COMPLEX PREDICTIVE EYE PURSUIT IN MONKEY: A MODEL SYSTEM FOR CEREBELLAR STUDIES OF SKILLED MOVEMENT

R.E. KETTNER[1*], M. SUH[2], D. DAVIS AND H.-C. LEUNG[3]

[1] Department of Physiology and Neuroscience Institute, Northwestern University Medical School, Chicago, IL 60611, [2] Department of Physiology/Neuroscience, New York University School of Medicine, New York, NY 10016 and [3] Department of Psychology, State University of New York, Stony Brook, NY 11794, USA.

INTRODUCTION

In an age where computers challenge chess grand masters and allow navigation of the solar system, we continue to be astounded by the grace of a ballerina and the agility of a skilled athlete. No robot can equal this motor ability. Highly skilled motor control is perhaps most apparent in the production of music. Exquisite control of the mouth and vocal cords are required to generate a Puccini aria or the lament of an Irish ballad. No robotic hand rivals the touch and feel of the concert violinist, flautist, or pianist.

The scientific examination of skilled motor behaviors is made difficult by their complexity. One complexity associated with many skilled behaviors arises from the need for precise coordination of large numbers of muscles. How this multi-muscle control is accomplished behaviorally and neuronally is an active area of research. One approach has been motivated by robot control systems. This work has focused on brain processing that might allow the conversion of relatively simple kinematic control signals into the more complex dynamic control signals needed for successful execution of complex limb and body motion. These transformations are made complex when muscle-force output is highly nonlinear, when the load being moved is unknown, and when inertial and Coriolis forces come into play.

Another fundamental aspect of skilled motor control is the ability to predict and prepare for upcoming events. Prediction is critically important for biological systems because sluggish neural elements introduce appreciable delays in sensory recognition and motor activation. Beyond this need to compensate for processor and actuator delays, predictive control is also required by engineers who work with much faster mechanical systems. One can never escape the simple idea that to pass a car on a crowded two-lane road, one must initiate carefully timed turns of the steering wheel well before the car begins to turn in and out of ongoing traffic. Similarly, in dance one can only match the beat by beginning movement before the beat occurs, not by responding after the beat.

Smooth eye movements are a good choice for studies of predictive processing during skilled behavior. The eye can pursue targets with high accuracy and very

*Address for correspondence: Dr. R.E. Kettner, Department of Physiology M211, Northwestern University Medical School, 303 East Chicago Ave., Chicago, IL 60611, USA. Tel. (312) 503-0456, Fax (312) 503-5101, E-mail: r-kettner@nwu.edu

small lags along complex trajectories. Given the slow processing of brain systems, these movements are only possible using rather sophisticated forms of predictive control. In addition, accurate pursuit is only observed in primates including man. This suggests a link to the improved cognitive processing observed in these species and the large amount of brain tissue devoted to oculomotor control. These analyses are facilitated by the relative simplicity of the eye movement system: the oculomotor plant drives eye motion using a very few muscles under conditions of constant load. This simplifies the interpretation of behavioral, neural, and modeling results that can be muddied by the complicated dynamics of arm and body control. Monkeys were selected as subjects because they allow accurate measurements of eye motion using surgically implanted eye coils and single-neuron recording during pursuit performance. Other scientists have also noted these advantages. As a result, there is a wealth of background information about the behavior, physiology, and anatomy of the oculomotor system.

The following is a description of our recent progress in studying complex predictive control using behavioral, neural-recording, and modeling studies in monkey (10, 12, 13, 17, 18, 32, 33).

BEHAVIORAL STUDIES

To understand predictive control, one first needs to know how quickly the smooth pursuit system can respond to unpredictable changes in ongoing target motion. This was studied by having the monkey track a circular target motion for several cycles before executing an abrupt right-angle change in target direction along a circle meridian. The time and location of the right-angle perturbation was varied so that the monkey could not predict its occurrence. The results are shown in Figure 1A. The eye accurately followed the circular trajectory before the right-angle perturbation. It then continued along the expected circular trajectory for about 90 ms, before it began to turn toward the altered target motion. This indicates a considerable delay in processing visual input about unexpected changes in target direction. Similar delays in visual processing have been reported for the initiation of pursuit after a moving target is turned on (7, 22).

It is therefore surprising that the delay between eye and target was only 5 ms during uninterrupted circular pursuit for the same monkeys (Fig. 1B). The smooth pursuit system appears to predict slow changes in target direction before visual information about these changes has been processed with a 90 ms delay. Put another way, this is not what one would expect from simple feedback controllers driven directly by image slip on the retina. For such systems, one would expect much poorer performance with lags of about 90 ms after changes in target motion. Other investigators have also described accurate pursuit of sinusoidal, circular, and other simple periodic motions (1, 2, 16, 23, 29, 35).

A more obvious form of prediction is required when a target is briefly turned off. This happens when the eye continues to pursue a bird that flies behind a tree.
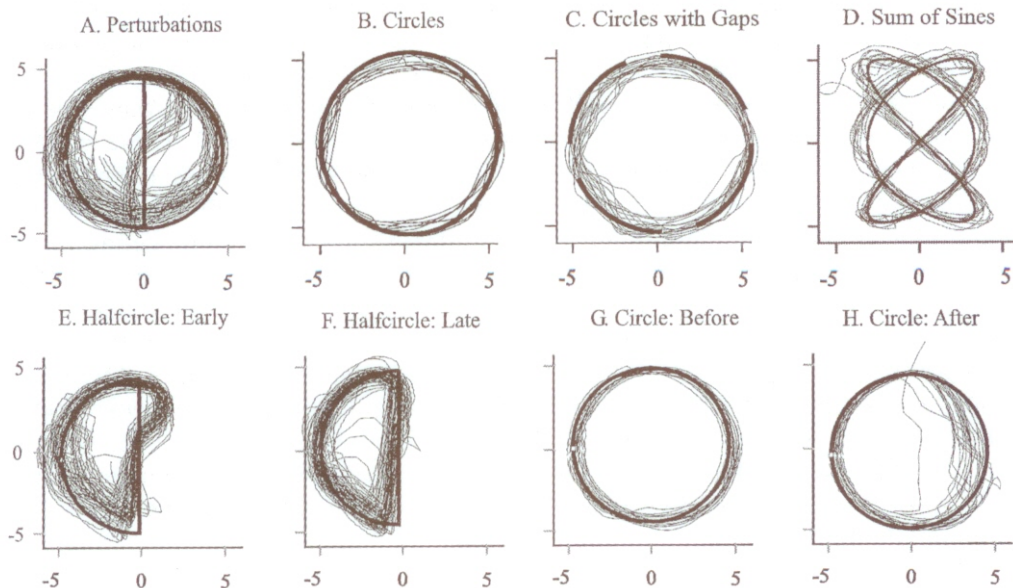
Fig. 1. - *Pursuit behavior (thin lines) is illustrated for a variety of target motions (thick lines).* Compare the pronounced error after (A) unexpected perturbations from circle pursuit with the accuracy of pursuit along predictable (B) circle, (C) circle with target gaps, and (D) sum-of-sines trajectories. Bottom panels illustrate the affect of repeated training on a half-circle trajectory: (E) early overshoot is gradually reduced until it is nearly absent (F) late in training. Aftereffects during circle pursuit are apparent in comparisons (G) before and (H) after training. Scales indicate eye position in degrees.

Experimentally, we studied this type of prediction by blinking off the target for 100 ms at up, down, right, and left locations during a circular target motion (Fig. 1C). The monkeys showed no difference in pursuit lag for performance on circular trajectories with and without target gaps. This result is interesting because one would expect declines in performance for controllers driven by visual inputs about 90 ms after the target was turned off. The continuation of pursuit during short target gaps has also been observed for straight-line trajectories (25). Of course, one expects some breakdown in pursuit performance for gaps of extended duration (4). To test this idea, we have recently begun to examine the effects of unexpectedly turning off the target for a longer period of 300 ms during circular pursuit. Preliminary results indicate that initial declines in performance during these longer gaps became smaller across several days of training.

To rule out the idea that a simple biological oscillator, a simple transformation such as a differentiation or integration, or a simple shift in phase in visual input might be driving these zero-lag behaviors, we next examined pursuit along more complex target motions. Figure 1D shows pursuit performance along a two-dimensional trajectory created by summing sinusoids of different frequency on horizontal and vertical axes. Although complex, this sum-of-sines trajectory had a relatively short repeat period that made predictive control possible. As for the circle trajectories performance was excellent. The average delay was 4 ms for four sum-of-two-

sines trajectories that were studied. In fact, a slight average lead of 9 ms was observed for four sum-of-three-sines trajectories. Both averages were much smaller than the 90 ms delay expected for controllers based on visual feedback.

It should be noted that sum-of-sine trajectories have also been used to generate pseudo-random target motions. Here the primary intent was to study pursuit without the influence of predictive control. Compared to our trajectories, these sum-of-sines motions were constructed using larger numbers of component sinusoids with frequencies that were not integral multiples of each other. This resulted in complex waveforms that did not repeat during a single presentation period. Even so, these studies demonstrated small phase lags for high-frequency components and even a tendency toward phase leads for low-frequency components (3, 5, 6, 11, 36). Thus, the pursuit system is able to use regularities in these trajectories to generate performance that is much better than expected from visual control alone. Monkeys performed at even higher levels in our experiments due to the shorter repeat periods of our trajectories and longer training periods extending for several weeks.

If one believes that a predictive controller uses past experience about a particular trajectory to improve future performance, then this suggests that predictive control is learned. To test the idea, we studied whether monkeys could learn to successfully navigate the right-angle perturbation illustrated in Figure 1A with extended training. In these experiments, the monkeys pursued a repeated half-circle trajectory for thou-
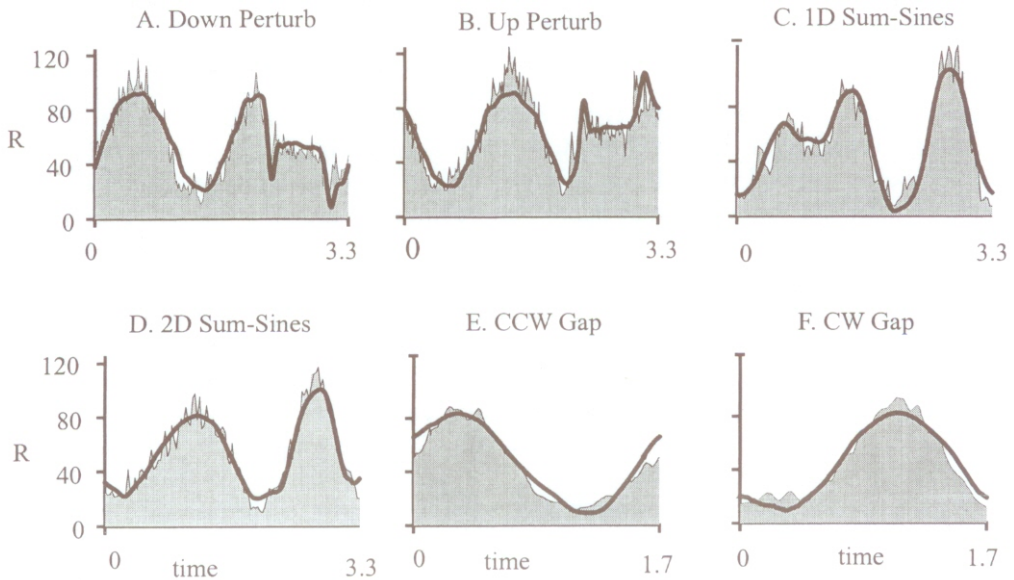

Fig. 2. - *Neural response histograms (in gray) during pursuit are well explained by Equation 1 (thick lines) as a combination of eye-position, eye-velocity and eye-acceleration sensitivities.*
Examples illustrate good fits during abrupt changes in horizontal motion for (A) downward and (B) upward perturbations from circle pursuit, as well as for complex (C) one-dimensional and (D) two-dimensional sum-of-sines motions. A lack of visual control is indicated by the lack of interruption during target gaps for (E) CCW and (F) CW circle pursuit with gaps.

sands of cycles. Initially, the eye overshot the target as previously observed for unexpected right-angle perturbations during circular pursuit (Fig. 1E). However, after several hundred repetitions of the half-circle pursuit performance improved until the right angle was executed with little or no error (Fig. 1F). In addition, a comparison of circle tracking before (Fig. 1G) and after (Fig. 1H) half-circle training indicated clear aftereffect errors during the previously well-executed circle trajectory. These aftereffects remained for several hundred cycles until accurate circle pursuit was again observed. The fact that accurate half-circle pursuit required hundreds of cycles and that aftereffects remained for hundreds of cycles indicates that permanent alterations in pursuit processing occur when one switches trajectories. Learned changes in the initiation of pursuit have also been observed (9).

BRAIN STUDIES

To better understand the neural mechanisms controlling predictive pursuit, we recorded from single neurons during many of the paradigms described above. The flocculus/paraflocculus region of the cerebellum was selected for initial study because several experiments have indicated its significance in pursuit processing. Lesions of this region produce severe declines in pursuit (37) and single neuron responses are highly correlated with pursuit behavior (19, 20, 24, 26, 30).

Our studies have verified the existence of strong correlations between the responses of individual Purkinje cells and eye motion along sinusoidal, circular, sum-of-sines, and gap trajectories, as well as the execution of unexpected right-angle turns during circular pursuit. Figure 2 shows average response histograms (gray filled areas) of Purkinje firing during sum-of-sines, gap, and perturbed pursuit. These observations were quantified by expressing the instantaneous firing rate of each neuron as the sum of two-dimensional eye-position, eye-velocity and eye-acceleration sensitivities using the following equation:

$$R(t) = \beta + \rho \cdot \mathbf{P}(t + \tau) + \nu \cdot \mathbf{V}(t + \tau) + \alpha \cdot \mathbf{A}(t + \tau). \quad (1)$$

Here R is the neural firing rate, t is the time, β is the baseline firing rate, ρ, ν and α are sensitivity vectors, $\mathbf{P}$, $\mathbf{V}$ and $\mathbf{A}$ are eye-position, eye-velocity and eye-acceleration vectors, τ measures the time difference between neural firing and eye motion, and vector multiplication is via the dot product. The dark lines in Figure 2 indicate the excellent regression fits provided by this model. These analyses indicated that eye-position and eye-velocity sensitivities accounted for most of the observed variation in firing rate. Interestingly, eye-position and eye-velocity sensitivities were generally maximal for different directions.

Purkinje cell responses were not related to visual input (image slip on the retina). This result is based on a lack of improvement in fit when visual position, velocity, and acceleration terms were added to Equation 1. This is a surprising because it suggests a lack of visual drive in this brain region. For sum-of-sines, circle, and gap trajectories

this finding can be explained by the accuracy of pursuit behavior: there was no consistent pattern of retinal-slip to drive predictive pursuit during these well-executed behaviors. Less expected was the lack of visual influence during unpredictable perturbations: these perturbations were designed to produce consistent periods of tracking error that generated visual error signals. However, responses both before and during perturbed pursuit were again explained by sensitivities to eye motion alone. Interestingly, some neurons showed reduced activity during unpredictable perturbations in comparison to pursuit along predictable target motions. We hypothesize that brain regions external to the flocculus/paraflocculus made up the difference by supplying increased levels of visual drive during unpredictable target motion.

Importantly, estimates of τ from Equation 1 allowed us to determine whether Purkinje cell responses led or lagged eye motion. On average, Purkinje cell responses led eye motion by 12 ms during predictable sum-of-sines pursuit, 6 ms during circle pursuit with gaps, and only 2 ms during unpredictable right-angle perturbations. Given the 9-ms transmission delay between flocculus stimulation and eye motion (21, 27), this result suggests that the flocculus/paraflocculus drives pursuit during predictable motions, but plays a follow-up role during unpredictable perturbations. An intermediate role is suggested for trajectories with gaps.

In combination, these findings support the idea that the flocculus/paraflocculus is involved in predictive control during pursuit and acts in conjunction with other brain regions that generate visual control signals. During well-learned predictable trajectories, flocculus/paraflocculus predictive signals drive eye motion while other brain areas provide relatively weaker visual control signals. During unpredictable pursuit, visually driven signals from other brain regions dominate the control of pursuit, while flocculus/paraflocculus plays a relatively weaker and delayed role.

COMPUTER MODELING STUDIES

To account for these results, we have utilized neural network modeling techniques based on the known anatomy and physiology of the flocculus/paraflocculus system. Our current model (10) can generate all of the predictive behaviors described above. Furthermore, the model accounts for many features of flocculus/paraflocculus physiology and anatomy. It explains the dominance (~ 80%) of mossy-fiber input related to eye motion and the relative paucity (~ 5%) of visual mossy-fiber input to flocculus/paraflocculus. It also accounts for the strong Golgi-cell inhibition observed in cerebellar glomeruli. The model utilizes the long-term plasticity observed at parallel-fiber-to-Purkinje-cell synapses to learn new trajectories. Finally, it explains why complex spikes triggered by inferior olivary inputs occur at very low frequency. This new model is noteworthy, along with a previous model (12), in being the only pursuit model that has been able to provide biologically realistic mechanisms for generating predictive pursuit.

Mossy fiber input to the model is based on empirical studies (20, 24) that describe a linear increase in firing rate with progressive eye movement in an "on" direction after a threshold eye position is exceeded. Importantly, this threshold varies across

mossy fibers. This means that different subpopulations of mossy fibers are activated as the eye moves throughout two-dimensional space. Golgi-cell inhibition within synaptic glomeruli further fractionates these activation patterns so that distinct subpopulations of parallel fibers are active at each point along a trajectory. The model generates predictive control by linking these subpopulations to specific Purkinje output cells via appropriate parallel-to-Purkinje synaptic connection weights. For example, the subpopulation of parallel fibers activated as the eye move towards the top of the half-circle (Fig. 1F) is trained to activate Purkinje cells that drive the eye downward. This allows the predictive initiation of downward eye motion before the target begins to move downward and well before visual information about this change in trajectory is processed visually. Of course, this strategy only works when a right-angle change in target motion consistently occurs at a particular point on the half-circle motion.

The above description argues that predictive control is based on eye-motion instead of visual mossy-fiber input. This explains the observed predominance of eye-motion input within the flocculus/paraflocculus, the absence of visually driven Purkinje-cell responses, and neural lead times during predictive control compared to lags during visually driven pursuit. Model simulations support this idea. Initial versions of the model learned quite slowly because they used random combinations of eye-motion and visual mossy-fiber input. Subsequent simulations learned more quickly when eye-motion and visual mossy-fiber input were separated. In fact, when visual mossy-fiber input was completely eliminated the model still generated predictive pursuit. In these simulations, only a rudimentary saccade generator was needed to occasionally correct eye position errors as observed during natural eye pursuit.

The model learns new trajectories by modifying parallel-fiber-to-Purkinje-cell synapses using a computer algorithm (14, 34) that is motivated by empirical studies of long-term plasticity. Put simply, synapses are modified when they are active during poor behavior and not altered when they are associated with accurate performance. This simple rule eventually leads to accurate pursuit performance. In the model, infrequent (500 ms refractory period) climbing-fiber pulses signal performance errors as measured by visual error (8, 15, 28, 31) and synaptic traces signal parallel-fiber activation. When both are active, synaptic strengths are altered. A similar algorithm based on a continuous climbing-fiber error signal was used in a previous model (12). Interestingly, the slower discrete climbing-fiber signals used in the newest model make it more stable, a possible explanation for the low occurrence of complex spikes observed in biological systems during pursuit.

DISCUSSION

Sophisticated brain systems allow the elegant and precise motor control that is observed in skilled athletes and musicians. These systems also generate smooth and accurate eye pursuit along complex target trajectories by using predictable features of these trajectories to improve performance. This is particularly important given the sluggishness (~ 90 ms delay) of biological systems in processing visual information.

Predictive control allows changes in eye motion to be initiated at the proper time and well before visual information about changes in target motion are processed. This control is so successful that the target image is stabilized on the retina and visual drive for pursuit is essentially eliminated. The only neural signals that remain to drive predictive pursuit are related to eye motion. For the oculomotor system, these signals arise from neurons that either directly or indirectly drive eye muscles. Brain systems controlling other movements can also utilize efference copy information to improve performance in addition to proprioceptive information derived from somatosensory, joint, and muscle-spindle input.

We suggest that the flocculus/paraflocculus region of the cerebellum generates this non-visual predictive control. Its activity is highly correlated with eye motion and only weakly correlated with visual image motion. In addition, neural activity in this brain area leads predictable target motion but lags unpredictable target motion. Our modeling efforts indicate how the flocculus/paraflocculus might generate predictive control. Specific sub-populations of its parallel-fiber input become active as the eye moves along a well-practiced trajectory and these sub-populations generate appropriate motor outputs via their connectivity strengths with Purkinje-cell output neurons. Appropriate parallel-fiber-to-Purkinje-cell synaptic strengths are learned using an algorithm based on cerebellar long-term depression. A prediction of this model is that relatively arbitrary trajectories can be acquired with extended practice and that this learning interferes with previously learned behaviors. This prediction was confirmed by behavioral studies of pursuit learning that demonstrate dramatic improvements in half-circle pursuit with extended training and the existence of aftereffects during a previously well-executed circle trajectory. Aside from their importance in understanding oculomotor control, these ideas should also prove useful in understanding the cerebellum's role in controlling other skilled movements.

SUMMARY

Smooth pursuit eye movements provide a good model system for cerebellar studies of complex motor control in monkeys. First, the pursuit system exhibits predictive control along complex trajectories and this control improves with training. Second, the flocculus/paraflocculus region of the cerebellum appears to generate this control. Lesions impair pursuit and neural activity patterns are closely related to eye motion during complex pursuit. Importantly, neural responses lead eye motion during predictive pursuit and lag eye motion during non-predictable target motions that require visual control. The idea that flocculus/paraflocculus predictive control is non-visual is also supported by a lack of correlation between neural activity and retinal image motion during pursuit. Third, biologically accurate neural network models of the flocculus/paraflocculus allow the exploration and testing of pursuit mechanisms. Our current model can generate predictive control without visual input in a manner that is compatible with the extensive experimental data available for this cerebellar system. Similar types of non-visual cerebellar control are likely to facilitate the wide range of other skilled movements that are observed.

REFERENCES

1. BAHILL, A.T. AND MCDONALD, J.D. Smooth pursuit eye movements in response to predictable target motions. *Vision Res.,* **23**: 1573-1583, 1983.
2. BARNES, G.R. AND ASSELMAN, P.T. The mechanisms of prediction in human smooth pursuit eye movements. *J. Physiol., Lond.,* **439**: 439-461, 1991.
3. BARNES, G.R., DONNELLY, S.F. AND EASON, R.D. Predictive velocity estimation in the pursuit reflex response to pseudo-random and step displacement stimuli in man. *J. Physiol., Lond.* **389**: 111-136, 1987.
4. BECKER, W. AND FUCHS, A.F. Prediction in the oculomotor system: smooth pursuit during transient disappearance of a visual target. *Exp. Brain Res.,* **57**: 562-575, 1985.
5. COLLEWIJN, H. AND TAMMINGA, E.P. Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *J. Physiol., Lond.,* **351**: 217-250, 1984.
6. DALLOS, P.J. AND JONES, R.W. Learning behavior of the eye fixation control system. *IEEE Transactions on Automatic Control.,* **8**: 218-227, 1963.
7. FUCHS, A.F. Saccadic and smooth pursuit eye movements in the monkey. *J. Physiol., Lond.,* **191**: 609-631, 1967.
8. FUSHIKI, H., SATO, Y., MIURA, A. AND KAWASAKI, T. Climbing fiber responses of Purkinje cells to retinal image movement in cat cerebellar flocculus. *J. Neurophysiol.,* **71**: 1336-1350, 1994.
9. KAHLON, M. AND LISBERGER, S.G. Coordinate system for learning in the smooth pursuit eye movements of monkeys. *J. Neurosci.,* **16**: 7270-7283, 1996.
10. KETTNER, R.E. AND SUH, M. Biological realism improves the performance of a flocculus/paraflocculus model of predictive smooth pursuit eye movements. *Soc. Neurosci. Abstr.,* **24**: 1410, 1998.
11. KETTNER, R.E., LEUNG, H.-C. AND PETERSON, B.W. Predictive smooth pursuit of complex two-dimensional trajectories in monkey: component interactions. *Exp. Brain Res.,* **108**: 221-235, 1996.
12. KETTNER, R.E., MAHAMUD, S., LEUNG, H.-C., SITKOFF, N., HOUK, J.C., PETERSON, B.W. AND BARTO, A.G. Prediction of complex two-dimensional trajectories by a cerebellar model of smooth pursuit eye movement. *J. Neurophysiol.,* **77**: 2115-2130, 1997.
13. KETTNER, R.E., SUH, M. AND DAVIS, D. Smooth eye movements improve with training and predictability along half-circle trajectories in monkey. *Soc. Neurosci. Abstr.,* **26**: 1330, 2000.
14. KLOPF, A.H. *Brain Function and Adaptive Systems - Aeterostatic Theory,* Bedford, MA: Air Force Cambridge Research Laboratories (AFCRL-72-0164), 1972.
15. KOBAYASHI, Y., KAWANO, K., TAKEMURA, A., INOUE, Y., KITAMA, T., GOMI, H. AND KAWATO, M. Temporal firing patterns of purkinje cells in the cerebellar ventral paraflocculus during ocular following responses in monkeys. II. Complex spikes. *J. Neurophysiol.,* **80**: 832-848, 1998.
16. KOWLER E. AND STEINMAN R.M. The effect of expectations on slow oculomotor control - I. Periodic target steps. *Vision Res.,* **19**: 619-632, 1979.
17. LEUNG, H.-C. AND KETTNER, R.E. Predictive smooth pursuit of complex two-dimensional trajectories demonstrated by perturbation responses in monkeys. *Vision Res.,* **37**: 1347-1354, 1997.
18. LEUNG, H.-C., SUH, M. AND KETTNER, R.E. Cerebellar flocculus and paraflocculus purkinje cell activity during circular pursuit in monkey. *J. Neurophysiol.,* **83**: 13-30, 2000.

19. LISBERGER, S.G. AND FUCHS, A.F. Role of primate flocculus during rapid behavioral modification of vestibuloocular reflex. I. Purkinje cell activity during visually guided horizontal smooth-pursuit eye movements and passive head rotation. *J. Neurophysiol.,* **41**: 733-763, 1978.

20. LISBERGER, S.G. AND FUCHS, A.F. Role of primate flocculus during rapid behavioral modification of vestibuloocular reflex. II. Mossy fiber firing patterns during horizontal head rotation and eye movement. *J. Neurophysiol.,* **41**: 764-777, 1978b.

21. LISBERGER, S.G. AND PAVELKO, T.A. Brain stem neurons in modified pathways for motor learning in the primate vestibulo-ocular reflex. *Science,* **242**: 771-773, 1988.

22. LISBERGER, S.G. AND WESTBROOK, L.E. Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *J. Neurosci.,* **5**: 1662-1673, 1985.

23. LISBERGER, S.G., EVINGER, C., JOHANSON, G.W. AND FUCHS, A.F. Relationship between acceleration and retinal image velocity during foveal smooth pursuit in man and monkey. *J. Neurophysiol.,* **46**: 229-249, 1981.

24. MILES, F.A., FULLER, J.H., BRAITMAN, D.J. AND DOW, B.M. Long-term adaptive changes in primate vestibuloocular reflex. III. Electrophysiological observations in flocculus of normal monkeys. *J. Neurophysiol.,* **43**: 1437-1476, 1980.

25. NEWSOME, W.T., WURTZ, R.H. AND KOMATSU, H. Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J. Neurophysiol.,* **60**: 604-620, 1988.

26. NODA, H. AND SUZUKI, D.A. The role of the flocculus of the monkey in fixation and smooth pursuit eye movements. *J. Physiol., Lond.,* **294**: 335-48, 1979.

27. SHIDARA, M. AND KAWANO, K. Role of Purkinje cells in the ventral paraflocculus in short-latency ocular following responses. *Exp. Brain Res.,* **93**: 185-195, 1993.

28. SIMPSON, J.I. AND ALLEY, K.E. Visual climbing fiber input to rabbit vestibulo-cerebellum: a source of direction-specific information. *Brain Res.,* **82**: 302-308, 1974.

29. STARK, L., VOSSIUS, G. AND YOUNG, L.R. Predictive control of eye tracking movements. *IRE Transactions Human Factors in Electronics,* **HFE-3**: 52-57, 1962.

30. STONE, L.S. AND LISBERGER, S.G. Visual responses of Purkinje cells in the cerebellar flocculus during smooth pursuit eye movements in monkeys I. Simple spikes. *J. Neurophysiol.,* **63**: 1241-1261, 1990.

31. STONE, L.S. AND LISBERGER, S.G. Visual responses of Purkinje cells in the cerebellar flocculus during smooth pursuit eye movements in monkeys II. Complex spikes. *J. Neurophysiol.,* **63**: 1262-1275, 1990.

32. SUH, M., DAVIS, D. AND KETTNER, R.E. Smooth eye movements improve with training during random target gaps in monkey. *Soc. Neurosci. Abstr.,* **26**: 1716, 2000.

33. SUH, M., LEUNG, H.-C. AND KETTNER, R.E. Cerebellar flocculus and ventral paraflocculus purkinje cell activity during predictive and visually driven pursuit in monkey. *J. Neurophysiol.,* **84**: 1835-50, 2000.

34. SUTTON, R.S. AND BARTO, A.G. Toward a modern theory of adaptive networks: expectation and prediction. *Psych. Rev.,* **88**: 135-170, 1981.

35. WESTHEIMER, G. EYE movement response to a horizontally moving visual stimulus. *AMA Arch. Ophthalmol.,* **52**: 932-941, 1954.

36. YASUI, S. AND YOUNG, L.R. On the predictive control of foveal eye tracking and slow phases of optokinetic and vestibular nystagmus. *J. Physiol., Lond.,* **347**: 17-33, 1984.

37. ZEE, D.S., ATSUMI, Y., BUTLER, P.H. AND GÜÇER, G. Effects of ablation of flocculus and paraflocculus on eye movements in primate. *J. Neurophysiol.,* **46**: 878-899, 1981.