step 4a. Reinforcement was available on both regular and probe trials when the ball hit the target.

*Ai.* The nomenclature of training steps is the same as for Pendesa.

*Step 1.* Baseline with stationary target (5 sessions, each of 32 trials.)

*Steps 2 and 3a.* Ai had no training with these procedures.

*Step 3b.* Training with the target moving back and forth in a linear path with the same four trial configurations as for Pendesa (22 sessions, each of 32 trials). Because this was the first condition with a moving target for Ai, the target's movement speed was increased gradually over the first 18 sessions from 70 to 350 pixels/s (20 cm/s).

*Step 3c.* Testing with non-moving target probes (5 sessions, each of 32 trials).

*Step 4a.* Training with the target moving in a clockwise rectangular pattern (10 sessions, each of 48 trials). The speed of target movement was increased from 250 to 550 pixels/s over the first 5 sessions and then kept at 550 pixels/s (32 cm/s).

There was no opportunity for further training and testing of Ai on this task.

## Results

Both subjects easily acquired the task of transporting the ball to the moving target and developed efficient performance strategies. The results are presented as images of travel paths and as quantitative summary data to enable an analysis of performance changes within and across experimental conditions.

### Baseline with stationary targets, step 1

In step 1, which served as a baseline of ball movement with a stationary target, both subjects readily moved the ball to the target because this movement was nearly identical to the movement required in the drawing tasks they had acquired previously using the same equipment. The top row in Fig. 2 shows examples of nearly linear movement paths in three individual trials, and the second row shows examples of slightly curved movement paths. In this and subsequent figures, the finger's movement path is shown as a series of small dots with each dot representing a contact point on the screen. These dots are shown here only for path analysis and did not appear on the screen for the subject, who saw only the target and the ball. For the subject, the ball moved with the finger and the ball's last location was therefore on top of the target. However, for the purpose of illustration, the figures show the ball's initial location. Speed of ball movement can be sensed by the spacing of individual contact points; when they are spread out the ball is moved quickly, and when they are dense the ball is moved slowly. Most commonly the subjects moved the ball relatively slowly at the beginning and at the end of a trajectory and relatively quickly during the middle portion of the trajectory, as seen for the second trial in row 2 in Fig. 2.
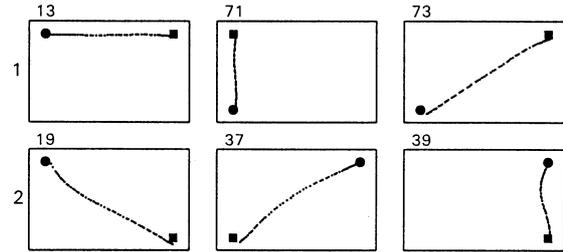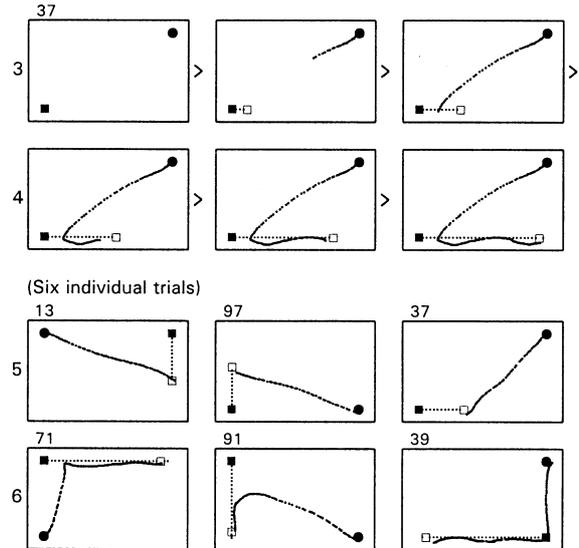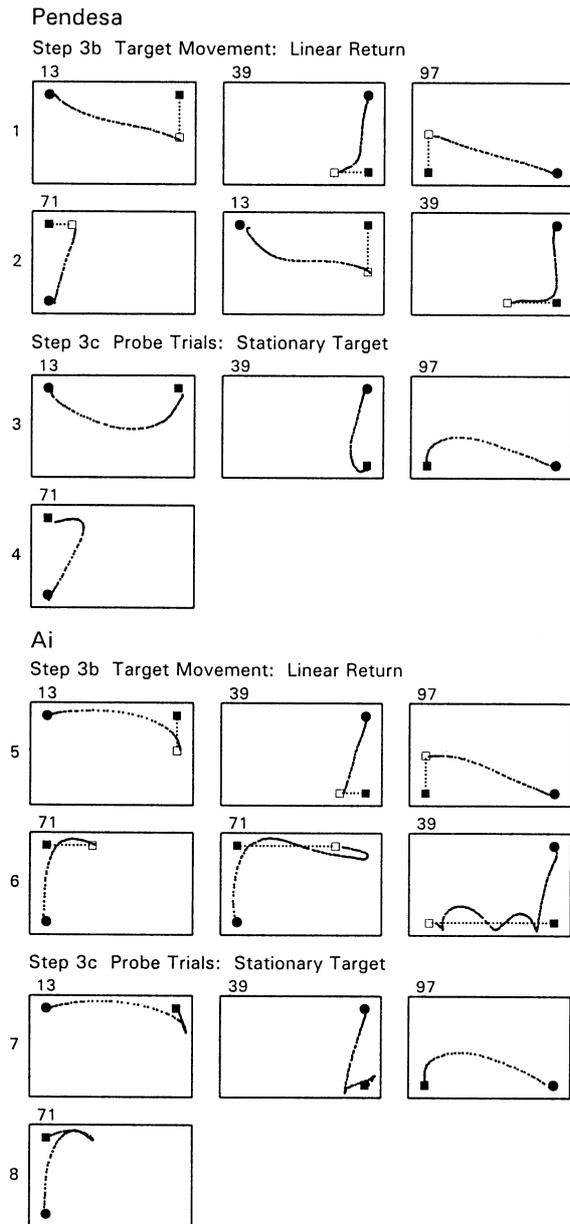


**Fig. 2** Selected individual trials show the ball's movement path for step 1 with a stationary target and for step 3a with the target moving in linear return. The ball is shown here in its initial position at trial start although it moved with the finger during sessions. A string of *small dots* indicates the path of finger movement that transported the ball from its start location to the target. These dots did not appear on the monitor during the task. To illustrate the relative, simultaneous movement of ball and target within a trial, rows 3–4 show six cumulative frames for a single trial (the *arrowheads* between frames indicate the successive temporal order). *Numerals* above each frame identify the trial type (see Fig. 1)

### Preliminary training, step 2

When the target moved along a linear path but in an unpredictable direction in step 2, Pendesa moved the ball so that it followed the target at an increasing speed until it reached the target. Data are not presented from step 2 because this phase served only as preliminary performance assessment and program development (Ai did not have step 2 training).

### Linear target movement, steps 3a and 3b

In step 3a, the target moved in a predictable direction depending on the initial position of ball and target, as is shown in the eight possible trial types in rows 1 and 2 in

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Pendesa

Step 3b Target Movement: Linear Return

Step 3c Probe Trials: Stationary Target

Ai

Step 3b Target Movement: Linear Return

Step 3c Probe Trials: Stationary Target

**Fig. 3** Selected individual trials show the ball's movement path for step 3b (linear return target movement) for Pendesa and Ai. For each subject the first six trials show performance on regular trials with target movement and the next four trials show examples of performance on probe trials with no target movement. *Numerals* above each frame identify the trial type (see Fig. 1)

analysis purposes and did not appear on the screen for the subjects). At first Pendesa moved the ball straight toward the target but then turned in a sharp angle and chased the target until she reached it. This movement pattern, which is here characterized as "target chasing," occurred on practically all trials during the first three sessions in step 3a. Over sessions, Pendesa developed a different strategy of moving the ball toward a point in the target's path where the target would later arrive, as shown in row 5 in Fig. 2. On these trials, Pendesa moved the ball directly toward a future rendezvous point thereby anticipating the target's movement. Such efficient linear ball movement is here characterized as "target interception." However, on other trials Pendesa first moved the ball toward a rendezvous point but missed the target and then chased it, as shown in the first trial in row 6, or she first moved the ball toward the target's initial location and then later adjusted the path to chase the target, as shown in the last two trials in row 6 in Fig. 2.

Because the performance was unstable the task was simplified in step 3b by removing four trial types, leaving only the four trial types shown in row 1 in Fig. 1. Pendesa quickly developed target interception performance on the majority of the trials, as exemplified by the trials in row 1 and the first two trials in row 2 in Fig. 3. On a few trials (especially type 39), Pendesa still first moved the ball to the target's initial location and then chased it, as shown in the last frame in row 2. ESM S2 shows a video clip of Pendesa's performance on one trial (type 13) from step 3b.

Ai did not have step 2 or step 3a training but quickly learned the task of transporting the ball to the moving target in step 3b. As did Pendesa, Ai chased the target in the first sessions and later began to intercept the target's movement. Rows 5 and 6 in Fig. 3 show examples of how Ai typically transported the ball. Row 5 and the first trial in row 6 show data for each trial type. For trial types 39 and 97, Ai clearly anticipated the target's movement and transported the ball very efficiently with no redundant movement. On trial type 13, however, Ai first moved the ball straight toward the target's initial location (at a high speed) and then chased it (at a much slower speed). Similarly, for trial type 71, the performance shows only a slight anticipation of the target's movement followed by a chase. Ai on occasion missed the target, as shown in the last two trials in row 6. In the second trial after she missed the target, Ai moved the ball ahead of the target and "attacked" it from the front. In the last trial at right, Ai missed the target three times even though the initial ball movement showed evidence of anticipating the target's movement.

*Test with non-moving targets, step 3c*

These probe trials with a stationary target tested to what extent target anticipation was determined by the stimuli presented at trial start. Fig. 3 shows examples of performance on probe trials for both subjects. Pendesa first moved the ball toward a point in the target's ordinary movement path. Because the target did not move on probe

Fig. 1. In the first few sessions, Pendesa at first moved the ball directly toward the target (as in step 1) but then changed course during the trial as the target was moving away from its initial position. Rows 3 and 4 in Fig. 2 show six cumulative frames from one single trial to illustrate the spatial relationship between ball and target as the trial progressed. The target is shown both in its initial position (solid square in the lower left corner) and in its forward moving position (as an open square – although it was solid on the screen); dots in the target path indicate previous target locations (these dots are presented here for

**Table 1** Quantitative performance measures across all trial types for steps 1, 3a, and 3b presented as averages and standard deviations (in parentheses, except for perfect anticipation, for which a standard deviation was not defined). Definitions of the performance measures are given in the text. Parenthetical information following step identification indicates which sessions were used for quantitative assessment

| Step | Path redundancy | Perfect anticipation | Anticipation angle | Completion time (s) |
|---|---|---|---|---|
| Pendesa | | | | |
| 1 (last 3) | 0.02 (0.03) | 93.1% | 2.6°  (6.2°) | 0.69 (0.45) |
| 3a (first 3) | 0.33 (0.38) | 6.9% | 6.4°  (7.4°) | 1.24 (0.69) |
| 3a (last 3) | 0.24 (0.31) | 27.7% | 11.1° (12.0°) | 1.12 (0.73) |
| 3b (3 only) | 0.10 (0.11) | 59.4% | 20.9°  (5.3°) | 0.73 (0.32) |
| Ai | | | | |
| 1 (last 3) | 0.07 (0.11) | 79.3% | −1.7° (3.7°) | 0.73 (0.52) |
| 3b (3 early) | 0.26 (0.21) | 17.2% | 7.1° (7.2°) | 1.28 (0.82) |
| 3b (last 3) | 0.17 (0.15) | 38.0% | 13.7° (6.2°) | 1.04 (0.40) |

trials, she adjusted the movement without lifting the finger from the screen about halfway through the trial to steer the ball back to the stationary target. Hence, the movement paths are curved. The paths show that Pendesa's initial movement closely anticipated the target's ordinary movement. ESM S3 shows a video clip of Pendesa's performance on one probe trial (type 13) with stationary target from step 3c.

Ai, too, showed evidence of anticipation of target movement based on the stimuli on the screen before the target began to move, as seen for probe trials types 39 and 97 in row 7 in Fig. 3. However, on the other two trial types, Ai moved the ball rapidly toward the target and then turned as if to chase the target. For example, the trial in row 8 shows that even though Ai did not initially move the ball in anticipation of target movement, she did move it in anticipation later when it approached the path that the target normally traveled (from left to right along the top of the screen in this case). Only for trial types 39 and 97 did Ai anticipate the target's movement from trial start.

*Quantitative performance analysis for step 3b*

Because the subjects always moved the ball to the target on every trial, the performance cannot be described adequately by a simple "percent correct." Instead, we developed several performance measures to examine how the performance changed with practice, with task changes, and during tests. *Trial completion time* is the time from initial contact with the ball to the moment the ball hit the target. *Path length* is the length of the ball's movement path from first screen contact with the ball to the ball's position when it hit the target; the length was the sum of the distance between successive contact points; path length data are not presented here but are integrated with the next measure. *Path redundancy* is the path length ($a$) minus the shortest linear distance between the ball's initial position and the target's last position ($b$) divided by the path length, that is $(a–b)/a$. This ratio yields a value of zero for perfect "target interception" with a linear path and a value between zero and one for curved paths for "target chasing"; hence, the higher the value is the more redundant is the movement path. Path redundancy can be expressed as a percentage score such that a ratio of, for example, 0.2 translates

into a path that has 20% redundant movement. *Perfect anticipation* is the percent of trials with a redundancy score of less than 5%; such trials had a nearly linear movement path. *Anticipation angle* is the angle between two imaginary lines; line A connected the initial locations of the ball and the target, and line B was a projection of the finger's initial movement path defined as the line between the fifth and tenth contact point (these points were used because earlier points commonly were not representative of the movement because initial screen contact often involved some turning of the finger as the movement began).

Table 1 presents the quantitative performance measures averaged across all trial types for step 1, the first and last three sessions of step 3a (eight trial types), and the three sessions of step 3b (four trial types) for Pendesa. For Ai, Table 1 shows data from step 1 and three early sessions and the last three sessions of step 3b (the three early sessions are the first three sessions where the target moved at the speed that was kept constant thereafter).

In step 1, with a stationary target on all trials, path redundancy was very small and the anticipation angle was close to zero because the subjects moved the ball directly toward the target in a nearly linear path. For Pendesa in step 3a, the path redundancy was at first large and the anticipation angle small because she first moved the ball toward the target and then changed course as she chased the target. By the end of step 3a, she anticipated better and movement redundancy was reduced. When the number of trial types was reduced from eight to four in step 3b, Pendesa's performance immediately improved with a reduction in redundancy (i.e., more paths became linear), an increase in perfect anticipation, and a large increase in anticipation angle. Ai (who did not have step 3a training) showed a similar pattern of improvement within step 3b. The trial completion time also decreased for both subjects as they improved because the ball's travel path became shorter.

The overall averages are useful for an appreciation of the general changes in performance. However, the subjects did not perform equally well on all four trial types in step 3b, as shown in Table 2. A perfect interception performance would mean a low redundancy score, a high score of perfect anticipation, a large anticipation angle, and a short completion time. Such measures were obtained for trial types 13 and 97 by Pendesa and for trial type 97 by

**Table 2** Quantitative performance measures for each trial type for step 3b presented as averages and standard deviations (in parentheses, except for perfect anticipation for which a standard deviation was not defined). Definitions of the performance measures are given in the text. For trial type, the first digit refers to the ball's initial location and the second digit refers to the target's initial location (see Fig. 1)

| Trial type | Path redundancy | Perfect anticipation | Anticipation angle | Completion time (s) |
|---|---|---|---|---|
| Pendesa | | | | |
| 13 | 0.05 (0.10) | 81.3% | 31.4° (5.1°) | 0.67 (0.17) |
| 39 | 0.21 (0.16) | 6.3% | 16.1° (9.0°) | 0.86 (0.25) |
| 97 | 0.06 (0.11) | 81.3% | 19.6° (7.9°) | 0.68 (0.21) |
| 71 | 0.11 (0.17) | 68.8% | 16.7° (3.5°) | 0.73 (0.20) |
| Ai | | | | |
| 13 | 0.20 (0.10) | 0% | 5.9° (5.1°) | 1.04 (0.17) |
| 39 | 0.14 (0.16) | 54.2% | 20.7° (9.0°) | 1.26 (0.25) |
| 97 | 0.06 (0.11) | 87.5% | 25.7° (7.9°) | 0.64 (0.21) |
| 71 | 0.28 (0.17) | 8.3% | 3.5° (3.5°) | 1.22 (0.20) |

**Table 3** Quantitative performance measures for the individual trials shown in Fig. 3. Performance measures are defined in the text. For trial type the first digit refers to the initial ball location and the second digit refers to the initial target location (see Fig. 1). Data for regular trials are from step 3b, and data from probe trials are from step 3c

| Trial type (row in Fig. 3) | Path redundancy | Anticipation angle | Completion time (s) |
|---|---|---|---|
| Subject: Pendesa | | | |
| Regular trials, moving target | | | |
| 13 (1) | 0.02 | 35.3° | 0.53 |
| 39 (1) | 0.07 | 15.3° | 0.47 |
| 97 (1) | 0.01 | 22.4° | 0.50 |
| 71 (2) | 0.01 | 14.5° | 0.35 |
| 13 (2) | 0.06 | 51.7° | 0.65 |
| 39 (2) | 0.23 | 1.4° | 0.62 |
| Probe trials, stationary target | | | |
| 13 (3) | 0.17 | 38.9° | 0.83 |
| 39 (3) | 0.16 | 15.1° | 0.66 |
| 97 (3) | 0.19 | 20.3° | 0.56 |
| 71 (4) | 0.32 | 31.5° | 0.56 |
| Subject: Ai | | | |
| Regular trials, moving target | | | |
| 13 (5) | 0.08 | –6.3° | 0.41 |
| 39 (5) | 0.01 | 19.2° | 0.33 |
| 97 (5) | 0.03 | 22.7° | 0.42 |
| 71 (6) | 0.23 | 3.8° | 0.52 |
| 71 (6) | 0.43 | 5.8° | 1.09 |
| 39 (6) | 0.37 | 21.8° | 2.55 |
| Probe trials, stationary target | | | |
| 13 (7) | 0.25 | –12.1° | 0.93 |
| 39 (7) | 0.45 | 17.2° | 0.99 |
| 97 (7) | 0.23 | 26.5° | 0.50 |
| 71 (8) | 0.56 | 1.9° | 0.86 |

Ai. Pendesa did poorly on type 39 with only 6.3% of all trials showing perfect anticipation, and Ai did poorly on type 13 with no evidence of anticipation.

For probe trials with no target movement in step 3c, the overall average anticipation angle was 23.6° for Pendesa and 9.2° for Ai. Broken into individual trials, the averages for Pendesa were 38.4° for trial type 13, 11.3° for type 39, 18.1° for type 97, and 26.6° for trial type 71. For Ai, the average anticipation angle was –7.1° for trial type 13, 20.3° for type 39, 21.2° for type 97, and 2.4° for type 71. Thus, both subjects showed anticipation angles on probe trials (cf. Fig. 3) that were similar to the anticipation angles on regular trials (shown in Table 2).

The relationship between the quantitative performance measures and the actual movement paths can be examined at the level of individual trials. Thus, Table 3 shows the performance measures for each of the individual frames in Fig. 3. For example, the first trial in row 1 had a path redundancy of 0.02, an anticipation angle of 35.3°, and a completion time of 0.53 s.

One difference between the subjects was that Ai moved the ball much faster than did Pendesa at the beginning of a trial. Initial ball speed was defined as the distance the ball traveled from the 5th to the 15th screen contact point divided by time taken to move the ball that distance. Based on an analysis of the last three sessions of step 3b, the overall movement speed was 347 pixels/s (SD=64) for Pendesa but 507 pixels/s (SD=98) for Ai. For Pendesa, the initial movement speed was quite uniform across trial types ranging from 284 to 414 pixels/s. For Ai, however, the speed was much faster at 718 pixels/s for trial type 71 than for any of the other trial types. Thus, Ai moved the ball very rapidly at the beginning of trial type 71 although the target did not move very far (target speed was constant whereas the ball could be moved at any speed). Thus, moving the ball very rapidly toward the target and then chasing the target a short distance (cf. Fig. 3, row 6, trial type 71) is a different performance strategy from moving the ball in a nearly linear path toward a future rendezvous point (cf. Fig. 3, row 5, trial types 39 and 97).

*Quantitative analysis of movement path changes on probe trials, step 3b*

An examination of the movement paths on probe trials indicated that a common break point seemed to occur when the angle of change between two successive contact-point segments exceeded 3° [i.e., the angular difference between an imaginary line from $(x_{i-1}, y_{i-1})$ to $(x_i, y_i)$ and a line from $(x_i, y_i)$ to $(x_{i+1}, y_{i+1})$]. We determined the time

from movement initiation to this break point. For Pendesa the average was 0.32 s (SD=0.05) with a range from 0.22 to 0.42 s. For Ai the average was 0.44 s (SD=0.16) with a range from 0.24 to 0.78 s. However, on some probe trials Ai moved the ball directly toward the target and then apparently chased a non-moving target before she turned the ball at a 180° angle back toward the target (e.g., trial types 13 and 71 in rows 7 and 8, respectively, in Fig. 3). When the analysis excluded the data from such probe trials for Ai, the average time to the break point was 0.31 s (SD=0.06), which was nearly identical to Pendesa's value. Thus, both subjects began to turn the ball toward the stationary target about 300 ms into the movement.

*Training with clockwise target movement, step 4a*

In step 4a the target moved clockwise around the monitor. The ball and target appeared in novel constellations at trial start compared to earlier training steps. In addition, the ball appeared in a new position at the center of the screen on some trials. Thus, step 4a featured 12 trial types (see rows 3–5 in Fig. 1). Figure 4 shows examples of data from individual trials from the first few sessions to illustrate both perfect transfer and failure of transfer of the performance to novel trial types. Row 1 shows examples of the first trials with ball and target in a novel constellation where Pendesa moved the ball in a perfect linear path



**Pendesa**
Step 4a  Target Movement:  Clockwise Rectangular

**Ai**
Step 4a  Target Movement:  Clockwise Rectangular

**Fig. 4** Selected individual trials show the ball's movement path for step 4a (clockwise rectangular target movement) for Pendesa and Ai. *Numerals* above each frame identify the trial type (see Fig. 1)

to a future rendezvous point. When the ball occupied the center position, which it never had previously, Pendesa also on some trials moved the ball in perfect anticipation of target movement, as shown in row 2. However, Pendesa also on several trials missed the target on one or more occasions within a trial. Row 3 shows examples of trials in which the target moved along two, three, or four sides of the rectangular path before it was hit. Even when she moved the ball inefficiently, it was evident that Pendesa often anticipated the target's movement during correction of the ball's movement (e.g., row 3). As summary data for the first three sessions with this procedure, Pendesa showed perfect anticipation on 55.5% of the familiar trial types (i.e., Fig. 1, row 3) and on 40.5% of the novel trial types (i.e., Fig. 1, rows 4, 5). The path redundancy was 0.22 on familiar trial types and 0.39 on novel types. The anticipation angle was 32.6° on familiar trial types and 16.2° on novel types. Pendesa's performance improved only marginally during the 15 sessions with this procedure.

Ai had only 10 sessions with this procedure and also anticipated target movement although not as well as did Pendesa. All trials in row 4 and the first trial in row 5 in Fig. 4 are selected to illustrate how Ai moved the ball when she anticipated the target's movement. Ai also had a different strategy of moving the ball very rapidly toward the target's initial position and then changing course to chase the target, as shown for the last two trials in row 5. To compare the two subjects after a similar number of sessions, summary data were calculated from the last three sessions for Ai and for sessions 7–10 for Pendesa. Data are presented for Ai first and for Pendesa in parentheses; the anticipation angle was positive on 66.6% (97.3%) of all trials, the anticipation angle was 6.7° (29.5°), perfect anticipation occurred on 17.0% (36.4%) of all trials, the redundancy score was 0.59 (0.32), and the completion time was 1.74 s (1.69 s). The subjects had very different strategies of approaching this task. Pendesa had a lower redundancy score because she moved the ball in better anticipation of target movement and therefore intercepted the target more often than she chased it. Ai, on the other hand, most often chased the target. The reason for the difference between the subjects is probably that Ai moved the ball much faster than did Pendesa. In summary, the average ball speed for Ai was 1,132 pixels/s whereas for Pendesa it was 769 pixels/s. Considering the overall trial completion time, which was nearly the same for the two subjects, both subjects were equally efficient in spite of having developed very different movement strategies.
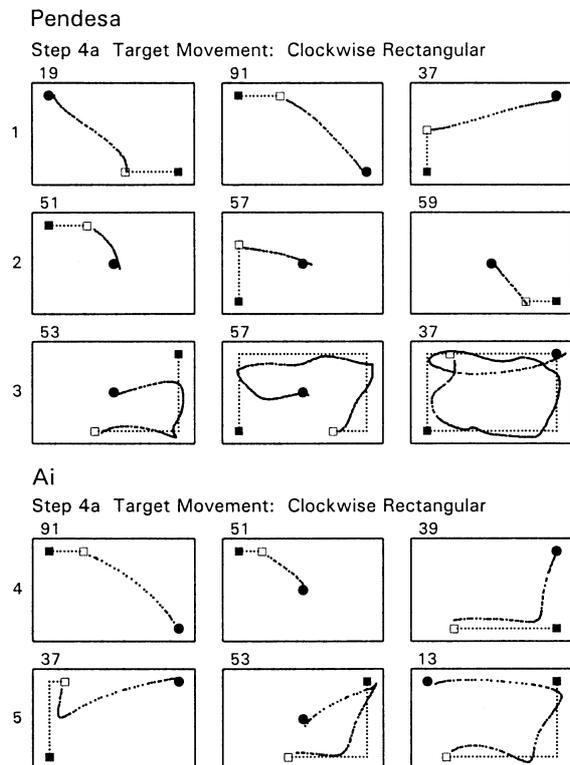
*Test with non-moving targets*
*for clockwise target movement, step 4b (Pendesa only)*

When the target did not move during occasional probe trials, Pendesa moved the ball in anticipation of target movement as on regular trials and then adjusted the ball's movement so as to reach the stationary target. Figure 5 shows a comparison of performance on selected regular

Pendesa

Step 4b Target Movement: Clockwise Rectangular



Step 4b Probe Trials: Stationary Target
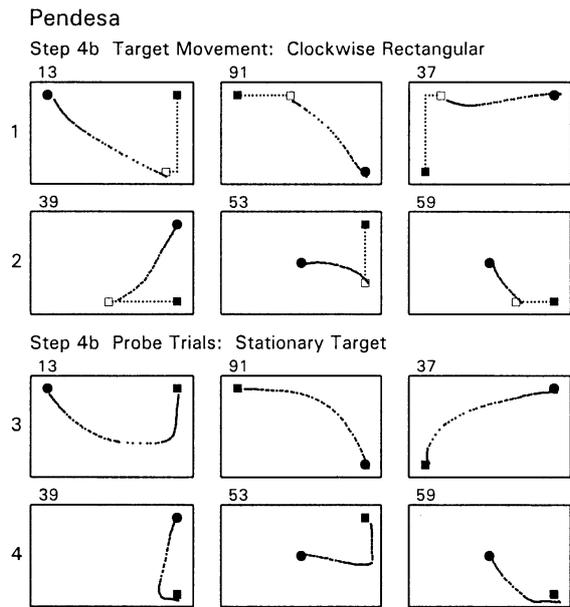
**Fig. 5** Selected individual trials show the ball's movement path for step 4b (clockwise rectangular target movement) for regular trials with target movement and for probe trials with no target movement. *Numerals* above each frame identify the trial type (see Fig. 1)

trials and probe trials with the same initial ball/target locations. The anticipation angle was very similar on regular and probe trials. On all probe trials Pendesa quickly changed the finger's path to move the ball to the target. In summary, all anticipation angles were positive on probe trials (range 17.1° to 57.4°) as well as on regular trials (range 14.8° to 69.3°), and the average anticipation angle was 33.9° on probe trials and 32.1° on regular trials. Thus, Pendesa had learned how the target moved. Based on the previous experience with the consistent rectangular clockwise target movement, the initial positions of the ball and the target were now sufficient stimuli to generate ball movement in anticipation of the target's movement. We were unable to schedule any probe tests with non-moving targets for Ai in step 4b.

## Discussion

Both subjects developed anticipatory interception performance in this task. No particular training was necessary other than what the subjects had learned previously when they moved a finger on a touch monitor to draw or bring a ball to a target within a maze of obstacles (e.g., Iversen and Matsuzawa 2001a, 2001b). The subjects' behavior changed from inefficient to efficient strategies of intercepting the path of the moving target. At first, they chased the target by simply following it and then increasing the speed of the ball sufficiently to catch the target from behind, so to speak. Next, they began to move the ball away from the target's path toward a point where the target would later arrive. Then they refined this interception further by moving the ball ahead of the target and then sometimes turning so as to "attack" the target from the front. An important aspect of the experiment was that the interception point was determined by the subject and not by the procedure; that is, the interception point was unmarked in this experiment. Some interception tasks with human subjects have used a pre-specified and marked interception point (e.g., Dubrowski and Carnahan 2001). Therefore, there was no distal stimulus on the screen that the subject moved the ball toward (except for step 1 and for probe trials with a stationary target in steps 3c and 4b). The stimuli that control ball movement are thus very complex and involve the relative movement and spatial positioning of two simultaneously and independently moving objects (ball and target). These stimuli control the anticipatory interception performance in relation to the subject's previous experience with the target's typical (fixed) speed and movement trajectory as well as in relation to the typical speed and trajectory of the subject's own hand.

The interception performance became very efficient on many trials with nearly linear movement paths that predicted target movement right from the beginning of the trial, even before the target began to move. The subjects completed such trials quickly, usually in less that 1 s. On probe trials, where the target was stationary, the subjects moved the ball so as to intercept the target as it would normally have moved and then turned the ball back toward the target's resting point. These results demonstrate that once interception performance becomes efficient, the stimulus elements that control the anticipatory movement are present at trial start. Essentially, given the experience with consistent target movement, the constellation of ball and target at trial start is sufficient to determine the ball's (finger's) initial movement path. The curved anticipatory paths on probe trials illustrate how the interception performance became so efficient that seeing the target move no longer was a necessary stimulus for the subject to steer the ball toward a spot where it would later arrive.

An interesting issue is whether the subjects had learned to intercept a moving target based on ongoing dual movement cues from ball and target or had learned fixed motor movements dictated by the constellation of ball and target at trial start. Apparently the subjects had learned both. Thus, when the subjects on occasion missed the moving target on regular trials, they immediately initiated a new path to intercept the target at a new location. Such interception was adaptive and did not reflect a fixed motor pattern. On the other hand, the probe trials with a stationary target indicated that the initial ball and target locations controlled at least the beginning of the hand's movement in a predictable way such that the initial movement direction could be labeled "fixed" and controlled by prevailing stimuli. However, the subjects quickly adjusted the ongoing movement on probe trials so as to steer the ball to the unexpectedly resting target. The evidence therefore suggests that the subjects clearly intercepted the target in a dynamic manner. Efficient interception is thus a combination of an initial quick and fixed movement, which is acquired from previous experience with the target's predictable movement, and a subsequent more adaptive

movement where the subject continuously adjusts the ball's speed and direction according to ongoing, shifting locations of ball and target.

The movement change on probe trials with a stationary target illustrates the subjects' prompt adaptation to a new task situation. A basic question regarding movement control is this: at what point in time does a sudden stimulus change control a movement change? In examinations of motor performance in interception tasks using human subjects, a common "constant" is that it takes about 110 ms for new visual information to influence ongoing hand movement (e.g., Brenner and Smeets 1996). In our experiment (probe trials in step 3b) this "constant" seemed to be near 300 ms. However, our experiment and prior experiments used for assessment of movement change in human subjects are sufficiently different to render a species comparison premature. The present task could also be used with human subjects and maybe with other primates so that a more direct assessment can be made of species differences in the "constants" of dynamic motor performance.

## Experiment 2

The purpose of this experiment was to determine how quickly the chimpanzee would adjust to a novel direction of target movement. The target now moved in a counterclockwise rectangular pattern along the periphery of the screen, exactly opposite to the target movement in experiment 1. To determine the generality of the interception performance, we examined in probe trials whether the subject also could anticipate the target's movement when the ball or the target appeared in a novel location at trial start. If the subject could accurately intercept the moving target when the ball or the target began to move from a new location then the subject had learned the ball and the target's general movement characteristics and not just specific motor movements based on the configuration of ball and target at trial start.

Method

*Subject*

Only Pendesa participated in this experiment, which was conducted after a 16-month break following experiment 1.

*Procedure*

Pendesa was first retrained on the same task as in step 4a. The target's movement speed was increased from 70 to 650 pixels/s (the latter equal to 38 cm/s) during the first eight sessions and then kept at the latter speed. Retraining was continued for 48 sessions, each of 48 trials.

*Step 5a*. Training with counterclockwise target movement (4 sessions, each of 48 trials). The target moved in a rectangular pattern as in step 4a but in the opposite direc-

tion. Target speed was the same at 650 pixels/s. In anticipation of Pendesa having some initial problems moving the ball to the target when it moved in the opposite direction, the contact area between ball and target was expanded to an 80-pixel diameter invisible circle around the center of the target so as to make it easier to hit the target with the ball (the diameter of this circle was previously 40 pixels). At trial start, the target was in one of the four corners of the screen, and the ball was at the center or at one of the three remaining corners (except the corner that would bring the target toward the ball's initial location).

*Step 5b*. Testing with new ball and target locations (4 sessions, each of 48 trials). The target moved in a counterclockwise rectangular pattern along the periphery of the monitor at a speed of 650 pixels/s, as in training step 5a. To determine whether Pendesa could generalize the interception performance to new target and ball locations, probe trials presented the target or the ball in an initial novel position on the screen. In all, 28 different probe trials were used, and each probe was tested once. Each session had 7 probe trials and 41 regular trials. On the regular trials the ball and target appeared as in training step 5a. Test sessions alternated with regular sessions without probe trials. Reinforcement was given on both regular and probe trials.

Results

*Training with counterclockwise target movement, step 5a*

When the target moved in a counterclockwise rectangular pattern in step 5a, which was directly opposite to the target movement in experiment 1, Pendesa at first chased the target erratically, as shown for the very first trial with this procedure (first trial in row 1 in Fig. 6). Pendesa chased the target continuously for 9.5 s before she hit it. After just a few trials, Pendesa moved the ball toward the target and then chased the target, as shown in the next two trials in row 1. By the fourth session she anticipated the target's movement and intercepted the target on most trials with a highly efficient movement trajectory, as shown in the three trials in row 2 in Fig. 6 (to illustrate the progress, the selected trial types are the same in rows 1 and 2). Pendesa had a more rapid progress on this task than when the target previously moved in a clockwise pattern in steps 4a and 4b. Thus, after just four sessions, the average redundancy was only 0.18, the anticipation angle was –33.1° (the anticipation angle is negative for a counterclockwise target movement), the trial completion time was 0.65 s, and 33.3% of the trials had a near perfect linear path. Pendesa, therefore, quickly adapted to the novel direction of target movement and in fact performed better on this task than when the target moved in a clockwise pattern. ESM S4 shows a video clip of performance on a single trial.

Before the nearly linear anticipation paths developed, Pendesa's performance went through an intermediate strategy of development that had not been seen previously in experiment 1. Toward the end of the first session and

Pendesa
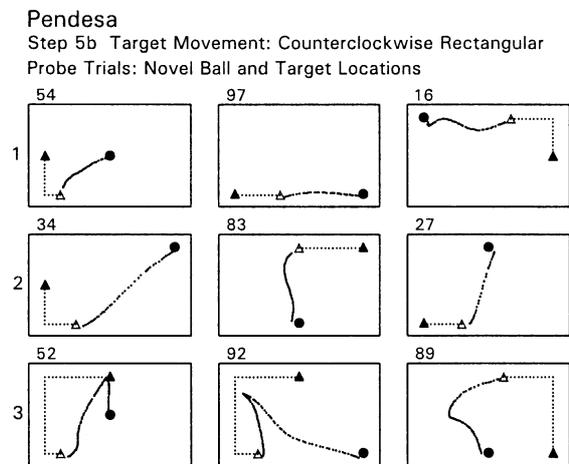Step 5a Target Movement: Counterclockwise Rectangular
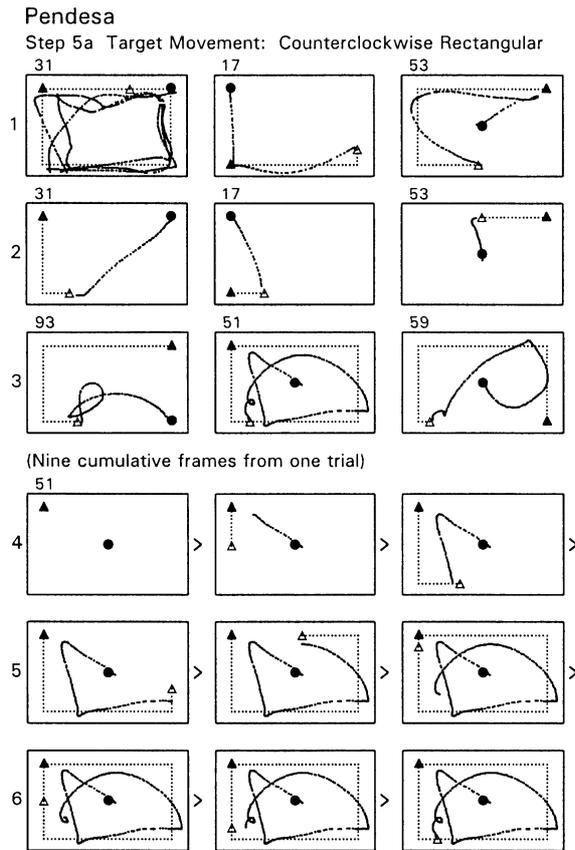


**Fig. 6** Selected individual trials show the ball's movement path for step 5a (counterclockwise rectangular target movement) for regular trials (rows 1–3). Rows 4–6 show nine cumulative frames of ball movement for a single trial (the *arrowheads* between frames indicate the successive temporal order). *Numerals* above each frame identify the trial type (see Fig. 1)

during the second session of step 5a, Pendesa began to move the ball in loops within a small spatial area. Such movement advanced the target toward the ball without moving the ball very much spatially. The first two trials in row 3 in Fig. 6 show examples of such performance. The performance can be characterized as serving to "lure" the target to approach the finger that moves the ball. To illustrate this dynamic spatio-temporal relationship between ball and target, rows 4–6 show one trial cut into nine cumulative segments. At first Pendesa moved the ball toward the target's initial location while the target moved away downward. Then Pendesa moved the ball to intercept the target as it moved along the lower edge (third frame in row 4), but she missed the target. Then she tried to intercept the target while it moved vertically on the right side of the screen (first frame in row 5) but again missed it and also missed it while it moved left along the top of the monitor (the second frame in row 5). Next, Pendesa slowed the ball movement (the movement path is denser) and looped the ball around until the target came very close to the ball, as seen in the first two frames in row 6. Last, Pendesa hit the target when it was right under the ball. ESM S5 shows a video clip of performance on

this trial. Such loops occurred on 14 trials during the first two sessions and then never again. The loops became progressively smaller and were replaced with small "kinks" of slow movement, as shown in the last frame in row 3, before they disappeared when the movement path became a nearly straight line, as shown earlier in row 2. Interestingly, the loops always occurred in the lower left-hand corner of the monitor. While moving the ball in loops was an efficient way of "moving the target toward the finger," while not moving the finger very much, such movement nonetheless took time and was replaced by the much quicker strategy of moving the ball in a nearly straight path.

*Testing with novel ball and target locations, step 5b*

On most probe trials with novel ball or target locations in step 5b, Pendesa moved the ball in nearly perfect anticipation of the target's movement, as shown in selected trials in Fig. 7. Particularly noteworthy is the performance on the second trial in row 1 where Pendesa moved the ball directly toward the target. On training trials, the ball had never faced the target's movement path on any trial. On the four probe trials of this type (13, 97, 79, and 17) the average redundancy was 0.07 and the anticipation angle was 6.1° (notice that for this particular probe type a perfect anticipation angle is 0°). For probe trials with a novel target location, with the ball in the center position, as for the first trial in row 1 (trial types 52, 54, 56, and 58), the average redundancy was 0.46 and the average anticipation angle was −33.3°. On most of these trials Pendesa moved the ball directly toward the target's initial position and then redirected the ball's movement, as for the first trial in row 3. On the remaining probe trials with a novel target location (types 16, 18, 34, 38, 72, 76, 92, and 94) the average redundancy was 0.42, and the average anticipation

Pendesa
Step 5b Target Movement: Counterclockwise Rectangular
Probe Trials: Novel Ball and Target Locations



**Fig. 7** Selected individual trials show the ball's movement path for step 5b (counterclockwise rectangular target movement) during probe trials with new ball and target locations. *Numerals* above each frame identify the trial type (see Fig. 1)

angle was –18.1°. The performance was either nearly perfect anticipation followed by immediate target interception, as shown in the last trial in row 1, or nearly perfect anticipation and then a failure to intercept the target on the first attempt, as shown in the second trial in row 3. For the last probe type with a novel ball location (types 21, 27, 29, 43, 47, 49, 61, 63, 67, 81, 83, and 89), the average redundancy was 0.20, and the average anticipation angle was –46.7°. Again, the performance was nearly perfect anticipation on some probe trials, as for the last two trials in row 2, a failure to intercept the target on the first attempt, or a strangely exaggerated anticipation movement, as shown for the last trial in row 3, which had an anticipation angle of –110.5°; such performance occurred on three trials with novel ball locations. Considering all the probe trials together, Pendesa showed an appropriate initial anticipation angle on 26 of the 28 trials. Thus, the interception performance for counterclockwise target movement readily transferred to novel ball and target locations even after just four sessions of training on this task.

Discussion

The experiment demonstrated a remarkable adaptability of the subject's interception performance. Within one or two sessions, Pendesa adjusted her ball movement to accommodate a complete reversal of the target's movement from a clockwise rectangular pattern in experiment 1 to a counterclockwise pattern in experiment 2. The quantitative performance measures indicated that Pendesa in fact performed more efficiently with the counterclockwise pattern than with the previous clockwise pattern even after only 4 training sessions compared with over 50 sessions of training and testing with the former pattern. We cannot determine the source of this difference based on the present experiment with only one subject. An intriguing temporary pattern of ball movement developed in the first 2 sessions as Pendesa began to move the ball in small loops, which apparently served to bring the target closer to the finger while the finger did not move very much spatially. Such performance did not occur earlier in experiment 1 for either subject. This performance was quickly replaced with moving the ball in a straight line to the anticipated rendezvous point.

When novel ball and target locations were presented in probe trials, Pendesa on most trials moved the ball to anticipate the target's movement. In short, Pendesa demonstrated that she had learned the target's general movement pattern so that she could predict where it would move to regardless of where it moved from. Similarly, Pendesa could move the ball in a novel path toward the target's path when the ball appeared in a novel position at trial start. Thus, the interception performance was not restricted to the trained constellations of initial ball and target locations. Instead Pendesa demonstrated evidence of generalized interception performance.

General discussion

In this interception task the subjects received reinforcement on each trial because they always hit the target whether they chased it or intercepted its movement. Why did the subjects develop anticipatory movements when such movements were not required? We surmise that a sufficient procedural element for this performance to emerge is that as the subject gradually improves the skill of moving the ball, the movement path becomes shorter, and the trial therefore is completed faster. Hence, such improvement in skill reduces the time to reinforcement. Although the subjects were not food deprived, and the reinforcement given was just a tiny piece of apple, they nonetheless collected and consumed each piece. The reinforcement contingencies operating in this task enabled continuous feedback between performance and reduced workload (shorter movement path and quicker access to reinforcement) to direct the development of effective target interception. Research on reinforcement effects indicates that animals in general select behavior that produces even very short reductions in expected time to reinforcement (e.g., Fantino and Abarca 1985). Similarly, research on complex motor skills indicates that speed of skill acquisition depends critically on minute changes in the degree of immediacy of feedback (e.g., Henderson 1977). Thus, if a slight behavior change in an existing skill results in a slightly shorter time to reinforcement then that change is likely to be selected so that the existing skill may be replaced with a slightly more efficient skill. Over time, such repeated slight changes may alter the overall performance from one form to a completely different form. In our experiment, the subjects' performance accordingly developed from time-consuming and inefficient target chasing to quick and efficient target interception, which are qualitatively different performances. The mechanism of such ontogenetic behavior change within a short time period resembles the mechanism that operates in the method of shaping a novel behavior, called "shaping by successive approximation" (e.g., Gleeson 1991; Iversen 2002).

In a broader sense, efficient interception performance is consistent with optimal foraging theory, which states that behavior develops so as to minimize energy expenditure and maximize food value (e.g., Kamil et al. 1987). Spontaneous development of anticipatory control also may have its roots in natural behavior and thus may not necessarily have emerged in the present task as a novel behavior in the subjects' repertoire. The observation of interception performance during spontaneous social behaviors noted in the Introduction serves as just one example (incidentally, the chimpanzee that performed the masterful interception and rescue was Pendesa). One may speculate that the interception performance demonstrated in the present experiments is parallel to interception skills observed during foraging and hunting in natural settings. Thus, Goodall (1986) reported many instances of hunting and foraging (e.g., capture of moving insects) among wild

chimpanzees that may involve intercepting the path of a moving target. Similarly, Boesch and Boesch-Achermann (2000) reported instances of anticipatory travel paths in wild chimpanzees hunting colobus monkeys. Target interception also has been reported for a variety of other animals in natural prey–predator situations such as bats intercepting flying insects (Simmons et al. 1996), archer fish swimming to the location where prey dislodged with a water jet will fall (Rossel et al. 2002), or dragonflies intercepting their prey during flight (Olberg et al. 2000). Target interception is obviously also germane to a variety of human endeavors such as hunting and sports (Bruce et al. 1996; McBeath et al. 1995). The present experiments offer a laboratory model that allows for detailed examination of development of interception performance in primates.

Monkeys have previously been trained on interception tasks (e.g., Filion et al. 1996; Washburn and Rumbaugh 1992). However, a comparison between the performances of chimpanzees and monkeys in interception tasks is not particularly straightforward at the present time because the tasks that have been used are quite different. Our task focused on using the hand in an attempt to simulate natural hand movement, as in trying to grab something that moves, whereas other tasks with monkeys have focused on using a joystick that moves a cursor on a monitor some distance from the hand (e.g., Washburn and Rumbaugh 1992). An additional task difference is that the ball (or cursor) in our task was moved at whatever speed the subject moved it at, whereas the cursor in the joystick task always moved at a fixed speed with only the direction of movement controlled by the subject. Furthermore, in the experiments reported for monkeys the target speed typically was very slow in the 2.5–5 cm/s range. In our experiment the target speed was 20 cm/s or even 38 cm/s, which is more than 10 times faster. We did not attempt to manipulate target speed systematically, and we increased it so as to match the general speed of hand movement in other tasks on the touch monitor with the same subjects. Also, in the present experiment, trials were typically completed in less than 1 s once efficient interception performance was established, as compared to about 10 s with monkey subjects (8.6 s is the fastest average speed in Washburn and Rumbaugh 1992). An additional difference is that the present experiments demonstrated anticipation of target movement in probe trials with stationary targets. Such performance illustrates that the subjects had learned the general characteristics of the target's movement. In addition, one subject that was tested with novel target and ball locations demonstrated generalized interception. Neither probes with stationary targets nor novel target locations were tested in prior research with monkeys as subjects. Thus, the present experiments offer a considerable expansion of knowledge about interception skills in primates. The present task provides a relatively simple way to monitor development of complex and dynamic anticipatory motor performance in non-human primates. The task was acquired with practically no explicit training given the subjects' background of experience with visually guided hand movements. In addition, the task can readily be used with human subjects for assessment of species similarities and differences.

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