Reprinted from the **Journal of Motor Behavior**, published by HELDREF PUBLICATIONS,
4000 Albemarle Street, N.W., Washington, D.C. 20016.
Journal of Motor Behavior
1989, Vol. 21, No. 3, 185–204

Cues and Control Strategies in Visually Guided Tracking

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ABSTRACT. Detailed quantitative models are required to investigate the neurological basis of motor behavior. Previous studies of visually guided manual tracking have either identified a variety of control signals (cues) for planning tracking movements or analyzed how a single cue is used (i.e., one-tracking strategy). A systematic, quantitative analysis of the effects and interactions of cues in terms of human manual-tracking performance is presented here together with measurements of concomitant eye movements. These measurements help to define the routes by which information reaches the CNS, and the analysis elucidates how the control signals are processed and combined. The results quantify not only the large improvement in performance observed when the target waveform being tracked is predictable but also the extent to which this improvement depends on the availability of current information about target movements and positional error. Target information is shown to provide short-term prediction independent of the error signals used in on-line negative feedback control.

VISUALLY GUIDED HAND MOVEMENTS are interesting for a variety of reasons. Psychologists studying human behavior have found them to be a convenient experimental paradigm for exposing many features of motor control. (Keele, 1981; Pew, 1974; Poulton, 1974). Engineers have sought to quantify human performance in order to improve the design of man-machine interfaces (e.g., McRuer & Krendel, 1959). The differing motivations of these two groups have led to distinctive experimental approaches and characteristic models. Psychologists have identified a large number of cues and strategies that subjects may use and have often summarized their results in terms of qualitative "black box" models (e.g., Poulton, 1981). Engineers typically limit the

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The authors are indebted to the Wellcome Trust, the Medical Research Council, and Trinity College, Oxford, for financial assistance. We would also like to thank Patricia Riddell and Jonathan Winter for expert technical assistance and the reviewers for their helpful comments. Dr. Weir's current address is: GEC Hirst Research Centre, Wembley, Middlesex, U.K.

Apparatus

A schematic diagram of the tracking paradigm is shown in Figure 1. Subjects were seated in a darkened room, 60 cm (approximately) from a 22-in. (55.88 cm) black-and-white monitor on which both target and monitor spot were displayed. The target, consisting of two vertically aligned dots (pixels) with a space between them, moved horizontally across the screen. The monitor spot (single pixel) was moved horizontally by the joystick, and subjects attempted to position it between the two target pixels. Each pixel had a diameter smaller than 1 mm, thus subtending less than 0.1° at the retina. The brightness and contrast of the display were adjusted at the beginning of each experimental session so that the subjects reported a clear image that did not smear due to persistence as the target and monitor spot moved around the screen.

The display was generated by a Research Machines 380Z microcomputer equipped with an 8-bit A/D interface. Target and monitor spot positions were updated every frame, giving the impression of smooth movement without flicker. Target waveforms were set up to cover 70% of the monitor spot's full range, allowing adequate room for overshoots. This corresponded to 25.2 cm (23.7°) on the screen. A 0.3 Hz sinusoid, with this amplitude, led to target velocities with an average of 14.2°/s and a maximum of 20.1°/s.

Subjects controlled the position of the monitor spot by moving a low inertia, linear, inductive joystick (RS components 162–984), held in the right hand, generally with the thumb, index, and middle fingers. Movements were primarily a function of wrist flexion or extension. The joystick was free to move in all directions within the horizontal-vertical plane, but only the horizontal component of its movements affected the position of the monitor spot. The joystick was 14 cm long and could move 50° (13 cm at its tip) before hitting mechanical stops. These stops corresponded to the extremes of the monitor spot's range.

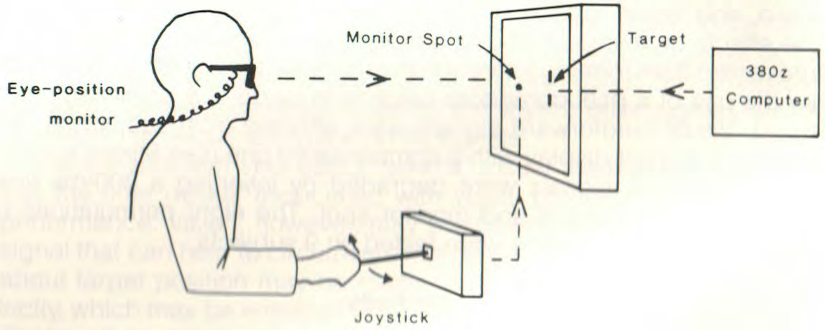


Figure 1. A schematic diagram of the paradigm used, in pursuit display mode. In this mode, the subject, whose head was stationary, tracked the moving visual target with movements of both hands and eyes. Movements of the joystick were reflected by movements of the monitor spot either instantaneously or after a 300-ms delay. In the compensated mode, the monitor spot was positioned a distance away from the middle of the screen equal to the current error between target and joystick signals, and a visual target was fixed in the screen's center to indicate zero error.

During tracking, the subjects rested an elbow on a comfortably positioned support and were asked to keep their heads still on a chin rest. The joystick was positioned so that subjects were unable to see their tracking hand. Those subjects (6 out of 9) who did not normally wear glasses had their horizontal eye movements measured by an infrared reflectometry technique (Carpenter, 1977).

Two modes of display, pursuit and compensated, were used. In pursuit mode, target and joystick position signals controlled the visual target and monitor spot positions, respectively. In compensated display mode, joystick and target position signals were compared to give a positional error signal. The monitor spot was plotted a distance away from the center of the screen equivalent to the current value of the error signal, and a stationary visual target was placed in the middle of the screen to indicate zero error. Thus, when actively tracking with a compensated display, subjects received feedback about their error but no direct information about the target signal.

A 0.3 Hz sinusoid was chosen as a suitable predictable target function on the basis of previous work (Leist, Freund, & Cohen, 1987; Navas & Stark, 1968), and was produced by a function generator (Feedback TWG501). A second 380Z microcomputer was used both to generate an unpredictable target function and to act as a switchable, 300-ms delay line between the joystick and the monitor spot. The unpredictable function used was pseudorandom, repeating every 150 s, and consisted of a series of ramps, random in direction, velocity, and duration. The amplitude of the ramps was between 20% and 80% of the target's range, and they lasted between 0.5 and 4.5 s. Unpredictable functions used in previous studies, such as the sum of randomly phased sine waves (Stark, 1968) or filtered white noise (Michael & Melville-Jones, 1966), have a relatively flat frequency spectrum (power) but a probability density function (PDF, Figure 2, e.g., *Gaussian* white noise) that is tightly centered around its midpoint. The existence of the range effect (Searle & Taylor, 1948, Slack, 1953) implies that subjects can use information derived from stochastic features of a target waveform such as the PDF to improve their tracking. For example, subjects might learn the PDF of a sum-of-sinusoids target waveform and decide not to track the target if it moved far from the center of its range, for they know it will return soon. The unpredictable target function used in this study had both a flat frequency spectrum and a more uniform PDF than a sum-of-sines or Gaussian white noise spectrum (Figure 2).

Protocol

The three experimental manipulations described earlier were combined to produce 8 tasks (Table 1). These 8 tasks were presented to information available to the subjects in an attempt to force them to use a single-tracking strategy that can then be analysed and described in the same way as a control circuit (Bekey, 1962; Licklider, 1960; Stark, 1968).

Neuroscientists investigating the role of neural structures underlying visuomotor control have also used control theory models to interpret lesion and recording data from the oculomotor system (Robinson, 1981; Skavenski & Robinson 1973). Before this approach can be applied to the control of arm movements, however, a model of visually guided manual tracking is required that combines the two approaches described above, that is, a quantitative model that takes into account as many of the cues and control strategies used as possible.

In order to define a framework for such a model, we have sought to delineate the roles of various cues that may be used to guide the limb in a combined eye- and hand-tracking paradigm (Figure 1). Subjects were required to track a continuously moving visual target, displayed on a TV screen, using a hand-held joystick that controlled the position of a monitor spot on the screen. In this paradigm, the cues for tracking may come from vision (both retinal and oculomotor signals), memory, and proprioception from the tracking arm. Proprioception alone cannot set the goal of movements in such a visual task and is subservient to vision and/or memory (Klein & Posner, 1974; Posner, Nissen, & Klein, 1976). If vision and proprioception are made to conflict by inserting a time delay between joystick and monitor spot, vision dominates (Miall, Weir, & Stein, 1985; Pew, 1974). Proprioception is not essential to generate any of the signals that might be used in planning movements in this paradigm and for simplicity was not experimentally manipulated.

Vision can provide a number of potential control signals in this paradigm. Subjects may use the positional error between target and monitor spot and its derivatives to directly drive their movements using a servomechanism-like strategy or, on a longer time scale, to calibrate the relationship between movements of the joystick and those of the monitor spot. Because the use of error signals implies that a negative feedback tracking strategy is being employed, error signals will be referred to as visual feedback (VFB) signals.

A major problem with using "on-line" visual feedback strategies is that the time delays associated with visual processing limit tracking performance. Vision, however, may provide a second class of control signal that can help to circumvent this problem. Short-term predictions about target position may be made using signals, such as target velocity, which may be employed to drive feedforward control processes. These will be labelled visual feedforward (VFF) signals. Evidence for the use of current target information (VFF) in visually guided movements has been provided by Campos, Chiezi, and Bolzani, (1986), Pelisson, Prablanc, Goodale, and Jeannerod (1986), and Poulton (1952b).

The long time delays associated with visual processing may also be circumvented by longer term predictions based on memorized internal representations of the target waveform. An improvement in performance resulting from following predictable target waveforms has been demonstrated in both oculomotor (Dallos & Jones, 1963; Michael & Melville-Jones, 1966) and manual-tracking (Poulton, 1974; Stark, 1968; Stark, Lida, & Willis, 1961) paradigms. Internal representations need not be exact replicas of the target waveform; they may also be stochastic models of the target's trajectory. In other words, movements may be preplanned on the basis of average features of the target waveform (Poulton, 1957). Slack (1953) has demonstrated that subjects can use the average target step-size of a random amplitude series to improve their performance. This ability was christened the "range effect" by Searle and Taylor (1948).

Good evidence exists, therefore, for the use of VFB, VFF, and memorized internal representations of the target waveform (memory) as cues for the planning of tracking movements. This evidence, however, comes from separate experiments and a variety of paradigms, which makes a quantitative comparison of the effects and interactions of each cue difficult. Many studies demonstrate the use of a particular cue by measuring the overall tracking error with and without that cue (e.g., Poulton, 1952a). The study presented here employed four measures of tracking performance: overall tracking error, shape matching between target and track, overall lag, and relative amplitude (gain). As we will show, some of the cues can have highly significant effects on one index of performance, such as lag, without significantly effecting overall tracking error. Finally, to be of use to neuroscientists, the model should include details of which physiological pathway is taken by which cue. Therefore, we measured the eye movements made by subjects during manual tracking in order to assess which cues were carried by retinal and which by oculomotor signals.

In order to study systematically the role of memory, visual feedforward, and visual feedback signals, each was disrupted in turn, and the effects on manual-tracking performance examined. Subjects were prevented from forming internal representations of the target waveform by the use of a pseudorandom function in place of a predictable sinusoid. Visual feedforward signals were withheld from subjects by replacing a pursuit display with a compensated one (see Methods), and visual feedback signals were degraded by inserting a 300-ms time delay between joystick and monitor spot. The eight permutations of these three manipulations were tested on 9 subjects.

Methods

Subjects

Nine neurologically normal subjects (8 males, 1 female) were studied. They ranged in age from 20 to 30 years. All of the subjects had normal or corrected-to-normal vision and used their right hand for tracking. Participation was encouraged by the promise of a bottle of wine for the most accurate tracking!

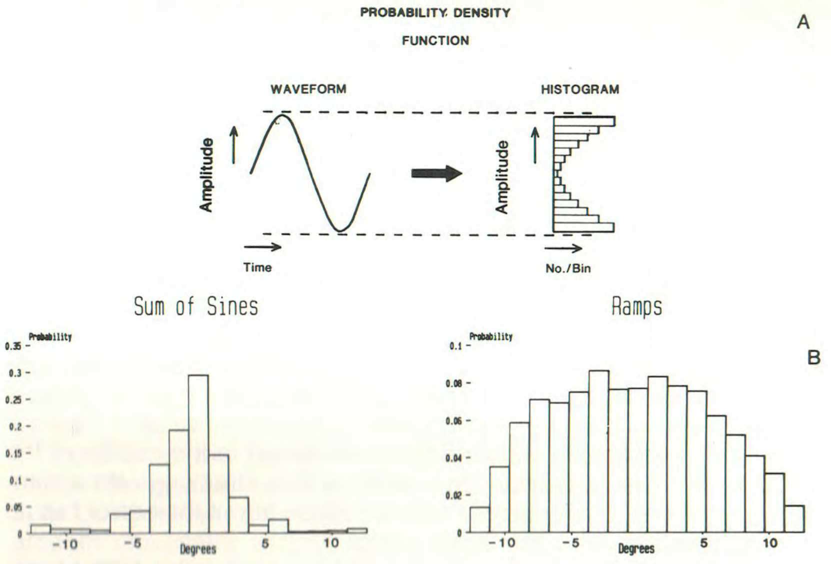


Figure 2. A, The probability density function of a sinusoid. This function is a measure of the likelihood of finding the target in a part of its range. It might serve as a stochastic model of the target waveform, allowing subjects to improve their tracking on the basis of memorized nonuniform PDFs. B, The PDF of two pseudorandom waveforms. Both waveforms had the same range and were sampled at 100 Hz for 150 s (after which they repeated). The sum-of-sines waveform (16 nonharmonic sines of equal amplitude and random phase) has been used in previous studies as an unpredictable target function (Miall et al., 1986; Stark, 1968). It has, however, a highly nonuniform PDF clustered around the middle of its range. In contrast, a ramps waveform (see text for details), which has a relatively uniform distribution, was used in this study (also see Poulton, 1957).

subjects as part of a larger series of 48 different tasks. This series was split into two sessions, tested on separate days. Each test session lasted approximately 1 hour and started with a calibration section, during which target, joystick, and eye movement signals were adjusted and recorded. The subject was then asked to practice tracking a 0.3 Hz sine wave for 1 min in order to get the "feel" of the joystick. The subject was then instructed to "Track as accurately as possible. Attempt to minimize your error." Each task lasted approximately 2 min, followed by a 30-s rest. The subjects were split into three groups. Each group was presented with the 8 tasks in a different order, which was chosen to encourage subjects to change strategy if this was advantageous. Thus, tasks alternated between the two display modes, and the same target waveform was rarely used on consecutive tasks.

Methods of Analysis

The best 50-s period of manual tracking from each task was selected by eye, and digitized (12-bit resolution) at 50 Hz. The positional

Table 1
Summary of Task Details and 4 Measures of Tracking Performance

	Task details		Task conditions		Average performance scores for each task			
						Cross-correlation		
Task	Sources of information available to the subject	Delay (ms)	Target	Display	Error (%)	Peak (Coeff.)	Lag (s)	Regression slope
A	VFB, Memory, VFF	0	S	P	16.95	0.978	0.025	0.977
B	VFB, Memory,	0	S	C	40.09	0.936	0.173	0.847
C	VFB, , VFF	0	PR	P	33.65	0.855	0.169	0.777
D	VFB, ,	0	PR	C	37.65	0.897	0.291	0.728
E	, Memory, VFF	300	S	P	33.32	0.953	0.093	1.040
F	, Memory,	300	S	C	48.61	0.898	0.224	0.904
G	, , VFF	300	PR	P	49.36	0.792	0.393	0.747
H	, ,	300	PR	C	51.11	0.802	0.533	0.596

Note. The error measure used was the absolute error over 30 s, expressed as a percentage of the error that would have resulted if no movement had been made. A regression slope gain of 1.0 would correspond to a track with an equal amplitude to the target. The results are the average of 9 subjects.

Key: VFB, Visual feedback signals; VFF, Visual feedforward signals; S, 0.3 Hz Sine; PR, Pseudorandom; P, Pursuit; C, Compensated.

error during this period was calculated from the difference between monitor spot and target position signals. The 30-s period of tracking that showed the least error was then chosen visually. An overall performance score was calculated by rectifying and integrating the error signal over the chosen 30 s. This error score was expressed as a percentage of the value that would have resulted if the subject had not moved at all (Poulton, 1974).

Overall performance was then broken down into three separate measures:

1. *Waveform shape matching.* A cross-correlation function was calculated between target and monitor spot position signals for the chosen 30 s. The peak coefficient of the correlogram was taken as a measure of the similarity in waveform shapes.
2. *Waveform timing (lag).* The position of the correlogram's peak was noted to determine the overall lag/lead between target and monitor spot signals.
3. *Waveform gain.* The joystick waveform was shifted relative to the target by the overall lag/lead calculated in 2 above. The slope of a regression line, fitted by the "least squares error" technique, was taken to indicate the gain (or multiplication factor) between target and monitor spot position signals.

The effects of removing each source of information (memory, VFF, VFB), intersubject variation, and task order on the four statistics—overall error, peak cross-correlation coefficient, peak cross-correlation time, and regression slope—were then assessed using analysis of variance (ANOVA) procedures. The statistical model used (Type 1) assumes that the variance associated with each class represents a sample from a population with the same variance (homogeneity of variance). This assumption was tested and, because the results were found to be equivocal, the ANOVA results were confirmed with paired *t* tests between tasks. Both statistical procedures found the same significant differences between groups of tasks.

Results

Qualitative results

Eye Movements. All subjects moved their eyes so as to follow the visual target rather than the monitor spot in every task. Hence, if a pursuit display was in use, the subjects attempted to match their eye movements to those of the target as best they could. When a compensated display was employed, subjects fixated the stationary central target (Figure 3). The performance of subjects' eyes with a pursuit display did not differ qualitatively from that observed by others (Carpenter, 1977) in tasks where no manual tracking was required. Thus, if an unpredictable waveform was followed, the eyes performed smooth pursuit, with only an occasional saccade when the positional error became too large. Sine waves of the frequency (0.3 Hz) and amplitude (23.7°) used in these tasks are within the dynamic range of the smooth pursuit system (Carpenter, 1977) and saccades were rarely seen.

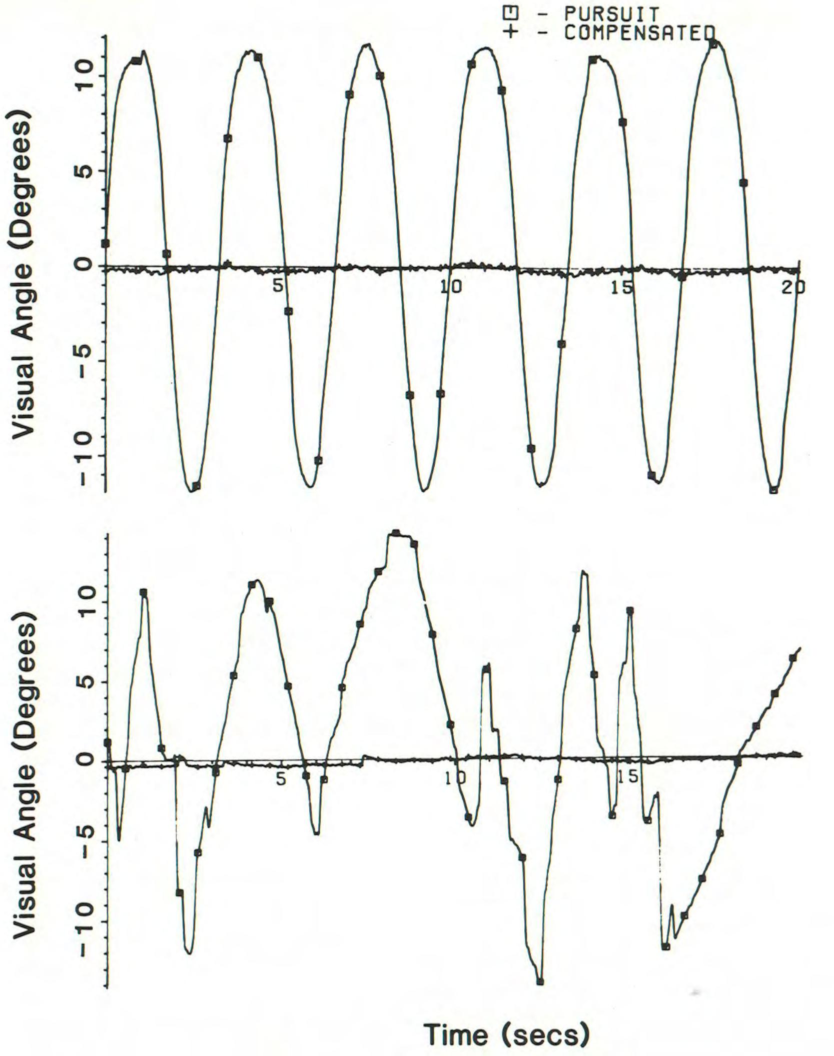


Figure 3. The eye movements made by a typical subject while tracking predictable (sinusoid) and unpredictable (ramps) target waveforms with pursuit and compensated displays. In all cases, the subjects' eyes attempted to follow the visual target. The eye movements were monitored using an infrared technique described in Carpenter (1977). 23.7° of visual angle corresponded to 25.2 cm on the screen.

Hand Movements Subjects who tracked a sinusoid displayed in pursuit mode also moved the joystick with a continuous smooth movement (Figure 4A). If, however, the sinusoid was replaced with a pseudorandom waveform, the joystick motion broke up into "step-and-hold"-like movements (Figure 4C). These discrete positional corrections (intermittency) can be seen most clearly during slow target ramps. Intermittency became more marked when subjects tracked with a compensated display. Under these conditions, it could be seen clearly even with the sinusoidal target waveform (Figure 4B). Subjects who followed pseudorandom waveforms with a compensated display showed very clear intermittency that was not only restricted to slow sections of the target waveform (Figure 4D). Thus, subjects' arm movements showed obvious intermittency when tracking unpredictable target waveforms or when independent viewing of target and joystick position signals was prevented by the use of a compensated display.

Addition of a 300-ms delay between the joystick and monitor spot did not greatly alter the nature of the tracking with a pursuit display (Figures 4E, G), although subjects consistently overshot the target when it reversed direction. If a compensated display was employed, however, tracking changed considerably (Figures 4F, H). For example, with a sinusoidal target waveform, the pattern of intermittent movement amplitudes over a target cycle altered markedly. Insertion of a delay led to the enlargement of the first movement after reversal of the target's direction of motion relative to the rest (Figure 4F). When tracking a pseudorandom target waveform with a compensated display and a 300-ms time delay between joystick and monitor spot, the tracking consisted largely of alternating intermittent movements, hunting around the target position (Figure 4H).

Quantitative results

Each of the three sources of information for guiding tracking (memory, VFF, VFB) was available in 4 of the 8 tasks. To demonstrate the effect of removing each source of information, Figure 5 shows the difference in each of the four measures of tracking between tasks, with and without each source of information.

Statistical analysis of the data was carried out using both analysis of variance and paired *t* tests (see Methods). The results of these two procedures were in close agreement and are summarized in Table 3. They show that removal of each of the three sources of information had a significant effect on overall performance and that there were clear interactions between sources.

Loss of the ability to memorize the target waveform (−memory, Figure 5) caused a large deterioration in all four measures of tracking performance. Two interactions with other cues were seen (Table 3): The effects on lag and regression slope were reduced if VFB signals were available (Figure 5C, D), whereas those on error and shape matching were largest if VFF information was present (Figure 5A, B). When target information (VFF) was removed, its interaction with memory was seen again: There was a significant effect on error, shape

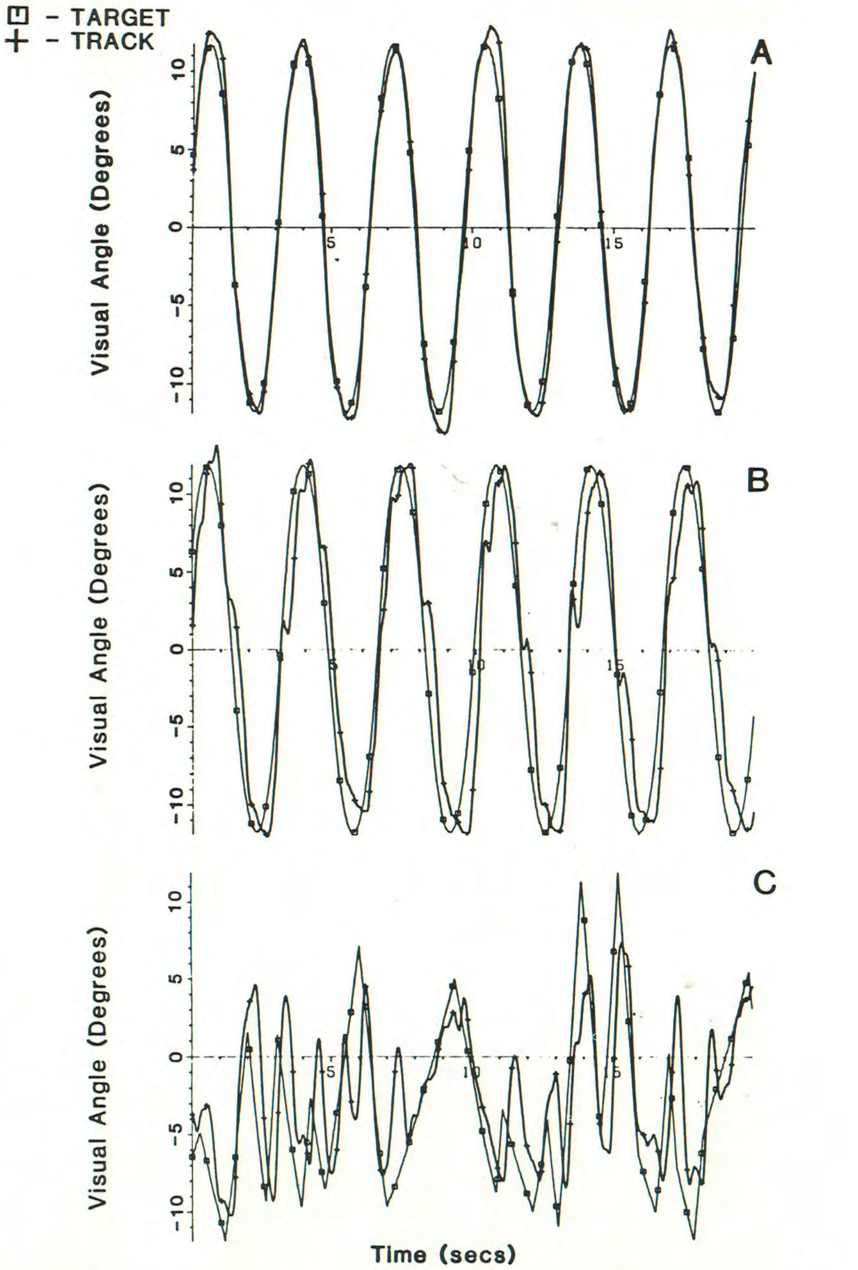


Figure 4. Records of target (light line) and joystick track (heavy line) from a typical subject performing the eight tasks (A-H) studied. The details of each task are given in Table 1. When both a predictable target waveform and pursuit display were used (Tasks A, E), a relatively smooth track was produced; in all other cases, the track consisted of intermittent movements.

Figure 4. **(continued)**

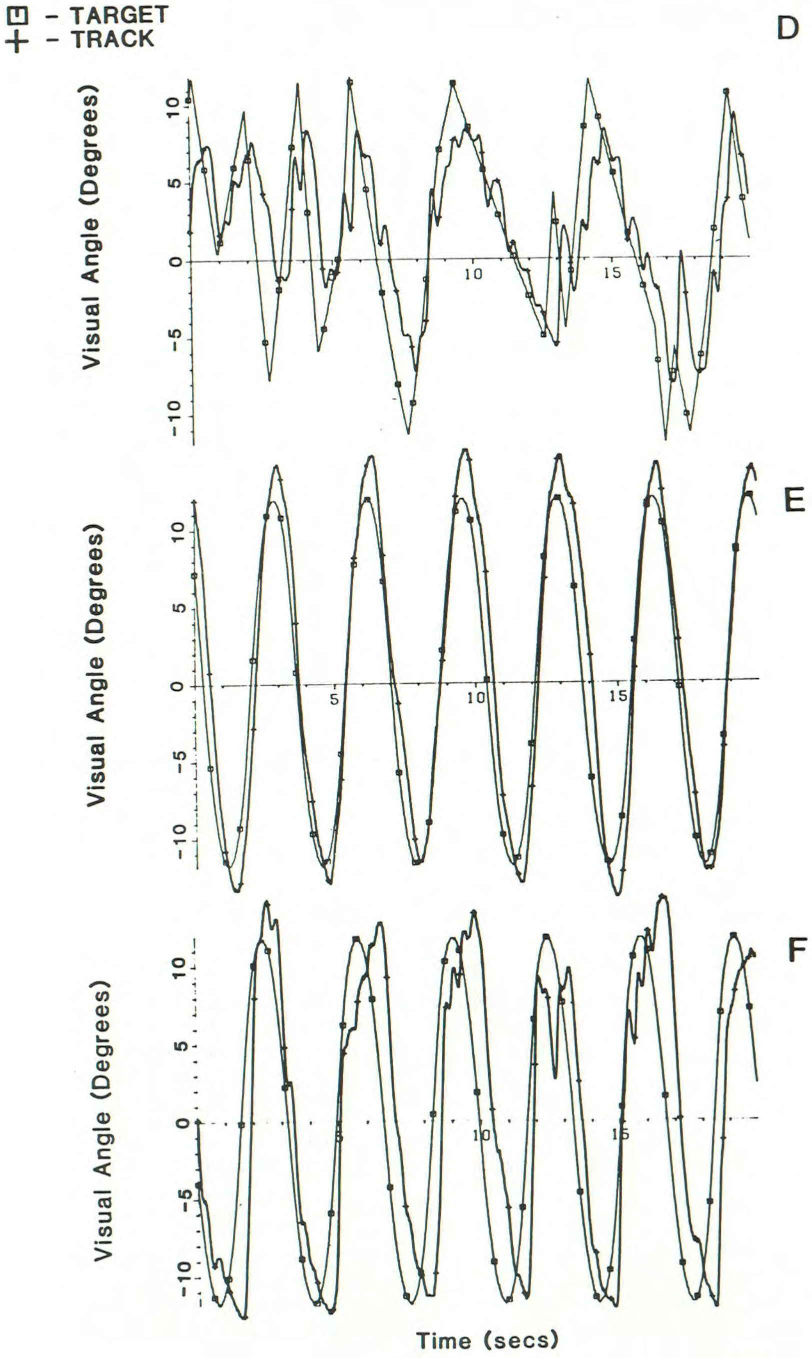
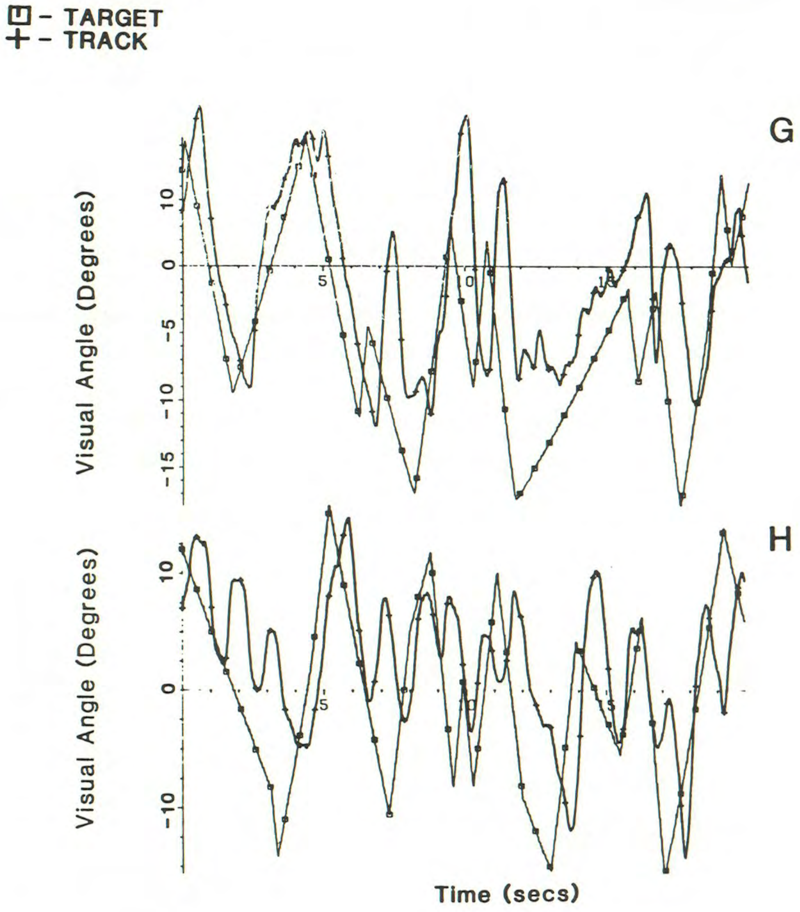


Figure 4. **(continued)**



matching, and regression slope only when a predictable waveform was being tracked. In contrast, there was a significant increase in lag (Figure 5C) irrespective of the waveform tracked. Insertion of a time delay between joystick and monitor spot (loss of VFB information) caused a decrement in all four measures of performance under some conditions. A clear interaction was observed in the lag measure (Figure 5C, Table 3): If the target waveform was predictable, subjects were able to compensate for the 300-ms delay placed between joystick and monitor spot.

Neither varying task order nor intersubject variability had a significant effect, $p = .01$, on overall performance (error), suggesting that transference of skill (Poulton, 1974) between tasks was negligible.

Discussion

Qualitative Results

Craik (1947a, 1947b) believed that human subjects, when tracking a visual target with their hands, behave like an "intermittent servomechanism." He also thought that, if information in addition to visual feedback (VFB) signals were available, the functioning of this servomechanism could be overlayed and smoothed by other processes.

The raw tracking records of a typical subject (Figure 4) agree very well with his views. Intermittency, which Craik thought indicated the action of the underlying servomechanism, was most marked when only VFB signals were available to subjects (Figure 4D). If these VFB signals were then delayed by 300 ms, subjects produced a series of slow, hunting movements (Figure 4H) similar to those that can be produced by an underdamped negative feedback process, such as a servomechanism.

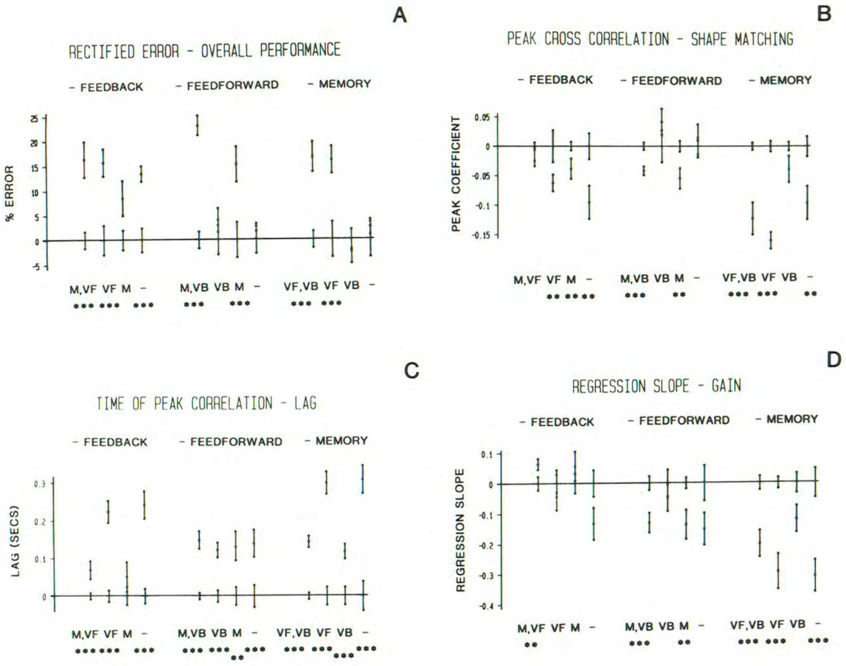


Figure 5. The effect of removing each source of information on four measures of manual tracking. Each source of information was presented in 4 of the 8 tasks (Table 1). The mean performance level (N = 9 subjects) before information source removal has been shifted to zero in each case, and the subsequent change in performance upon source removal plotted as an offset. The standard errors associated with the tasks before and after removal are plotted around zero and the offset, respectively. The source of information removed is displayed above each graph, and the sources of information remaining after the removal are displayed beneath each pair of points (M, memory; VF, visual feedforward; and VB, visual feedback). A paired t test was performed on the performance before and after removal and the results are indicated.
(**p = .05; ***p = .01.)

Table 2
Average Changes in Performance Measures Upon Information Removal

Source of information	Error (%)	Cross-correlation Peak (coeff.)	Cross-correlation Time (s)	Regression slope
Memory	8.2	−0.11	0.22	−0.23
VFF	11.1	−0.01	0.14	−0.12
VFB	13.5	−0.06	0.15	−0.01

Note. Average of 9 subjects. See Table 1 for a description of measures.

Table 3
ANOVA Significance of Removing Each Source of Information

Class	Error	Cross-correlation Peak	Cross-correlation Time	Regression slope
VFF	**0.0001**	0.3315	**0.0001**	**0.0001**
VFB	**0.0001**	**0.0001**	**0.0001**	0.6865
MEM	**0.0001**	**0.0001**	**0.0001**	**0.0001**
VFF*VFB	0.1486	0.3245	0.9999	0.2979
VFF*MEM	**0.0001**	**0.0022**	0.8121	0.5182
VFB*MEM	0.5365	0.0455	**0.0001**	**0.0085**
VFF*VFB*MEM	0.4205	0.6692	0.6348	0.3569

Note. Analysis of variance procedures were run with each of the four measures as the independent variable and with the three information sources and all possible interactions as dependent variables. All models (ANOVA Type 1) were highly significant ($p < .0001$) and had r^2 values of greater than 70%.

Key: * = interaction between.

If further sources of information were added to VFB signals, subjects did, indeed, smooth their intermittency as Craik had suggested. Addition of visual feedforward (VFF) signals by the use of a pursuit display (Figure 4C) led to smoother, but still intermittent, tracking. Provision of a predictable target function (enabling the required trajectory to be memorized) led to even smoother tracking. In fact, subjects were able to track the predictable 0.3 Hz sinusoid in pursuit mode almost completely smoothly (Figure 4A), with the only sign of intermittency being a series of small inflections in the tracking movement. The small size of these inflections and the tiny lag (25 ms) between target and track suggest that other, memory-based ("off-line") processes, had taken over from the intermittent servomechanism.

These off-line processes appear to require not only a predictable target function but also both VFF and VFB signals to function correctly. If VFB signals were delayed, smooth tracking was maintained with a small lag, but subjects consistently overshot the target when the VFB signal reversed direction (Figure 4E). When VFF signals were witheld, subjects returned to intermittent tracking (Figure 4B). This observation suggests that without VFF signals subjects were unable to produce a complete replica of the target waveform from an internal representation, and, therefore, the intermittent servomechanism was once again revealed. If both VFF and VFB signals were degraded (sinusoidal target, compensated display, 300-ms delay, Figure 4F), then intermittency again appeared, but the size of each intermittent movement was determined mainly by its position in the target's sine wave cycle. Under these circumstances, an internal representation may have been used to scale, rather than smooth, the output of Craik's intermittent servomechanism.

The raw tracking records therefore suggest that subjects used two distinct modes of tracking in the 8 tasks studied. When following a predictable target waveform with a pursuit display (VFF signals), subjects produced a smooth track with very little lag, implying that an off-line control strategy was in use. Unless both these sources of information were available, subjects tracked with a series of intermittent movements, probably produced by an on-line negative feedback process.

Quantitative Results

The effects of removing each source of information (Figure 5 and Table 2) show that each cue had a significant effect on error in at least one condition, a result that is in accord with previous studies that demonstrated that each of the three cues can improve tracking performance (Poulton, 1974). The systematic and quantitative analysis presented here (Figure 5 and Tables 2 and 3), however, allows further conclusions to be drawn about the relative importance and interactions of the three cues. Although removal of each cue had an effect on each measure of performance in at least one situation, the size of the change in performance was highly dependent on which other cues were present. Clear interactions were seen between cues: For example, the effect of removing VFF on overall performance was only significant if a predictable target waveform was tracked. In the following paragraphs, an analysis is presented of the effects of removing memorized, VFF, and VFB signals; this analysis is used to suggest mechanisms that can account for the observations.

Subjects who follow a predictable target waveform have the opportunity to memorize an internal representation of the target's trajectory, which subsequently may be played back off-line. An improvement in performance associated with tracking predictable waveforms has been shown in both eye (Michael & Melville-Jones, 1966) and hand (Poulton, 1974; Stark, 1969) tracking. The small lag observed when all three cues were present (Table 1, Task A) suggests that the time delays associated with visual processing had been avoided and that subjects behaved rather like a "function generator." Poulton (1952a, b) described this process as course anticipation, which he classified as a subset of perceptual anticipation. Such a predictive mechanism would require error signals (VFB) to scale the size of waveform produced, and the significant increase in regression slope seen when VFB was removed (leaving memory and VFF cues, Figure 5D) is consistent with the use of delayed error information in this way. An off-line function generator strategy also requires target information to be available in order to synchronize playback of the internally stored waveform. With such information, the subject could compensate for both externally imposed and internal time delays by changing the relationship between the observed target movement and the phase of the memorized function produced. When both VFF and memory cues were present, the lag observed was less than 100 ms (Table 1), and the addition of a 300-ms delay led to an increase of only 70 ms (Table 1, Tasks A and E).

The hypothesis that, for a subject to behave like a function generator, target information (VFF) is required to time the playback of the stored waveform correctly predicts a strong interaction between memory and VFF cues. The effect of removing memory when VFF was available should have been larger than otherwise. Figure 5 shows that this was the case; removal of memory only had a significant effect on overall performance (error) if VFF was present.

The effect of removing memory on lag (Figure 5C) contradicted the function generator hypothesis in two ways:

First, an interaction was seen between memory removal and VFB. This interaction, however, may have been an artifact of the method used to degrade VFB signals. Placing a 300-ms delay between joystick and monitor spot will increase the lag by the same amount in a passive system. If, as we have suggested, subjects can compensate for externally imposed delays when following a predictable waveform, then switching to a pseudorandom one should remove the ability to compensate and lead to a large increase in lag. This was observed (Figure 5C); subjects' lag rose most, following a change to an unpredictable target, if VFB signals had been degraded by an externally imposed lag of 300 ms.

The second observation that contradicted the function generator hypothesis was that replacing a sinusoid with a pseudorandom function had an effect on some of the performance measures even when subjects tracked with a compensated display. There was a significant change in the lag, shape matching, and gain measures (Figure 5C), although overall performance (error) was unaffected. The function generator hypothesis, put forward above, involves the assumption that VFF signals, and therefore a pursuit display, are required to play out a memorized representation of the target's waveform and thus to take advantage of its predictability. Poulton (1974) and Pew, Duffendack, and Fensch (1967) have measured the improvement in performance that occurs as subjects practice tracking single sinusoids with pursuit and compensated displays. Their results suggest that it takes subjects much longer than the 2-min trials used in this study to take advantage of a predictable target waveform when tracking with a compensated display. The detailed analysis presented here shows that, although the overall performance was unaffected, subjects were able to improve aspects of their performance quickly when given a sinusoid to track. Subjects reported that, although detailed target information was not available from a compensated display, they were able to sense when the target had reversed direction and thus to form and play out a partial representation of the sinusoidal target's trajectory. The two observations that appear to conflict with the function generator hypothesis can therefore be explained in terms of inadequacies in the methodology rather than in the hypothesis itself.

Removal of VFF when a predictable target function was being tracked had a much greater effect on overall performance than when the target's trajectory was pseudorandom (Figure 5A). This observation is further evidence of the strong interaction between VFF and memory predicted by the function generator hypothesis. The same interaction can be seen in the shape matching and regression slope measures (Figure 5B, D). In contrast, removing VFF caused a uniform increase in lag that was independent of which other cues were present (Figure 5C), suggesting a role for VFF signals that is not linked to memory. If the target's trajectory is pseudorandom, short-term predictions may nevertheless be made using signals such as target velocity (Poulton's speed anticipation, 1952b). Such predictions would reduce the effect of visual time delays and cut down the lag between target and track. Thus, although there was no significant effect on overall tracking performance (error), removal of VFF did have an effect on tracking lag.

In pursuit mode, subjects smoothly followed the visual target with their eyes. Hence, in these experiments, VFF signals were most probably provided by the oculomotor rather than the retinal system. It is possible to speculate that oculomotor signals reach movement planning centers more rapidly than retinal signals. For example, the lateral cerebellum has been implicated in the planning of movement (Stein, 1978; Strick, 1983), and eye velocity signals with an average latency of a few ms have been recorded in the lateral cerebellum of monkeys tracking square waves in this paradigm (Horvat, 1984; Noda & Mikami, 1986). In contrast, retinal signals caused by the target's movement or by a flash of light reach the lateral cerebellum with an average latency of around 80 ms (Horvat, 1984). The shorter latency of oculomotor signals than retinal signals may permit more accurate predictions of future target position.

The role of visual feedback in scaling the output of a memorized internal representation of the target waveform has been discussed above. Degrading VFB signals also had a significant effect on overall performance when the target waveform was unpredictable, pointing to an additional on-line role. An on-line negative feedback control strategy would suffer from the long time delays inherent in the processing of retinal signals and would be unable to compensate for extra delays placed in the visual feedback loop. The lag observed if only VFB signals were available to subjects (Task D, Table 1) was nearly 300 ms, and when an additional delay was inserted, the lag rose by 240 ms (Task H, Table 1)—almost the value expected from a passive system. In contrast, if subjects were given a predictable target function to track, the addition of a 300-ms delay between joystick and monitor spot was almost entirely compensated for, giving the impression of an interaction between memory and VFB. As discussed before, this result may be an artifact of the manipulation used and may reflect the ability of subjects to employ an off-line strategy capable of compensating for externally imposed delays. There was no clear interaction between VFB and VFF, and none would be expected from the strategy proposed of a servomechanism (VFB) augmented by short-term prediction (VFF), because these processes can operate independently of each other.

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Submitted June 1, 1988
Revised February 3, 1989