

Motion dependence of smooth pursuit eye movements in the marmoset

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Mitchell JF, Priebe NJ, Miller CT. Motion dependence of smooth pursuit eye movements in the marmoset. *J Neurophysiol* 113: 3954–3960, 2015. First published April 1, 2015; doi:10.1152/jn.00197.2015.—Smooth pursuit eye movements stabilize slow-moving objects on the retina by matching eye velocity with target velocity. Two critical components are required to generate smooth pursuit: first, because it is a voluntary eye movement, the subject must select a target to pursue to engage the tracking system; and second, generating smooth pursuit requires a moving stimulus. We examined whether this behavior also exists in the common marmoset, a New World primate that is increasingly attracting attention as a genetic model for mental disease and systems neuroscience. We measured smooth pursuit in two marmosets, previously trained to perform fixation tasks, using the standard Rashbass step-ramp pursuit paradigm. We first measured the aspects of visual motion that drive pursuit eye movements. Smooth eye movements were in the same direction as target motion, indicating that pursuit was driven by target movement rather than by displacement. Both the open-loop acceleration and closed-loop eye velocity exhibited a linear relationship with target velocity for slow-moving targets, but this relationship declined for higher speeds. We next examined whether marmoset pursuit eye movements depend on an active engagement of the pursuit system by measuring smooth eye movements evoked by small perturbations of motion from fixation or during pursuit. Pursuit eye movements were much larger during pursuit than from fixation, indicating that pursuit is actively gated. Several practical advantages of the marmoset brain, including the accessibility of the middle temporal (MT) area and frontal eye fields at the cortical surface, merit its utilization for studying pursuit movements.

eye movements; marmoset; primate; pursuit; vision

SMOOTH PURSUIT EYE MOVEMENTS have been extensively studied in rhesus monkeys and humans, providing critical insight into visual processing, choice, motor planning, and plasticity (for review, see Lisberger et al. 1987). Pursuit eye movements are voluntary movements that allow for the stabilization of slow-moving objects on the retina by matching eye velocity with target velocity. Pursuit is a voluntary behavior driven by the motion of a selected target. In contrast to ocular following responses that depend on wide-field motion, pursuit eye movements allow the viewer to stabilize small targets by extracting target motion signals from competing motion signals. For example, in tracking a bird flying in front of a grove of trees, the motion signals that drive pursuit eye movements are determined by the difference in eye and bird velocity. As noted

by Gregory (1958), however, the smooth movement of the eye produces motion signals from the stationary trees in the opposite direction. Those motion signals must be separated from the signals of the target. Of further interest, the target in this example, the bird, is perceived as moving, although during the closed-loop portion of pursuit it remains stable on the retina, whereas the background trees moving across the retina are perceived as stationary. These perceptual phenomena are consistent with the notion that oculomotor feedback drives pursuit as well as our perception of motion (Robinson et al. 1986; Yasui and Young 1975). Several studies confirm the perceived object motion, rather than retinal motion, influences pursuit velocity (Steinbach 1976; Stone et al. 2000, 2009). The ability to select a small moving target and to disambiguate it from background motion may be related to the selection of targets conferred by activity in frontal cortical areas, which have undergone a rapid expansion among primates (Chaplin et al. 2013), as well as unique primate visual areas, areas middle temporal (MT) and medial superior temporal (MST), that have neurons selective to real vs. retinal motion (Chukoskie and Movshon 2009).

In the current study, we examined the pursuit eye movements in a small-bodied New World species, the common marmoset (*Callithrix jacchus*). Some of the first primate transgenic lines have been developed in the marmoset, promising new opportunities for studying human neuropsychological disorders and providing genetic access for probing neural circuitry in primates (Sasaki et al. 2009; Shen et al. 2013). Furthermore, the marmoset presents advantages for modern imaging and array recording techniques because many of its visual cortical areas, as well as frontal cortical areas associated with eye movements, are accessible on the surface of its smooth lissencephalic brain. Although pursuit eye movements have been demonstrated in another New World primate, the squirrel monkey (Heiney and Blazquez 2011), no studies have yet examined the marmoset. Among primates, the marmoset is specialized for smaller size and faster breeding, and although the visual system remains highly similar in organization to that of larger species like the macaque (Mitchell and Leopold 2015; Solomon and Rosa 2014), much less is known about its oculomotor behavior or the organization of those frontal areas involved in pursuit. If pursuit behavior were conserved, the marmoset would afford unique opportunities for studying the neural circuitry involved, as both MT/MST and frontal eye field are accessible at the cortical surface.

We characterized visual motion dependence of smooth eye movement in marmosets trained to perform fixation tasks. We measured the eye movements evoked by target motion using

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the standard Rashbass (1961) step-ramp paradigm. We found that marmosets naturally pursue small moving targets with some degree of diligence without any further demands on their behavioral conditioning other than their initial fixation training. As seen in other primates, we find that initial pursuit is driven by the direction of target motion, with acceleration amplitude related to the target velocity. Furthermore, we find that eye movements evoked by small perturbations in target velocity are larger during pursuit than from fixation, indicating that distinct modes exist for tracking targets. These features resemble those of macaques and humans, although marmosets do complete much fewer trials than is typical of a highly trained macaque. We conclude that the marmoset does exhibit the pursuit behavior naturally and thus may provide a complementary model system in which to study the natural sensory-motor transformations involved in smooth pursuit.

METHODS

Eye movements were collected from two marmoset subjects with surgically implanted head posts for head stabilization. All procedures with marmosets were performed in the laboratory of C. T. Miller under the approval of the Institutional Animal Care and Use Committee at the University of California, San Diego. The design of the primate chair, surgery to install head implants, and behavioral conditioning under head restraint have been reported in earlier studies of auditory processing (Lu et al. 2001a,b; Osmanski et al. 2013; Remington et al. 2012). Two male marmosets participated in the current studies. Both had been trained to maintain fixation on a small central point using methods for eye tracking described in a previous study (Mitchell et al. 2014). All procedures conformed to National Institutes of Health guidelines. Both subjects were maintained on food control to provide motivation in behavioral tasks with their weight reduced from 5 to 10% of baseline.

Eye position calibration and stimulus presentation. Eye position of the right eye was continuously monitored with an infrared eye tracking system (120 Hz, spatial resolution 0.1 visual degrees root-mean-square error; ETL-200; ISCAN). The camera was placed to the lower right visual field (12–15° eccentricity), 15 cm away from the eye. In a small number of sessions, we repeated tests monitoring the left eye instead of the right eye. Stimulus presentation, data acquisition, and reward control were handled by National Institute of Mental Health (NIMH) Cortex software (<http://dally.nimh.nih.gov/>). The eye position was measured directly from the center of mass of the dark thresholded pixels corresponding to the pupil without use of the corneal reflection to correct for head motion as the head was fixed. Analog outputs of the eye position signals were oversampled at 500 Hz and stored digitally, with time stamps for stimulus events, using the software package Cortex. Eye position was calibrated as described previously (Mitchell et al. 2014). First preferential looking toward marmoset faces at discrete positions on the screen was used to obtain a rough calibration of the eye tracking system. This calibration was then followed by a fixation task in which the fixation target was positioned at the center and 5° eccentric from center in four directions (up, down, left, or right). The horizontal and vertical gains were adjusted in each daily session to ensure fixation was centered within a 1° radius window at each of these positions. Position error at these eccentric locations was <10%.

Fixation stimuli for tracking tasks were presented on a computer monitor that was adjusted for a high background luminance to constrict the marmoset pupil. Although many pursuit tasks in humans and macaques maximize stimulus contrast using a black background, this poses a problem for infrared video tracking because the marmoset pupil is large relative to the orbits of the eyes, and its edges can be easily occluded under the orbits in dim lighting. We used a gray

background of high luminance to ensure the pupil was constricted within the orbits. The background luminance was 90 cd/m² (Sony SDM-X95F; 1,024 × 768 pixels, 60 Hz). The spatial and temporal discretization does cause slight inhomogeneities in stimulus velocity, but these are generally small. Variations in target velocity due to discretization error had a root-mean-square error <12% of the mean target velocity for different stimulus speeds.

Behavioral tasks. We characterized smooth pursuit in marmosets by measuring the eye movements evoked by target motion using the standard Rashbass (1961) step-ramp paradigm. In this paradigm, the marmoset was rewarded for tracking a small circular fixation point (0.3° diameter, white color 226 cd/m²) that jumped to an eccentric position briefly and crossed back through central fixation at constant velocity. A task trial is depicted in Fig. 1A, with the horizontal position of a moving target indicated by the black dashed trace superimposed with the marmoset's horizontal eye positions shown as a solid trace. Each trial began with an initial period of fixation on a central point (fixation window 2° in diameter 300 ms) after which the point jumped to an eccentric position and began moving back to the central position at fixed velocity. The eccentricity of the jump was such that the point would cross central fixation after 250 ms (or 200 ms in some later sessions in trying to reduce saccades to the jump location). Target direction randomly varied between left and right motion or among the four cardinal directions on a trial-by-trial basis. A range of target velocities were further explored across and within sessions beginning with slower velocities in early sessions and progressively including trials with faster motion (3, 4, 6, 8, 10, 12, 14, and 16°/s). A juice reward was given if eye position was maintained within a window centered on the target (3° in diameter for velocities <6°/s, otherwise 4.5°). Initially, a grace period of 250 ms was also provided to allow the subject adequate time to acquire the moving target. Successful trials could result from either saccadic or slow eye movements as long as eye position was within the target window beyond the initial grace period. In a second version of the task, we measured eye movements to small perturbations in the velocity of the target. The perturbations had a sinusoidal velocity profile that had a duration of 250 ms, thus discretized to 15 video frames (Fig. 4, lower panels), and that ranged in amplitude from 2.5 to 10°/s and either occurred from fixation or during pursuit of a target moving at 4°/s. In the first subject, horizontal pursuit trials were initiated from a position equally eccentric from the central position such that the perturbation would occur at the center in passing to the other side. For the second subject, trials were initiated identically to the main Rashbass (1961) paradigm, with the perturbation occurring after crossing the central position. Trials were also included in both cases in which the target motion was constant, lacking the perturbation. In daily sessions, not including other tasks such as fixation, *marmoset P* completed on average 47.2 trials correctly (range 21–118 trials), and *marmoset B* completed on average 49 trials correctly (range 41–57 trials).

Preprocessing of eye movements and saccade removal. Saccades and smooth pursuit were both evoked by moving targets. Saccadic eye movements were cut from eye velocity traces by manually marking the start and end of saccades and interpolating eye velocity in between these times. We also analyzed the data without interpolating the velocity traces over intervals with saccades, instead cutting those intervals trial by trial out of the average, to insure it did not contribute to any effects. Individual eye position traces were differentiated using a finite impulse response filter with a bandwidth (−3 dB) of 21.5 Hz. Differential filters with higher frequency cutoffs did not alter our results. Trials were included for analysis if the marmoset tracked the stimuli within the window described above, regardless of whether smooth movements or saccades were used to maintain eye position in that window.

RESULTS

We began by studying the target motion parameters that evoked smooth eye movements in two adult marmoset subjects. The experimental protocol followed a Rashbass (1961) design in which animals initially fixate a centrally located target, which is then stepped to an eccentric location and moved at a fixed velocity (Rashbass 1961; Fig. 1). To be successful, the animals were required to maintain gaze within a fixation window around the target. After 0.7–2 s of target motion, the target stopped and then was extinguished and a drop of juice was given for successful trials. Trials were aborted if gaze fell outside of the fixation window, but rewards were not based on how the animals stayed within the fixation window. That is, it was possible for the animals to complete the trial successfully using saccadic or pursuit eye movements. Both animals had previously been trained to perform fixation tasks (Mitchell et al. 2014) but had not been exposed to tracking moving targets. Marmosets completed a variable number of trials in daily sessions, on average successfully tracking targets in 50 trials. Although small in number, these trials were sufficient to evaluate the core features of their pursuit behavior. No training was performed to shape marmosets toward making smooth movements, and thus our data reflect their natural behavior after fixation training.

The subjects successfully tracked the target motion using both saccadic eye movements as well as smooth eye movements. Smooth eye movements began ~200 ms following the start of target motion and went in the direction of the moving target. The beginning and end of saccades were marked by hand by looking for sharp excursions in the eye velocity traces to segregate saccadic eye movements from smooth eye movements (Fig. 1; see METHODS). To measure how target velocity influences pursuit eye movements in marmosets, we compared

the evoked smooth eye movements with targets moving horizontally that varied in speed from 3 to 16°/s (Fig. 2). We analyzed two aspects of the pursuit response. First, we examined the closed-loop eye velocity near the end of the target motion (after 400 ms from onset) to determine the overall gain of the pursuit eye movements relative to the target motion. The eye velocity averaged over trials from a single session at a variety of different tracking speeds is shown for each subject (Fig. 2, *A* and *E*). Pursuit initiated relatively slowly in both subjects, beginning ~200 ms after onset of target motion. We find that the relationship between eye velocity and target velocity increases for slow speeds, but for fast speeds the overall eye velocity declines with target velocity (Fig. 2, *B* and *F*). The gain for slow speeds nears 0.7–0.8, whereas for fast speeds it declines to 10% of the target speed (Fig. 2, *C* and *G*). To track faster moving targets, marmosets compensate for the low gain with larger saccadic eye movements. Marmosets exhibit a similar linear dependence on target motion as do humans and macaques, although their reduction in gain at speeds >10°/s differs from humans and macaques, which perform much closer to unity gain over a broader range of velocities.

We next examined the initial eye acceleration during the initial 100 ms following pursuit initiation (median pursuit latency: *marmoset P*, 178 ms; and *marmoset B*, 166 ms). We examined pursuit between 200 and 300 ms after motion onset to measure the open-loop pursuit, the pursuit that reflects the response to target motion without the influence that the eye movements have on target motion. In macaques and other primates, the amplitude of the initial eye acceleration is monotonically related to the target velocity for speeds <30°/s (Lisberger and Westbrook 1985). We found that initial eye acceleration was monotonically related to target

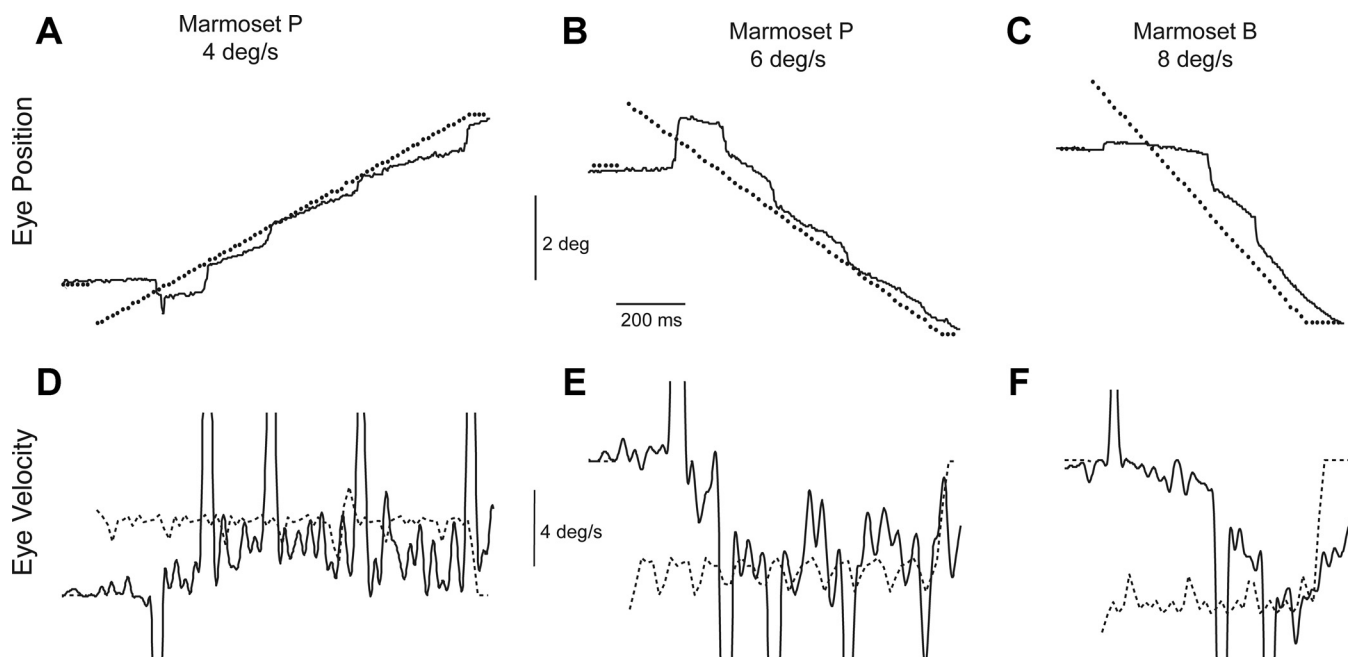


Fig. 1. The Rashbass step-ramp paradigm and typical single-trial eye movement responses for horizontal pursuit. *A–C*: each trial begins with fixation on a central target that jumps to a slightly eccentric position and moves back across the central position with continued linear motion that then lasts for 0.7–2 s (horizontal stimulus position shown as discrete dots on each video frame). Horizontal eye position traces are superimposed (solid line). *D–F*: the eye and target velocities are shown in the same trials (horizontal stimulus velocity indicated by the dotted line, eye velocity indicated by a solid line). Position and velocity calibration bars are indicated in *A* and *D*, respectively, and the time scale is indicated by the calibration bar in *B*. deg, Degrees.

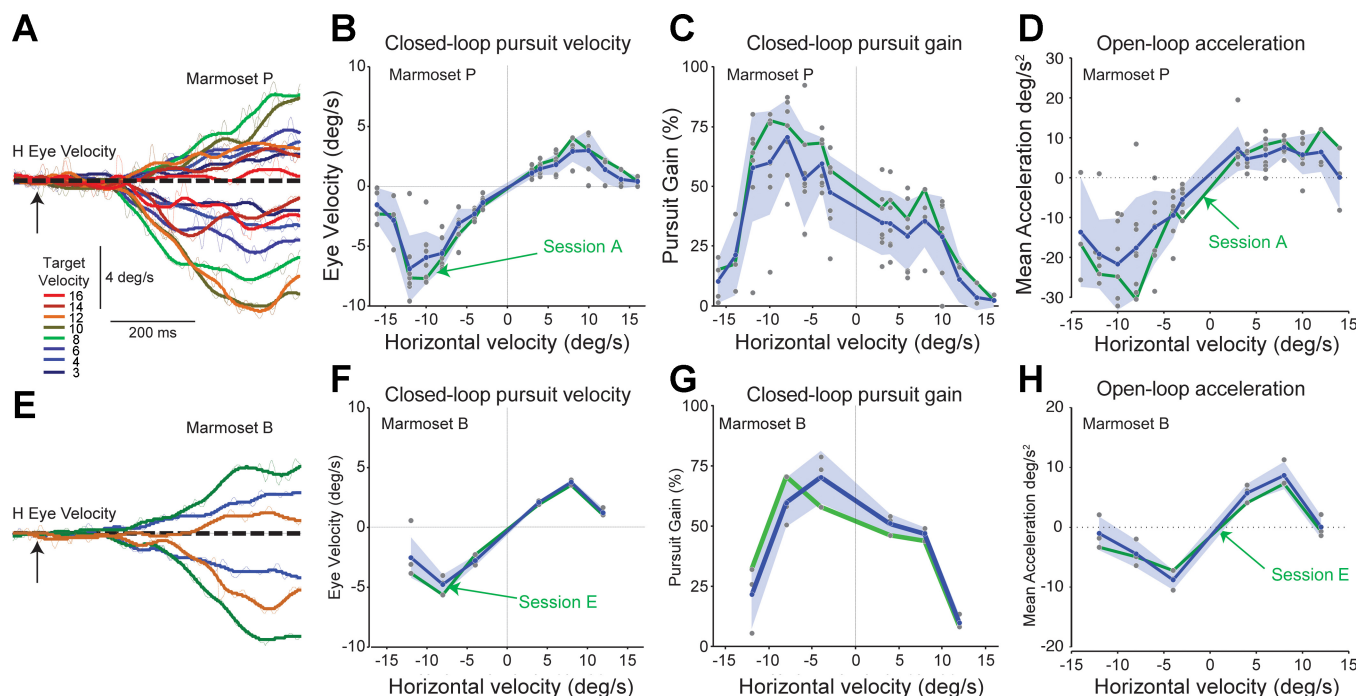


Fig. 2. Dependence of pursuit velocity and acceleration with target velocity. *A* and *E*: the mean horizontal (H) velocity for both subjects is shown time-locked to the onset of target motion for a set of different velocities sampled in a single behavioral session (velocity indicated by color with thick lines indicating a Gaussian smoothing, $\sigma = 20$ ms). The upward arrow indicates the beginning of target motion. Velocity and time calibration bars apply for both *A* and *E*. *B* and *F*: the closed-loop pursuit velocity measured in the interval from 400 to 600 ms is shown as a function of target velocity averaged across sessions (± 1 SD). The pursuit velocity shows a linear dependence for slower ($< 10^\circ$) target velocities. Each gray dot indicates the average value computed from trials completed at that velocity in a single behavioral session (marmoset *P*, 9 sessions; marmoset *B*, 3 sessions). Points for the example sessions shown in *A* and *E* are labeled in green. *C* and *G*: the closed-loop gain as a function of stimulus velocity reveals left and right asymmetries. *D* and *H*: the open-loop acceleration measured in the interval from 200 to 300 ms is shown as a function of target velocity averaged across sessions (± 1 SD). Same conventions as in *B* and *F*.

velocity in both marmosets examined but, as with closed-loop eye velocity, only for slow moving targets (Fig. 2, *D* and *H*). For slow speeds, $10^\circ/\text{s}$ or slower, initial eye acceleration monotonically increases with target speed. For speeds $> 10^\circ/\text{s}$, however, the relationship between initial eye acceleration and target velocity became weaker. Faster target motions elicited slower smooth eye movements rather than faster smooth eye movements. The marmosets were still successful at completing these trials but in doing so relied to a greater extent on saccadic eye movements than smooth eye movements.

Asymmetries were observed between rightward and leftward pursuit. Both animals exhibited higher initial eye acceleration and closed-loop eye velocity to leftward targets than rightward targets. This preference for leftward targets over rightward targets persisted across recordings and is most clearly evident in viewing the closed-loop gain as a function of eye velocity (Fig. 2, *C* and *G*). This could reflect the idiosyncratic abilities of individual animals, but because the same asymmetry was observed in both animals, we also suspect that this may be an outcome of the manner in which the eye movements were measured. The eye tracker used to make these measurements was placed on the right side of the video monitor, tracking the right eye, and may have introduced a looming stimulus in the lower right visual field ($12\text{--}15^\circ$ eccentricity). To determine whether the camera location was a factor in this asymmetry, we switched the camera to the left side and tracked the left eye in a single subject. We found that the asymmetry was nearly eliminated with only a 1% difference remaining in pursuit gain between left and right directions. However, we would have

expected the asymmetry to have reversed to the other side if it were solely due to the camera, therefore we expect that the difference in pursuit for right and left target motion also stems in part from the idiosyncrasies of these marmosets.

Pursuit eye movements were present both for horizontally moving targets as well as vertically moving targets, although pursuit was weaker for vertical motion (Fig. 3). Weaker pursuit for vertically moving targets existed both for the initial eye acceleration (Fig. 3*B*) as well as for closed-loop pursuit velocity (Fig. 3*C*). As in other primates, pursuit gain is higher for horizontally moving targets than for vertically moving targets (Grasse and Lisberger 1992; Heiney and Blazquez 2011).

Because pursuit is a voluntary eye movement that requires selection of a target, it is thought that the pursuit system must be engaged to allow tracking (Robinson 1965). One method to probe whether the pursuit system is activated is to measure the smooth eye movements evoked by small perturbations in the target motion. Previous studies in the macaque have demonstrated that small target perturbations during fixation evoke small smooth eye movements, whereas the same target perturbations during pursuit, when the pursuit system is engaged, evoke larger smooth eye movements (Churchland and Lisberger 2002; Mahaffy and Krauzlis 2011; Schwartz and Lisberger 1994). To determine whether the smooth eye movements measured here are also subject to the system being activated, we presented small sinusoidal perturbation of target motion from either fixation or during smooth pursuit (Fig. 4; see METHODS). Perturbations from fixation evoke very little smooth eye movement response (Fig. 4*A*), but when that same

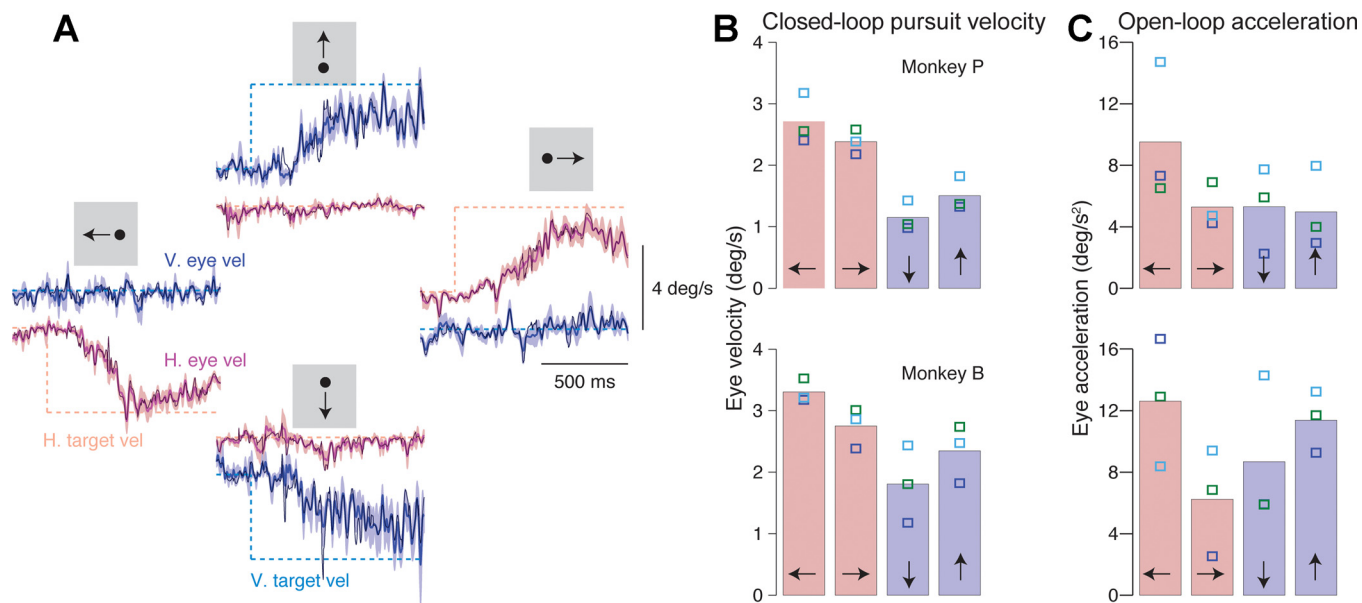


Fig. 3. Velocity and acceleration for horizontal and vertical moving targets. *A*: the mean horizontal (purple) and vertical (V.; blue) velocity (vel) are shown for different cardinal directions of motion averaged over a single session (± 1 SD) for a single subject (marmoset *P*). Averages without including saccade intervals (see METHODS) are superimposed (thin black line). *B*: closed-loop eye velocity averaged over sessions (individual session means shown as points) for each of the directions in both subjects. *C*: initial eye acceleration averaged over sessions (same conventions as in *B*).

target motion is presented during pursuit, the changes in eye velocity are more dramatic. To isolate the response to the target perturbation during pursuit, we measured the pursuit response to constant target motion and subtracted that from the response to pursuit that included the perturbation (Fig. 4*B*) as in previous studies (Churchland and Lisberger 2002; Schwartz and Lisberger 1994; Tavassoli and Ringach 2009). Although there is a small smooth eye movement response to the perturbation from fixation, it is far more modest than that observed when the pursuit system was engaged. We compared the response to the perturbation

during fixation and during pursuit in both animals and under varying perturbation amplitudes (from 2.5 to 10°/s) and found that similar eye movements evoked during pursuit were systematically greater than those during fixation (Fig. 4*C*). Therefore, it appears that, as in humans and macaques, marmoset pursuit eye movements depend on the engagement of the pursuit system.

DISCUSSION

We first characterized visual motion dependence of smooth eye movements in marmosets by measuring the eye move-

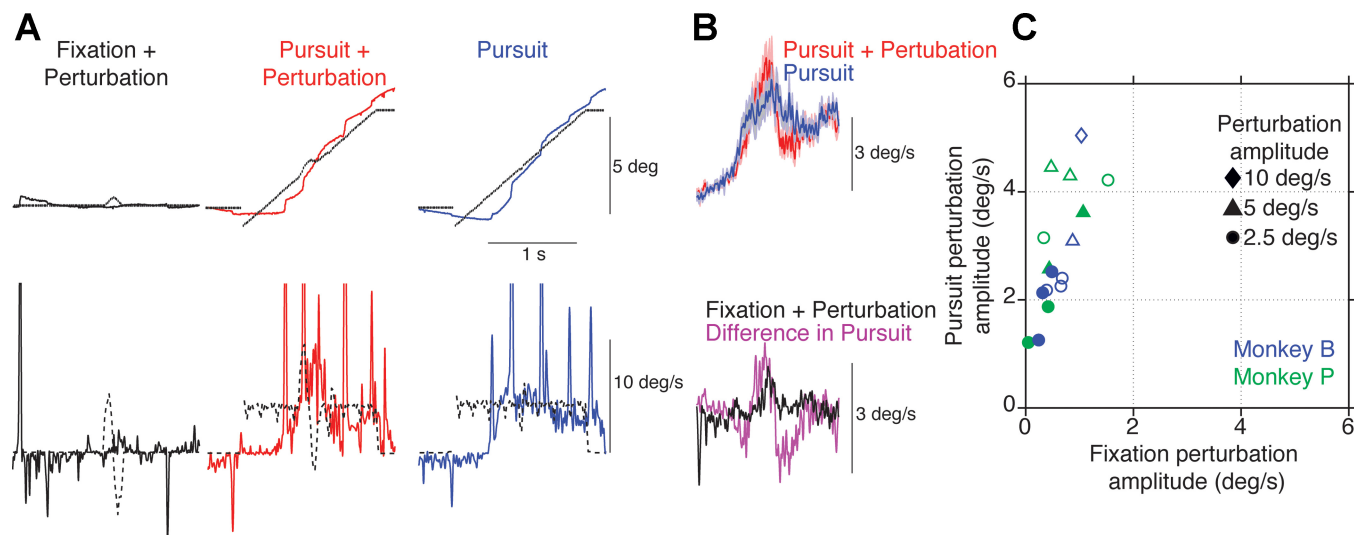


Fig. 4. Smooth pursuit following brief motion perturbations depends on whether the perturbation occurs from fixation or during pursuit. *A*, left: horizontal eye position (top) and eye velocity (bottom) during fixation of a central point as a 4-Hz sinusoidal perturbation in velocity occurs for a single trial (target position and velocity shown as discrete points and dashed lines, eye position and velocity as solid lines). Middle: eye position and velocity (red traces) to the perturbation during pursuit of a moving target. Right: eye position and velocity (blue traces) in the absence of the motion perturbation. *B*, top: average eye velocity over a session is shown for trials with (red) and without (blue) the motion perturbation. Shading indicates the standard error of the mean. *B*, bottom: eye velocity in response to the perturbation from fixation (black) or during pursuit is shown (purple; based on the difference in eye velocities shown in the top). *C*: mean amplitude of the smooth eye movements evoked by the motion perturbation are consistently larger in magnitude during pursuit relative to fixation as indicated by the points falling above the line of unity. Individual symbols are based on single sessions for rightward (open) and leftward pursuit (filled). Symbol color indicates the subject, and symbol shape indicates the perturbation amplitude.

ments evoked by target motion using the standard Rashbass (1961) step-ramp paradigm. As in other primates, initial smooth pursuit eye movements were in the direction of the target motion and not the step, indicating that pursuit was driven by target movement rather than target position. Furthermore, the initial eye acceleration strongly depended on the speed of horizontal target motion, with faster targets evoking monotonically larger eye accelerations, over a range of slower target motions. Both of these results indicate that, as in other primates, pursuit eye movements depend strongly on the motion signals of the target (Lisberger and Westbrook 1985).

To study whether pursuit eye movements depend on the engagement of the pursuit system, we measured the gain of smooth eye movements to small perturbations. When these perturbations occur during pursuit, large changes in smooth eye movements are observed, whereas when the perturbations occur from fixation, little to no smooth eye movements are observed. This change in the gain of smooth eye movements suggests that the marmoset pursuit system depends on voluntary engagement (Robinson 1965), similar to what is found in humans and macaques (Churchland and Lisberger 2002; Mahaffy and Krauzlis 2011; Schwartz and Lisberger 1994).

Several distinct cortical areas participate in the control of pursuit eye movements in macaques and humans (Lisberger 2010), including MT/MST, which specializes in motion analysis, and frontal areas such as the frontal pursuit area, which directs pursuit eye movements. Marmosets share a similar organization of motion-related visual areas and have well-identified frontal eye fields (for review, see Solomon and Rosa 2014), although little is known about a possible frontal pursuit area in marmosets. An earlier study reported that microstimulation at sites in the marmoset frontal eye fields resulted in smooth eye movements with a range of velocities, with sites located more frontally being more likely to evoke saccades rather than smooth movements (Blum et al. 1982). The basic metrics of pursuit behavior have been recently reported in another New World species, the squirrel monkey (Heiney and Blazquez 2011), and have been found to be comparable with macaques but, in accord with our data from the marmoset, also reveal that pursuit gain drops for targets moving faster than 10–15°/s. A similar decline in pursuit gain is also found in macaques when the contrast of targets relative to the background is low (Lisberger and Westbrook 1985). Accurate eye position tracking depended on having a small pupil, which required use of a bright background for these experiments, thus lowering contrast. The decline in pursuit gain for fast speeds may therefore be a consequence of our experimental setup. In addition, the decline in pursuit gain may reflect a dominance of head movements for orienting in the New World species, as their head is much smaller and has smaller inertial forces (Heiney and Blazquez 2011). We did not train these animals to pursue targets, and the decline in pursuit gain for fast targets may therefore reflect a natural tendency for marmosets to use head movements instead of eye movements for tracking, which may also be related to a more limited oculomotor range in these New World species when the head is fixed (Heiney and Blazquez 2011; McCrea and Gdowski 2003; Mitchell et al. 2014). It may merit further consideration how the oculomotor range may trade off with the gain in pursuit for faster moving stimuli that approach the periphery of the range and whether that gain might be sustained better for higher velocities with

shared head and eye gaze movements if the head were free. Only a few studies have examined pursuit eye movements among naïve macaques and humans, as done in the present study in marmosets, but those studies report lower pursuit gain and a higher proportion of catch-up saccades (Liston and Stone 2014). Finally, the decline in pursuit gain could reflect a difference in either motion sensation or the target selection process. A comparison of speed sensitivity between macaque and marmoset neurons in area MT has revealed an overall preference for slower speeds in the marmoset that could impact pursuit eye movements (Lui and Rosa 2015). In addition, frontal cortical circuits have undergone considerable expansion from New to Old World primates (Chaplin et al. 2013), and marmosets have specialized for smaller brain size, therefore it may also be worthwhile to consider that there are differences in the frontal circuitry mediating these behaviors.

In sum, we demonstrate that smooth pursuit eye movements occur naturally in marmosets and these eye movements have similar characteristics to the eye movements observed in other nonhuman primates. The marmoset provides several practical advantages for neural investigation of smooth pursuit because the parietal and frontal cortical circuits involved in this behavior all lie at the cortical surface of its lissencephalic brain. Although their behavioral performance appears more limited, we note that no attempt was made in the current studies to shape their behavior extensively, and thus continued study with more extensive training or paradigms better suited to their natural inclinations is merited. For certain lines of inquiry, the advantages for study in this system may offset the weaker behavioral performance, providing a valuable complement to the more extensively studied macaque.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

J.F.M. and N.J.P. conception and design of research; J.F.M. and N.J.P. performed experiments; J.F.M. and N.J.P. analyzed data; J.F.M. and N.J.P. interpreted results of experiments; J.F.M. and N.J.P. prepared figures; J.F.M. and N.J.P. drafted manuscript; J.F.M., N.J.P., and C.T.M. edited and revised manuscript; J.F.M., N.J.P., and C.T.M. approved final version of manuscript.

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