

# Kinematic Analysis of Manual Tracking in Monkeys: Characterization of Movement Intermittencies During a Circular Tracking Task

A. V. Roitman,<sup>1</sup> S. G. Massaquoi,<sup>2,3</sup> K. Takahashi,<sup>2</sup> and T. J. Ebner<sup>1</sup>

<sup>1</sup>Department of Neuroscience, University of Minnesota, Minneapolis, Minnesota 55455; and <sup>2</sup>Artificial Intelligence Laboratory and Laboratory for Information and Decision Systems and <sup>3</sup>Division of Health Sciences and Technology, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139

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**Roitman, A. V., S. G. Massaquoi, K. Takahashi, and T. J. Ebner.** Kinematic analysis of manual tracking in monkeys: characterization of movement intermittencies during a circular tracking task. *J Neurophysiol* 91: 901–911, 2004. First published October 15, 2003; 10.1152/jn.00261.2003. Segmentation of the velocity profiles into the submovements has been observed in reaching and tracking limb movements and even in isometric tasks. Submovements have been implicated in both feed-forward and feedback control. In this study, submovements were analyzed during manual tracking in the nonhuman primate with the focus on the amplitude-duration scaling of submovements and the error signals involved in their control. The task consisted of the interception and visually guided pursuit of a target moving in a circle. The submovements were quantified based on their duration and amplitude in the speed profile. Control experiments using passive movements demonstrated that these intermittencies were not instrumentation artifacts. Submovements were prominent in both the interception and tracking phases and their amplitude scaled linearly with duration. The scaling factors increased with tracking speed at the same rate for both interception and pursuit. A cross-correlation analysis between a variety of error signals and the speed profile revealed that direction and speed errors were temporally coupled to the submovements. The cross-correlation profiles suggest that submovements are initiated when speed error reaches a certain limit and when direction error is minimized. The scaling results show that in monkeys submovements characterize both the interception and pursuit portions of the task and that these submovements have similar scaling properties consistent with 1) the concept of stereotypy and 2) adding constant acceleration/force at a specific tracking speed. The correlation results show involvement of speed and direction error signals in controlling the submovements.

## INTRODUCTION

It has been known for over 100 yrs that human limb movements are not completely smooth, but instead are composed of intermittent submovements (Woodworth 1899). Manifested in the multi-peaked velocity profiles, submovements have been described for pursuit tracking (Hick 1948; Miall et al. 1986, 1988; Noble et al. 1955; Searle and Taylor 1948; Taylor and Birmingham 1948; Vince 1948), reaching (Meyer et al. 1982), interception of moving targets (Lee et al. 1997), pointing (Fitts 1954), rapid hand movements (Novak et al. 2000, 2002), and drawing (Massey et al. 1992). Submovements characterize both human and nonhuman primate limb movements (Miall et al. 1986). Disorders of the motor system including Parkinson's disease generally increase movement segmentation (Draper and Johns 1964; Flash et al. 1992; Hocherman and Aharon-

Peretz 1994). Segmentation also characterizes the velocity profile of a cursor movement generated during an isometric task (Massey et al. 1992). Irregular velocity profiles have also been found for body-powered prosthetic arms (Doeringer and Hogan 1995). During slow finger movements, segmentations were found in the EMG activity, demonstrating that the descending command is also inherently intermittent (Vallbo and Wessberg 1993). The prevalence of these submovements suggests that they play a fundamental role in the control of human and nonhuman primate limb movements. However, the exact nature of the submovements remains unresolved, including the scaling properties and the relevant control signals.

Most studies have emphasized submovements' role in feedback error corrections (Noble et al. 1955; Vince 1948), feed-forward control (Miall et al. 1986), or both (Novak et al. 2000, 2002). There is also the possibility that the submovements are themselves movement errors, i.e., the uncorrected consequences of musculoskeletal dynamics. Authors of the early pursuit tracking studies argued that reversals of the velocity profile were dependent on past visual input (Hartman and Fitts 1955). However, movement segmentation persists in the absence of visual feedback (Doeringer and Hogan 1998). Very slow reaching movements or those requiring extreme accuracy are characterized by submovements (Milner and Ijaz 1990), suggesting that submovements are corrective actions by which the hand eventually achieves the target (Milner 1992). This led to the hypothesis that a series of stereotypical submovements are used to make one composite movement (Milner 1992). Stereotypy is an appealing concept in that it reduces the control problem to manipulating scaled versions of a single prototype velocity profile. Based on this concept, submovements during reaching (Milner 1992) and interception (Lee et al. 1997) tasks have been modeled based on minimum jerk criterion (Flash and Hogan 1985) or individually fitted prototypes (Milner 1992).

Given the above stereotypy concept, the nature of the scaling properties remains unknown. Understanding submovement scaling is important to independently (i.e., without prior assumptions) examine the stereotypy hypothesis. The duration of a submovement is monotonically related to both the distance it covers (Miall et al. 1986) and its velocity amplitude (Milner 1992). However, the detailed properties of the scaling across a wide range of movement parameters have not been studied. Therefore the first aim of this study was to characterize the

Address for reprint requests and other correspondence: T. J. Ebner, 2001 Sixth St. SE, Suite 421, Minneapolis, MN 55455 (E-mail: ebner001@umn.edu).

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amplitude–duration scaling properties of submovements across different directions and speeds of circular manual tracking in the monkey. These scaling properties were used to critically test the concept of stereotypy. The results demonstrate that submovement amplitude scaled linearly with duration for both tracking and pursuit, and this scaling was a function of tracking speed.

If the submovements are an essential part of primate limb movements, it is reasonable to postulate that the neural systems involved employ control algorithms that exploit the intermittent nature of the motor system. For visually guided manual tracking, this would imply the use of an intermittent error correction strategy based on generating discrete submovements rather than continuously modifying the motor output. Recent work in humans has demonstrated that specific direction and speed errors provide adequate control signals for manual tracking at a global kinematic level (Engel and Soechting 2000). Therefore the second aim was to investigate the temporal relations between the speed of the submovements and on-line error correction. If there exist strong correlations, this would suggest that the intermittencies are driven by the feedback error signals and would be additional proof that submovements are neither passive mechanical events nor errors themselves. The results show that the movement intermittencies were correlated with specific direction and speed errors, suggesting that these signals play a role in controlling the submovements. An abstract of some of these findings has been presented (Roitman et al. 2001).

## METHODS

### Behavioral task

Experimentation was conducted according to the Guiding Principles in the Care and Use of Animals as endorsed by the American Physiological Society and was approved by the Institutional Animal Care and Use Committee of the University of Minnesota. Two female monkeys (“H” and “M,” *Macaca mulatta*, 5–6 kg, one right-handed and one left-handed) were trained to use a two-jointed manipulandum to make visually guided multi-joint arm movements in the horizontal plane (Fu et al. 1993; Johnson et al. 1999). The task included an initial interception of a circularly moving target from a centrally located hold target and a subsequent visually guided pursuit of the target for one rotation.

The trial sequence (Fig. 1) was initiated when the monkey held the cursor (1-cm black cross-hair) on the hold target (1.8-cm-diam red circle) for a random time between 1 and 2 s (Hold period). A cue target (2.5-cm-diam yellow circle) then appeared at a radius of 5 cm and moved around a circle centered on the hold target while the monkey maintained the cursor in the hold target (Cue period). After 180° of circular travel, the target changed color (red) signaling the onset of interception. The monkey had 65° of target travel to intercept the circularly moving target (Intercept period). After intercepting the target, the monkey continued to track the target for another 360° (Track period). Target speed, starting angle, and direction were varied in a randomized, blocked fashion. The six target speeds ranged from 3.1 to 9.6 cm/s, in 1.3-cm/s increments. One monkey (H) performed the task with the five lower target speeds (3.1–8.3 cm/s), and the other (M) worked at the five larger target speeds (4.4–9.6 cm/s). The starting angle of the Cue period varied from 0° to 270° in 90° increments. Target travel was also randomized between clockwise (CW) and counter clockwise (CCW) directions. For each trial type, 5–10 repetitions were obtained for a total of 200–400 trials per experiment. At any point in the trial sequence, deviation of the cursor from the hold

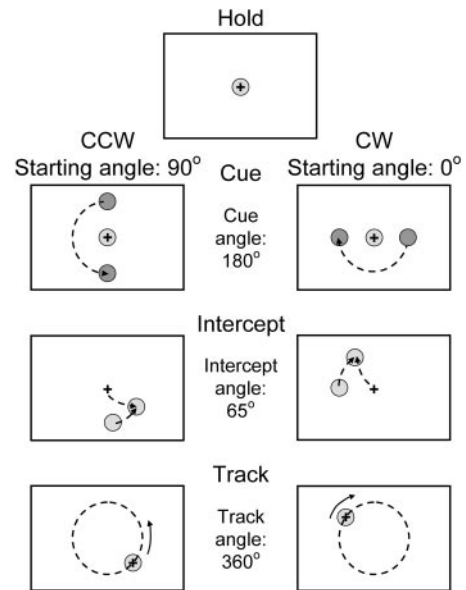


FIG. 1. Schematic of the 4 periods in the manual tracking task. Hold period: monkey is required to hold the cross-hair cursor in a centrally located hold box for a random time between 1 and 2 s. Cue period: monkey has to maintain the cursor in the hold box during the motion of the cue target through one-half a circle. Intercept period: monkey has to intercept the target within 65° of target travel. Track period: monkey has to track the intercepted target for another 360°. Speed, direction, and the starting angle of tracking were independently and systematically varied. *Left*: example tracking in a counterclockwise (CCW) direction with a starting angle of 90°. *Right*: example tracking in a clockwise (CW) direction with a starting angle of 0°.

or moving target aborted the trial. The monkeys could see their hands and manipulandum, but the task requirements demanded that the animal view the vertically positioned monitor.

### Data acquisition

Hand trajectory was digitized using the two potentiometers in the joints of manipulandum. The position data were acquired at 200 samples/s and used to drive the cursor position on the monitor. Both the mechanical manipulandum system and electrical data acquisition system will be referred to as instrumentation. Velocity was calculated by numerical differentiation of the position data and was filtered using a digital 12-Hz low-pass 12th order Butterworth filter. The filter was applied successively in forward and reverse directions to preserve the phase of the signal. The cut-off frequency of filtering was selected based on a comparative speed pulse analysis (see *Speed pulse analysis*) using a 5-, 12-, and 20-Hz low-pass filter. The 12-Hz filtering was found to preserve the majority of the large speed pulses present in Intercept and Track periods while eliminating high-frequency noise that occurred throughout all task periods. It is worth mentioning that most previous studies use considerably lower filtering thresholds (4–6 Hz), making the speed traces smoother and removing a large fraction of the speed pulses. Speed and direction of the movements were computed from the filtered velocity record.

### Speed pulse analysis

The analysis of the submovements in this study is based on the peaks in the speed profile, which we will refer to as *speed pulses*. The bell-shaped profiles of the speed pulses were identified by finding the local minima in the speed profiles (see Fig. 4A). Two measurements, duration and amplitude, were performed for each pulse. The base of the pulse was defined as the average speed value of two successive minima,  $S_{\text{start}}$  and  $S_{\text{end}}$ . The amplitude,  $\Delta S$ , was the difference be-

tween the peak speed  $S_{\text{peak}}$  and the base speed. The duration,  $\Delta T$ , of the pulse was defined as the time interval between successive speed minima. The simple linear regression equation

$$\Delta S = b_0 + b_1 \Delta T + \varepsilon \quad (1)$$

was used to determine the relation between these measures of the pulses. The last term in Eq. 1 represents the error term of the regression.

The regression analysis was carried out for both Intercept and Track periods separately at all experimental conditions. Initially, the means of the regression slopes of each period were tested for significant differences across five target speeds, four starting angles, and two directions of tracking using a three-way ANOVA followed by a post hoc comparison (Student *t*-test with a Bonferroni correction). The regression slopes from the Intercept and Track periods were then compared. For consistency, we limited further analysis to 15 data sets. Each data set consisted of 400 trials (2 directions, 4 starting angles, 5 speeds, 10 repetitions for each condition) so that the results from 10 trials of each type could be averaged together.

### Error-speed analysis

Various measures of tracking error were calculated based on the position and velocity of the hand and those of the target. The goal was to test not only the direction and speed errors suggested for the manual tracking (Engel and Soechting 2000), but also to examine a wide variety of possible error signals. The complete list of equations defining all error signals evaluated is presented in the APPENDIX. Here we limit ourselves only to the description of the two error signals that 1) yielded the largest correlations and 2) had the temporal profiles consistent with involvement in intermittent error correction. These signals were as follows. 1) Direction error (DE) (Engel and Soechting 2000),  $DE = \theta - \phi$ , where  $\theta$  is the present direction, and  $\phi$  is the desired direction of the motion:  $\phi = \angle[(\mathbf{r}_t - \mathbf{r}_h) + \tau \mathbf{v}_t]$ . In this and the following equations,  $\mathbf{r}$  and  $\mathbf{v}$  stand for the position and velocity vectors, respectively. The superscripts *t* and *h* denote the parameters of the target and hand, respectively.  $\angle$  denotes the angle between the vector in parentheses and the reference direction. The coefficient  $\tau$  is constant. 2) Modified speed error (MSE):  $MSE = [(\mathbf{r}_t - \mathbf{r}_h) + \tau(\mathbf{v}_t - \mathbf{v}_h)] \cdot \mathbf{t}'$ , where  $\mathbf{t}'$  is the unit vector in the desired direction  $\phi$  of the hand motion,  $\mathbf{t}' = (\cos \phi, \sin \phi)$ , and  $\tau$  is constant.

The constant  $\tau$  in DE and MSE has the dimension of time and represents the interval for which the simple linear prediction about the target behavior is made by the control system. This is discussed in greater detail in Engel and Soechting (2000).

Cross-correlation analysis was used to reveal coupling between these error signals and the speed pulses. First, the cross-correlation between each error signal and the speed profile was computed for the Track period of each trial. The resulting cross-correlograms were averaged over similar trials to yield an average cross-correlation profile. This was done separately for each of the four starting angles, two directions of tracking, and five target speeds. Then the extrema of these average cross-correlation profiles were found, and their values and lags were measured. Finally, these cross-correlation results were compared across speeds, starting angles, and directions of tracking using a three-way ANOVA followed by post hoc comparison (Student *t*-test with a Bonferroni correction). The same set of analyses was repeated for each of the error signals described in the APPENDIX.

### Control experiment

A simple control experiment was designed to ensure that the submovements analyzed were generated by the monkeys and were not instrumentation artifacts. This control experiment consisted of a balanced rotational setup (Rotational Inertial Accessory, PASCO Scientific ME-8953, mounted on a Rotating Platform, PASCO Scientific

ME-8951) connected to the manipulandum via a low-friction pin coupling. Position data were recorded from the manipulandum during free rotation at speeds comparable to those used in the tracking task. The acquired control data were analyzed in the same manner as the primate tracking data. This control experiment allowed the measurement of the instrumentation noise. A threshold of 3 cm/s was chosen based on the results of this control experiment and on those obtained from the animals during nonmovement periods (see Fig. 5).

## RESULTS

### General description of kinematics

Data from 97 data sets recorded from two monkeys (75 from monkey H and 22 from monkey M) were used in this study. Both animals successfully intercepted and tracked the target with the hand in this error-constrained task. Figure 2 shows averaged movement trajectories, speed profiles, and direction profiles for the hand and target for five target speeds (monkey H). The position trajectories followed the target except for small undershoots or overshoots during the interception. The speed profiles are notable for an initial bell-shaped peak during the Intercept period. This initial peak was followed by subsequent smaller amplitude peak-like overshoots and undershoots of the required target speed during the Track period. The delay in the initial speed increase relative to the target speed reflects the reaction time for this cued task. Using a threshold of 3 cm/s, the average reaction times were  $370 \pm 67$  ms for monkey H and  $203 \pm 126$  ms for monkey M. Monkey M attempted to predict the onset of the interception by beginning to move during the Cue period (yet staying within the Hold target) to a considerably larger extent than did monkey H. Therefore a considerable fraction of the reaction times of monkey M were lower than those of monkey H, hence, the lower average value and the larger SD of the reaction time. The direction profiles also demonstrate the reaction time followed by a parallel change in the direction of both the hand and target for approximately 300–500 ms. This change in direction was then followed by a rapid convergence of the hand movement to the target direction over the next 100 ms. Once the hand and target converged during the Intercept period, the direction profiles followed with great fidelity for the entire circle.

Single trial (i.e., not averaged) trajectories and speed profiles demonstrate an increased variability compared with the averaged traces during the Track period. The differences in the kinematics of the movement can be appreciated by comparing the averaged (Fig. 2) versus single trial trajectories and speed traces (Fig. 3). The single trial speed profiles are most notable for the prominent peaks during tracking. Qualitatively these peaks have bell-shaped profiles similar to those occurring during the interception period. Overshoots and undershoots during tracking were not locked in time or in space. Quantitative evaluation of the speed variance during the Track period confirms the increased speed variability: the values of the speed SD at the intermediate target speed of 5.7 cm/s were 0.69 cm/s for the averaged data versus 1.88 cm/s for the single trial data.

### Speed pulse analysis

The speed pulses during movement periods were not instrumentation artifacts but were properties of the monkey move-

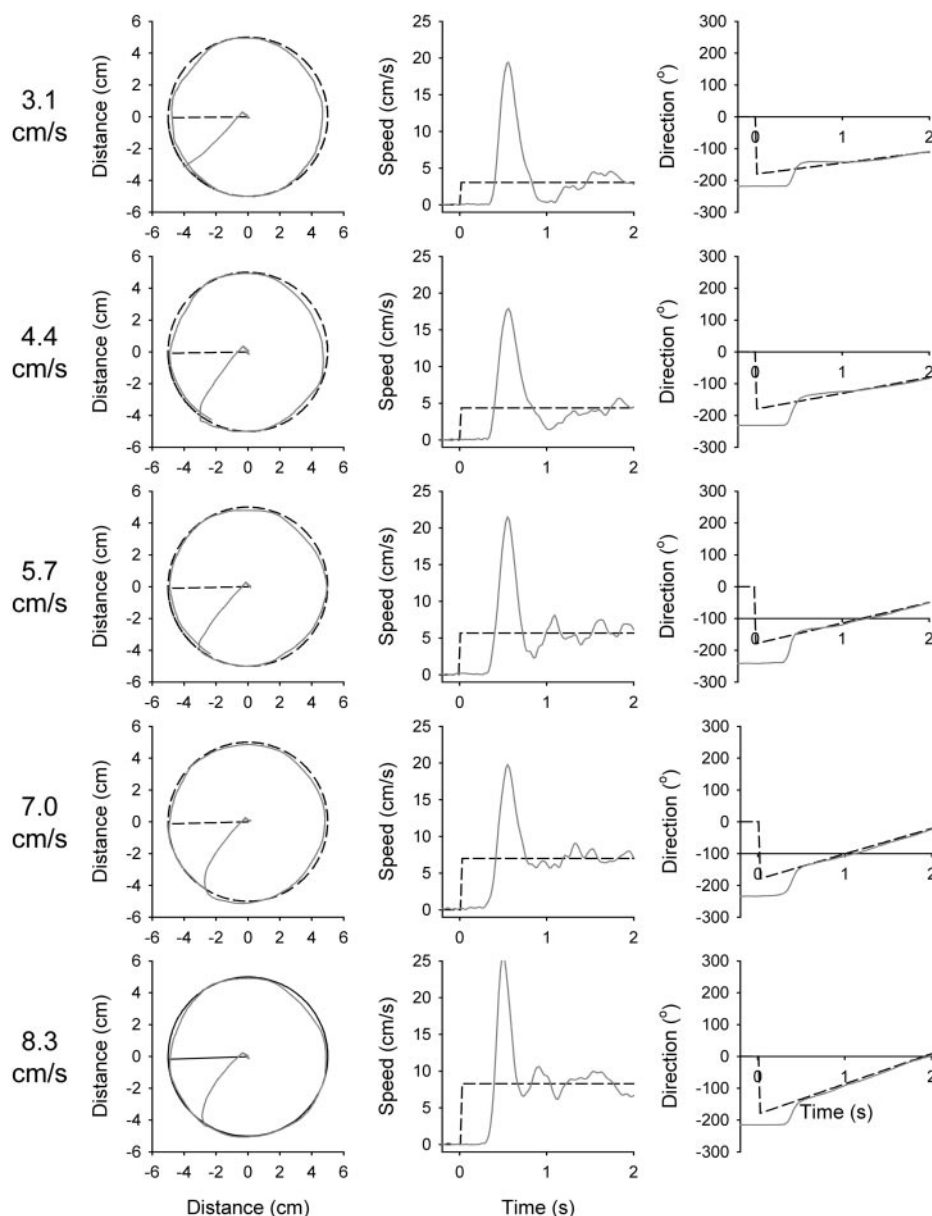


FIG. 2. Averaged position traces (*left*), speed profiles (*middle*), and direction profiles (*right*) for the hand (solid gray) and target (dashed black) for different target speeds. Each row is data from 1 target speed ranging from 3.1 cm/s (*top*) to 8.3 cm/s (*bottom*). Starting angle was 0°, and direction of motion was CCW. Averaged profiles are from 10 task trials. Zero time corresponds to the onset of the Intercept period.

ments. The amplitude of the speed pulses differentiated the submovements during movement (Intercept and Track) periods from the speed variations in the nonmovement (Hold and Cue) periods (Fig. 4B). As expected, the variations in speed were minor when the animal held the cursor on a stationary target. The pulse amplitudes did not exceed 4 cm/s for the Hold period and 2 cm/s for the Cue period, with only a few of the pulses (<0.4%) in the Hold period exceeding 3 cm/s. The normalized number of speed pulses decreased rapidly with pulse amplitude for Hold and Cue periods compared with the Intercept and Track periods. Therefore the amplitudes of the speed pulses in the Hold and Cue periods established an instrumentation noise level of approximately 3 cm/s.

The results of the control experiment using the balanced rotational setup demonstrated that the primate tracking speed irregularities are not due to the instrumentation noise during movement of the manipulandum. The speed pulse amplitudes during passive movement were comparable to those observed

in the Hold and Cue periods. The speed pulse amplitudes of the control experiment did not exceed 4 cm/s, with the vast majority (>99%) less than 3 cm/s (Fig. 4B). Therefore when a noise level of 3 cm/s is used, the instrumentation can be considered to be free of artifacts at constant rotational speeds, and the speed pulses during movement reflect the properties of the primate motion control system. One additional control evaluated whether the submovements could be attributed to oscillation at the natural frequency of the monkey's arm and manipulandum. Computation of the frequency spectrum of the speed profile (data not shown) revealed a smooth, continuous power density distribution monotonically declining with frequency, with no obvious peaks in the frequency range of the submovements.

A major goal was to evaluate the relationship between speed pulse amplitude and duration. Plots of the  $\Delta S$  against  $\Delta T$  of the speed pulses reveal a linear relation for both the Intercept and Track periods (Fig. 5). Simple regression analysis between  $\Delta S$

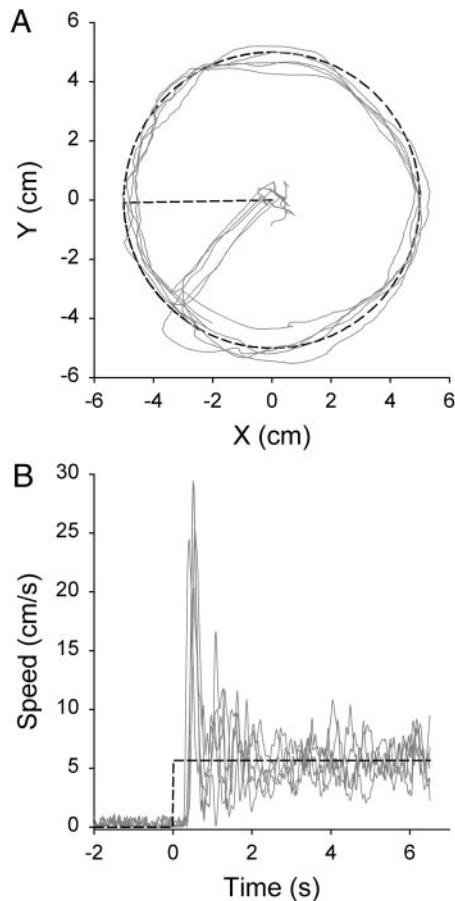


FIG. 3. Single trial movement trajectories (A) and speed profiles (B) at the intermediate target speed of 5.7 cm/s. Plotted are monkey hand data (solid gray) and target data (dashed black). Starting angle was  $0^\circ$ , and direction of motion was CCW. Profiles shown are from 5 task trials. Zero time corresponds to the onset of the Intercept period. Speed overshoots and undershoots are prominent in both Intercept and Track periods.

and  $\Delta T$  (Eq. 1) confirmed the linear dependencies. The grand average  $R^2$  (across starting angles, directions, and speeds of tracking for both animals) for the regressions was  $0.77 \pm 0.07$  and  $0.78 \pm 0.07$  for the Intercept and Track periods, respectively. Therefore speed pulse amplitude and duration are linearly related.

The next question was what parameters of tracking altered this relationship? If this scaling is a robust property of the speed pulses, it should be invariant with respect to most movement parameters. The regression slopes  $b_1$  (Eq. 1) were tested for significant differences across five target speeds, two directions, and four starting angles of tracking using a 3-way ANOVA. The slope of the Intercept period differed significantly across speeds ( $P < 0.05$ ). There were no significant difference ( $P > 0.05$ ) in the slope of the Intercept period between CW and CCW directions. There was a significant difference in the slope of the Intercept period across the four starting angles ( $P < 0.05$ ). However, post hoc analysis determined that only the two starting angles of  $180^\circ$  and  $270^\circ$  produced significantly different slopes. The slope of the Track period showed significant difference across speeds ( $P < 0.05$ ). There was no significant difference ( $P > 0.05$ ) in the slope of the Track period either between CW and CCW directions or across four starting angles of tracking.

Therefore tracking speed was determined to be the only significant factor consistently affecting the slope. Thus for further analysis, the slope values for both Intercept and Track periods were averaged across both directions and all starting angles of tracking. No significant relationship was found between the duration and the amplitude of pulses during Hold and Cue periods or those during the control experiment. This is further evidence that the pulses in the Intercept and Track periods are not passive but rather due to the active control mechanisms.

The scaling slope  $b_1$  between the amplitude and duration of speed pulses was a function of tracking speed. Examination of the  $\Delta S$  versus  $\Delta T$  plots revealed that the regression slope  $b_1$  increased linearly with increasing tracking speed for both the Intercept and Track periods (Figs. 5 and 6). This was explicitly tested by regressing the  $b_1$  on the target speed  $S_t$

$$b_1 = c_0 + c_1 S_t + \varepsilon \quad (2)$$

where the last term represents the error term of the regression. As shown in Fig. 6,  $b_1$  depended significantly ( $P < 0.05$ ) on target speed for both Intercept ( $R^2 = 0.73$ ) and Track ( $R^2 = 0.99$ ) periods. The values of the regression baseline  $c_0$  for the Intercept and Track periods were 32.5 and 2.1  $\text{cm/s}^2$ , respectively. This reflects that the values of  $b_1$  for the Intercept period were systematically higher than those for the Track period for all target speeds. The slope increased with the target speed at the same rate,  $c_1 = 2.5 \text{ s}^{-1}$ , for both Intercept and Track periods (Fig. 6). The same dependency of  $b_1$  on tracking speed was found for both monkeys. Therefore the common rate of increasing the slope  $b_1$  as a function of target speed points to a similarity between interception and pursuit tracking behaviors (see DISCUSSION).

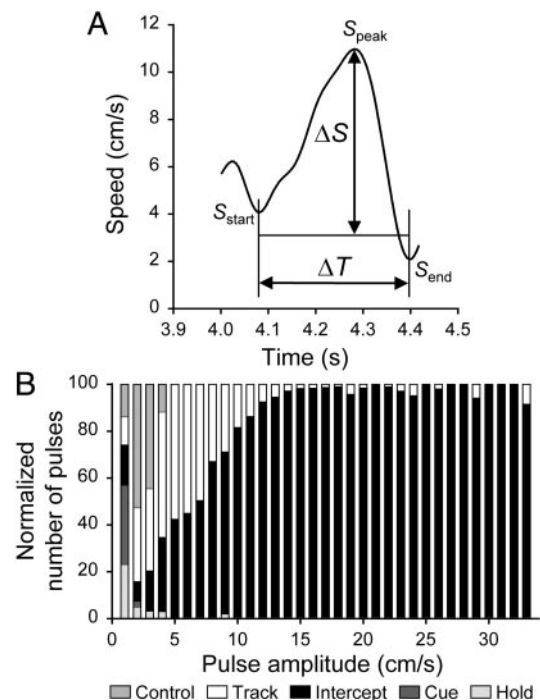


FIG. 4. A: measures of the speed pulse: amplitude ( $\Delta S$ ) and duration ( $\Delta T$ ). Shown is a speed pulse extracted from a speed profile. B: relative distribution of speed pulses as a function of their amplitudes for Hold, Cue, Intercept, and Track periods and for the Control experiment. Total number of pulses in each column normalized to 100%.

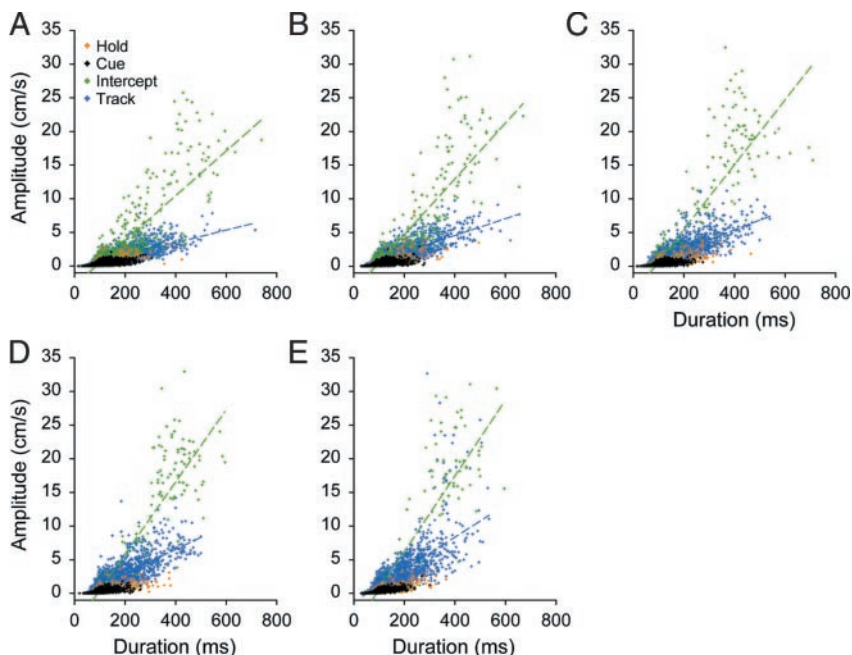


FIG. 5. Scaling of speed pulse amplitude as a function of pulse duration. This relationship is plotted for the Hold (orange), Cue (black), Intercept (green), and Track (blue) periods at the target speeds of (A) 3.1, (B) 4.4, (C) 5.7, (D) 7.0, and (E) 8.3 cm/s. Plotted are the speed pulse values from 400 trials in monkey H.

*Error-speed correlations*

Cross-correlations were performed between the various tracking error measures (APPENDIX, *Eqs. A1–A10*) and the speed profiles of the Track period using lags from  $-500$  to  $500$  ms. The results will concentrate on MSE and DE. The rest of the studied error signals yielded cross-correlograms that were either similar to that of MSE or negligible in amplitude (see APPENDIX for the details).

The cross-correlation between MSE and the speed trace reached its maximum at negative lags (i.e., MSE leads speed) of  $-227 \pm 47$  ms and its minimum at short positive lags of  $35 \pm 18$  ms (Fig. 7, *left*). Therefore the increases in MSE occurred prior to the increases in speed (speed pulses), and the decreases in MSE followed the speed pulses. The amplitudes of the cross-correlation were quite large, reaching the absolute value of 0.6. The cross-correlations between DE and the speed showed a reversed profile: high negative correlations occurred at short negative lags (leads) of  $-102 \pm 65$  ms and high positive correlations occurred at longer positive lags of  $196 \pm 69$  ms (Fig. 7, *right*). Therefore the decreases in DE preceded

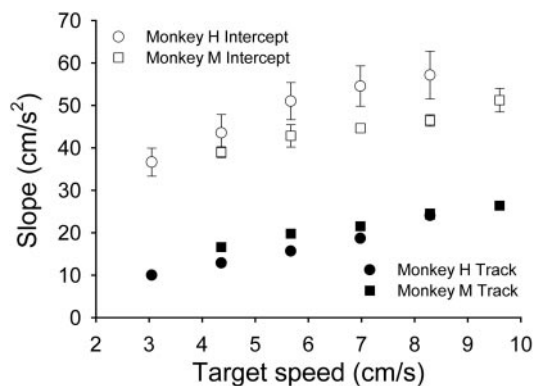


FIG. 6. Amplitude–duration regression slope dependence on the target speed. Shown are the amplitude–duration slopes for both monkeys at each target speed for the Intercept (open symbols) and Track (filled symbols) periods. Plotted are the means  $\pm$  SD.

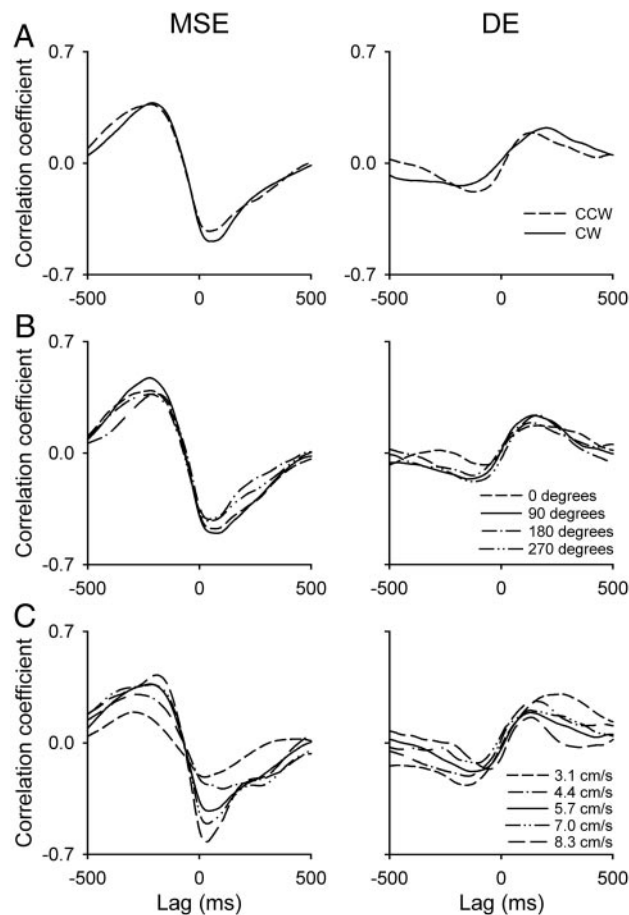


FIG. 7. Example cross-correlations of modified speed error (MSE; *left*) and direction error (DE; *right*) with speed across experimental conditions. A: cross-correlation profiles across 2 directions of tracking for intermediate target speed of 5.7 cm/s and starting angle of 270°. B: cross-correlation profiles across 4 starting angles for intermediate target speed of 5.7 cm/s and CCW direction. C: cross-correlation profiles across 5 target speeds for starting angle of 270° and CCW direction. Shown are the profiles averaged over 10 similar trials in monkey H.

the speed pulses, while the increases in DE followed the pulses. Again, the amplitudes of the correlation were quite large (absolute values  $\sim 0.3$ ), although smaller than those of MSE. The temporal structure and large amplitudes of the correlations suggest that these or similar signals are involved in the control of the speed pulses.

If MSE and DE are relevant control signals, they should be independent of direction and starting angle. Qualitatively, this is observed in the example cross-correlograms obtained from different directions and starting angles (Fig. 7, *A* and *B*). Therefore the latencies and amplitudes of the extremes from the average cross-correlations across tracking speeds, directions, and starting angles were analyzed statistically for MSE and DE signals. There were no significant differences (3-way ANOVA,  $P > 0.05$ ) in five of the eight tested measures between CW and CCW directions or across four starting angles of tracking. The three remaining measures (MSE maximum value, MSE minimum value, and DE minimum value) were isolated with significant differences ( $P < 0.05$ ) in starting angle (MSE minimum value), direction (MSE maximum value), or both (DE minimum value). Post hoc analysis determined that the detected differences in the correlation amplitudes of the above three measures were weak (0.01%, 0.5%, and 4.1%, respectively) and not consistent across tested measures. Therefore neither the latencies nor extrema of the cross-correlations depended strongly on either starting angle or the direction of tracking. For further analysis, the values and latencies of the cross-correlation extremes were averaged across both directions and all starting angles of tracking.

In contrast to the latter results, the cross-correlation analysis did reveal that the extrema and latencies for DE and MSE were a function of target speed (3-way ANOVA,  $P < 0.05$ ). The absolute values of the maximum and minimum for the MSE cross-correlations both increased with target speed, thereby sharpening the overall MSE cross-correlation profile (Figs. 7*C* and 8*B*). The latency (lead) of the MSE cross-correlation maximum increased (shortening the lead), while the latency (lag) of the MSE cross-correlation minimum became slightly longer with increased target speed (Fig. 8*C*). The DE cross-correlation maximum and minimum both decreased with target speed, flattening the cross-correlation profile (Figs. 7*C* and 8*B*). The latency (lead) of the DE cross-correlation minimum generally decreased (lengthening the lead) with the target speed and the latency (lag) of the DE cross-correlation maximum slightly decreased (Fig. 8*C*).

The constant  $\tau$  in SE (Eq. A5) and MSE (Eq. A6) has the dimension of time and represents the interval for which the simple linear prediction about the target behavior is made by the control system. Engel and Soechting (2000) found  $\tau$  to be on the order of 100 ms in humans. Therefore the value used in this study was set to 100 ms. Values ranging from 0 to 500 ms were also evaluated and yielded qualitatively similar cross-correlation results. The value of 100 ms yielded the largest cross-correlation amplitudes. However, the quantitative effect of  $\tau$  on the cross-correlation results was not studied in detail.

## DISCUSSION

### Existence and detection of submovements

The results demonstrate that arm movements during manual visual pursuit tracking in the monkey are not continuous, but

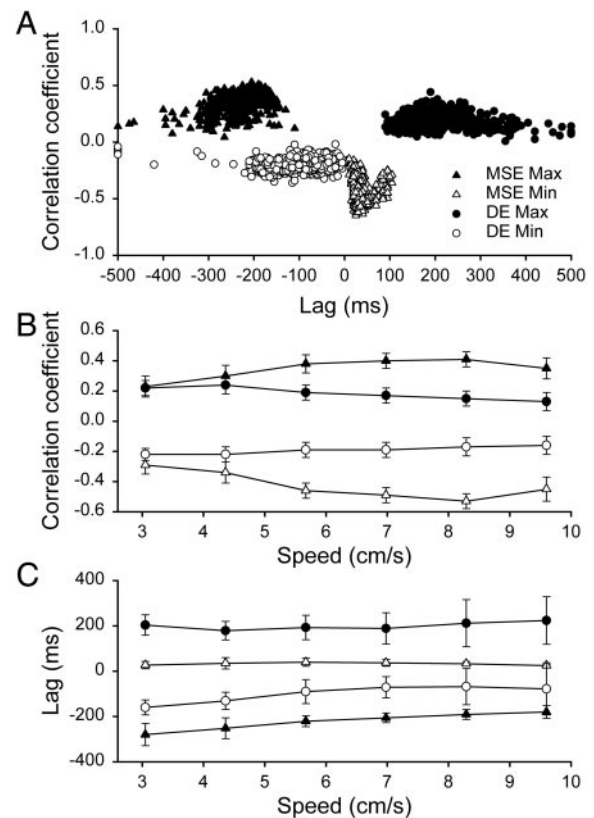


FIG. 8. *A*: cross-correlation extrema (maximum and minimum) of MSE and DE across all speeds and all datasets in both animals. *B* and *C*: speed dependence of cross-correlation extrema values (*B*) and lags (*C*) across all datasets in both animals. Plotted are the means  $\pm$  SD.

instead consist of submovements. These results confirm previous findings that the speed traces of virtually all human and nonhuman primate movements are not smooth (Doeringer and Hogan 1998; Hick 1948; Lee et al. 1997; Massey et al. 1992; Meyer et al. 1982; Miall et al. 1986, 1988; Milner and Ijaz 1990; Noble et al. 1955; Novak et al. 2000; Searle and Taylor 1948; Vince 1948).

The amplitude of the submovements and their properties were clearly distinguishable from any noise introduced by the acquisition system and were not present in passive movement. The amplitude and duration of submovements are not constant but instead span wide ranges with prominent scaling properties. The submovements are not fixed in time or space but instead are highly correlated with specific error signals. We interpret these findings to show that submovements are stereotypic corrective actions required by the task performance.

Arguments can be made that the submovements are the passive consequence of the complicated linked segment dynamics. This is highly unlikely because of the robust scaling properties and the strong cross-correlations observed across different limb configurations and different parameters of motion. Spectral power density analysis of the speed profiles also demonstrated that the submovements were not due to any resonant phenomena.

The submovement detection method used in this study does not allow for the speed pulses to overlap: the beginning of the speed pulse cannot occur before the end of the previous one. Although more elaborate detection algorithms exist (Lee et al. 1997; Milner 1992; Novak et al. 2000, 2002), the speed min-

ima method was chosen for its simplicity and the lack of a need to make assumptions concerning the underlying control strategy. For the submovements that overlap with the speed minimum in between, this method will detect two speed pulses with amplitudes and durations smaller than those of the overlapping submovements. For the submovements that overlap without the speed minimum in between, this method will detect one speed pulse with the larger amplitude and combined duration of the overlapping submovements. The distortion produced by each type varies depending on the size of the submovements and extent of overlap. Therefore when analyzing large numbers of speed pulses (approximately 100,000 in this study), the two types of distortions should approximately compensate for each other and average out.

### *Scaling properties of submovements*

Analysis of the speed pulses reveals three properties of the submovements. The first property is the linear relation between the amplitude and the duration of speed pulses at a fixed target speed (Fig. 5). Since the target speed and the average speed of tracking are nearly identical, this linear relation also holds true at a given tracking speed. Second is the linear relation between the scaling factor  $b_1$  and the target speed  $S_t$  (see Eq. 2). Finally, the scaling factor  $c_1$  is the same for both periods, suggesting a fundamental similarity between the generation of submovements in interception and pursuit.

The first property suggests that the mean acceleration and deceleration during a submovement remain constant across the wide range of submovement amplitudes and durations. From Eq. 1, one can infer the approximate mean acceleration from the regression slope  $b_1$  as  $\langle a \rangle = 2b_1$ . For a given target speed, the mean acceleration is constant and can be related to a constant average force. Therefore the three scaling properties can be restated as follows. For a given speed of tracking, the submovements are generated by a constant average force applied to the hand/manipulandum. Similarly, the average amount of force in a submovement increases linearly with tracking speed and the rate of the increase is uniform for both interception and tracking behaviors.

The acceleration/force arguments represent only a first approximation and could be challenged. First, it can be argued that the relationship between speed change and average acceleration in two dimensions is more complex than proportionality because of their vector nature. However, because the speed pulses are relatively short and the corresponding path segments are relatively straight, the average scaling properties can be well described by proportionality. Second, the speed pulses are not necessarily symmetric so that  $\langle a \rangle$  is not exactly twice as large as  $b_1$ . However, an evaluation of the average acceleration and deceleration for the pulses as a measure of symmetry yielded absolute value differences not exceeding 2.3% across all experimental conditions (average difference was  $1.4 \pm 0.7\%$ ). Third, the exact relation between the muscle forces and the produced acceleration depends on the complicated dynamics of the arm and its interaction dynamics with the manipulandum. These dynamics in turn depend on the state of joint angles and their derivatives (Hogan 1985). However, the proportionality is still a reasonable approximation because the results are averaged over the range of position and velocity space (i.e., the range of joint angles and their derivatives).

Therefore as a first approximation, interpreting the amplitude-duration scaling properties in acceleration/force terms is justified.

The scaling properties of the speed pulses are consistent with the notion of stereotypy (Milner 1992), which states that a complex movement is composed of scaled versions of a prototype velocity profile. Although submovements have been extracted based on minimum jerk criteria (Flash and Hogan 1985; Lee et al. 1997) or individually fitted velocity prototypes (Milner 1992), these approaches cannot verify the concept since they assume stereotypy. Without making any assumptions, our results show that the amplitude of the speed pulses scales with their duration; this is an independent confirmation of stereotypy.

The second and third properties of submovement scaling further extend the stereotypy concept (Milner 1992). The linear dependence of scaling factor  $b_1$  on movement speed reflects the adjustment of the prototype. Controlling faster movements may be achieved simply by scaling the amplitude of a prototype submovement. On the skeleto-muscular level, this can be performed by increasing the average force applied to generate a submovement. This is similar to the proposed pulse-height regulator that sets pulse size and thus the overall speed of movement (Vallbo and Wessberg 1993). Finally, the commonality of  $c_1$  (the rate with which the scaling factor  $b_1$  increases with tracking speed) across Intercept and Track periods points to similar strategy for both reaching and tracking movements.

### *Error-speed cross-correlation analysis*

The error-speed cross-correlation analysis showed that two of the error signals investigated, MSE and DE, are highly correlated with tracking speed. Furthermore, the amplitudes and time courses of the cross-correlograms are consistent across data sets and across animals. This consistency is further evidence of the nonrandom nature of the speed irregularities, because it is the peaks and valleys in the speed profile that contribute to the cross-correlation. The above error signals had these properties among several possible error signals examined.

Similar error signals, SE (see APPENDIX) and DE, were recently shown to be capable of adequately controlling manual tracking in humans with realistically delayed visual feedback information (Engel and Soechting 2000). The present study used a modified version of speed error, MSE. The cross-correlation profiles for SE were similar to those of MSE; however, the MSE amplitudes were significantly larger. Similarly, simple position error signals (PE and TPE, see APPENDIX) had comparable waveforms to those of SE and MSE. This is not surprising because each of these four error signals had a common contribution from the position error term (see Eqs. A1, A5, A6, and A7). We chose to focus on MSE because the amplitudes were larger than those for other signals. However, similar arguments apply to any of the other three signals.

The temporal profiles of the correlograms between MSE and DE and tracking speed are consistent with these signals participating in intermittent error correction. Considering the cross-correlation between MSE and the speed trace as the average MSE profile centered on the average speed pulse, the timing of the maximum correlation implies that the speed pulses are preceded by 220-ms increases in MSE. This sug-

gests that a sufficiently large MSE triggers the generation of a submovement. Conversely, the minimum correlation at a 35-ms lag shows that MSE was reduced by the submovement.

Similar reasoning can be used to interpret the relation between DE and tracking speed. The minimum correlation occurs at a lead of 100 ms, showing that DE is minimal preceding a speed pulse. Presumably, this reflects that the submovements must be generated in the correct direction and is consistent with the importance of directional information during limb movements (Fu et al. 1995; Larish and Frekany 1985; Rosenbaum 1980; Soechting and Flanders 1989). During manual tracking, a change in tracking direction is preceded by a speed decrease and is followed by a speed increase, even though target speed does not change (Engel and Soechting 2000). The DE maximum occurring at a lag of about 200 ms suggests that the direction becomes misaligned with the desired direction at the end of the pulse. This is not unexpected when trying to approximate curvilinear motion with piece-wise straight submovements.

Taken together, the cross-correlation results suggest the following scenario for the intermittent error correction process. First, a sufficiently large increase in MSE reaches a threshold and signals the need for a corrective submovement. However, DE must also be minimal so that the submovement is pointing in the correct direction. Therefore the motor control system (by a mechanism yet to be elucidated) aligns the direction of an upcoming submovement with the desired direction. Then, the submovement is generated with its speed increasing and then decreasing. Shortly after the speed peak, the MSE value drops as a result of the corrective movement performed. An increase in DE at the end of the submovement is an inevitable consequence of using an almost straight submovement while tracking a circularly moving target. Therefore MSE and DE may provide necessary control signals to generate the intermittent corrective movements during manual tracking. As the error signals have both feedback and predictive components, the submovements are implicated in both feedback and feed-forward types of control. The proposed sequence of events can be viewed as a threshold nonlinearity that generates a submovement only if the MSE overshoots a certain threshold.

The question of a sensory error threshold triggering a movement has been previously studied, for example, in the detection of unexpected load differences during fast goal-directed movements (Smeets et al. 1990). Although the proposed velocity error threshold did not stand a subsequent challenge (Shapiro et al. 2002), error signals other than a simple velocity mismatch may be operative. In this task, kinematic error measures appear to be adequate candidates for a signal that defines a critical threshold. It is entirely plausible that the value of the threshold is not fixed, but adjusted depending on the movement parameters (e.g., tracking speed). Unfortunately, the value of the MSE threshold cannot easily be obtained from the cross-correlogram, because this measures only the synchronization between speed pulses and the error signal. Other methods will be needed to identify the error threshold.

The time course of the DE correlogram is distinctly different from all other error signals evaluated (Figs. 7, 8A, and 9). The minimization of DE occurring prior to the speed pulse is additional evidence that a piece-wise intermittent error correction process occurs during two-dimensional tracking. Although a conceivable tracking strategy could have been to simulta-

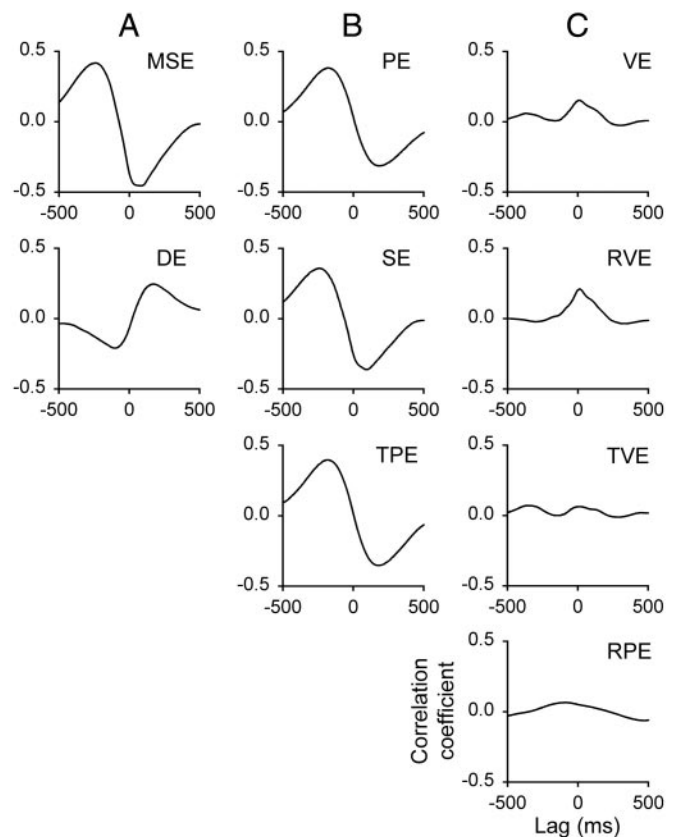


FIG. 9. Example cross-correlations between error signals and speed. *A*: cross-correlation profiles for MSE and DE. *B*: cross-correlation profiles for error signals similar to MSE: position error (PE), speed error (SE), and tangential position error (TPE). *C*: cross-correlation profiles for the other error signals investigated: velocity error (VE), radial velocity error (RVE), tangential velocity error (TVE), and tangential position error (TPE). Shown are the profiles averaged across directions and starting angles (80 trials) for intermediate target speed of 5.7 cm/s in monkey H.

neously reduce the position/speed error and change the direction of the movement, the results demonstrate the opposite. Instead, the observed strategy involves a “slow-down—change direction—speed-up” pattern. This is consistent with previous results for handwriting (Soechting and Terzuolo 1987) and tracking (Engel and Soechting 2000). Had the direction been controlled similarly to other movement parameters, all error signals including DE would have been reduced by the submovements.

The absolute values of MSE correlation amplitude increased with speed, and the absolute values of DE amplitude decreased with speed. This implies that, as tracking speed increased, the submovements were more coupled to MSE and less so to DE. This could be explained by a better ability to control speed than direction at higher speeds (Soechting and Terzuolo 1987; Viviani and Terzuolo 1982). Eventually, when the coupling with the DE becomes too poor, the corrective movements are no longer useful because they lack the correct direction (this is the case at extremely high speeds). Such misalignment of direction would place natural limits on the tracking speed. In this study, the highest tracking speeds used were the maximum at which we could train the animals.

The latencies of the extremes of the correlograms were also dependent on tracking speed. Both the MSE maximum lead and DE minimum lead became shorter as the speed of tracking

increased. This suggests that the correction system was responding to the control signals sooner when the motion was faster. This result is consistent with the observed scaling of the amplitude–duration ratio with tracking speed. Equivalently, the duration of the pulses of similar amplitude becomes shorter as the speed increases, thereby allowing for a faster response.

#### APPENDIX

The error signals studied in this paper were

##### 1) Position error (PE)

$$PE = |\mathbf{r}_t - \mathbf{r}_h| = [(x_t - x_h)^2 + (y_t - y_h)^2]^{1/2} \quad (A1)$$

In this and the following equations,  $\mathbf{r}$  stands for the position vector. The superscripts  $t$  and  $h$  denote the parameters of the target and hand, respectively.

##### 2) Velocity error (VE)

$$VE = |\mathbf{v}_t - \mathbf{v}_h| = [(v_{x,t} - v_{x,h})^2 + (v_{y,t} - v_{y,h})^2]^{1/2} \quad (A2)$$

In this and the following equations,  $\mathbf{v}$  denotes the velocity vector.

##### 3) Direction error (DE) (Engel and Soechting 2000)

$$DE = \theta - \phi \quad (A3)$$

where  $\theta$  is the present direction, and  $\phi$  is the desired direction of the motion

$$\phi = \angle[(\mathbf{r}_t - \mathbf{r}_h) + \tau \mathbf{v}_t] \quad (A4)$$

In the equation above,  $\angle$  denotes the angle between the vector in parentheses and the reference direction. The coefficient  $\tau$  is constant.

##### 4) Speed error (SE) (Engel and Soechting 2000)

$$SE = [(\mathbf{r}_t - \mathbf{r}_h) + \tau(\mathbf{v}_t - \mathbf{v}_h)] \cdot \mathbf{t} \quad (A5)$$

where  $\mathbf{t}$  is the unit vector in the tangential direction of the hand motion:  $\mathbf{t} = \mathbf{v}/|\mathbf{v}|$ , and  $\tau$  is constant.

##### 5) Modified speed error (MSE)

$$MSE = [(\mathbf{r}_t - \mathbf{r}_h) + \tau(\mathbf{v}_t - \mathbf{v}_h)] \cdot \mathbf{t}' \quad (A6)$$

where  $\mathbf{t}'$  is the unit vector in the desired direction  $\phi$  of the hand motion:  $\mathbf{t}' = (\cos \phi, \sin \phi)$ .

Note that the difference between MSE and SE is in the direction on which the error vector in brackets is projected: the direction of the actual motion ( $\mathbf{t}$ ) for SE versus the desired direction ( $\mathbf{t}'$ ) for MSE.

It is important to note that the term “speed error” (Engel and Soechting 2000) is not simply an error signal based on speed or velocity; instead, it refers to the proposed strategy of basing speed updates on this signal. In fact, both SE and MSE include a combination of position and velocity vector differences between the hand and the target projected onto a certain direction. We chose to express both SE and MSE with the dimension of length, which can be changed to the dimension of velocity by introducing a constant conversion factor.

##### 6) Tangential position error (TPE)

$$TPE = (\mathbf{r}_t - \mathbf{r}_h) \cdot \mathbf{t} \quad (A7)$$

##### 7) Tangential velocity error (TVE)

$$TVE = (\mathbf{v}_t - \mathbf{v}_h) \cdot \mathbf{t} \quad (A8)$$

##### 8) Radial position error (RPE)

$$RPE = (\mathbf{r}_t - \mathbf{r}_h) \cdot \mathbf{n} \quad (A9)$$

where  $\mathbf{n}$  is the unit vector in the direction normal to the trajectory of the hand motion.

##### 9) Radial velocity error (RVE)

$$RVE = (\mathbf{v}_t - \mathbf{v}_h) \cdot \mathbf{n} \quad (A10)$$

Cross-correlation analysis was used to reveal coupling between these error signals and the speed pulses as described in METHODS. Based on the cross-correlograms, the error signals were broken down into three groups. The first group included the MSE and DE signals (Fig. 9A) with nearly opposite time courses and large amplitudes. The maximum absolute amplitudes were  $0.39 \pm 0.11$  for MSE and  $0.20 \pm 0.11$  for DE across all conditions and all data sets. The second group included PE, SE, and TPE signals (Fig. 9B). The cross-correlograms for these signals were similar to that of the MSE but with significantly smaller (1-way ANOVA,  $P < 0.05$ , followed by post hoc comparison) maximum amplitudes ( $0.29 \pm 0.10$  for PE,  $0.29 \pm 0.11$  for SE, and  $0.32 \pm 0.11$  for TPE). The third group included VE, RVE, TVE, and TPE signals (Fig. 9C). The correlation amplitudes were small ( $0.12 \pm 0.08$  for VE,  $0.15 \pm 0.09$  for RVE,  $0.09 \pm 0.05$  for TVE, and  $0.07 \pm 0.04$  for RPE), and their time courses were not indicative of any delayed coupling, as opposed to the first two groups.

As described in the DISCUSSION, the temporal profiles of the correlations for MSE and DE suggested involvement of these error signals in the process of intermittent error correction (Fig. 7). Furthermore, the time courses were consistent across all data sets recorded from both animals (Fig. 8A). Although PE, SE, and TPE had cross-correlation profiles similar to that of MSE, the latter had significantly larger amplitude. Therefore the results and analysis of this study focused on MSE and DE.

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