Motion dependence of smooth pursuit eye movements in the marmoset

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Abstract

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 in order 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 areas MT and FEF at the cortical surface, merit its utilization for studying pursuit movements.

Introduction

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
Richard 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, while 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; Stone et al, 2009). The ability to select a small moving target, and to disambiguate
if 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 MT and
MST, that have neurons selective to real versus 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. While 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 though the visual system remains highly similar in organization to that of
larger species like the macaque (Solomon and Rosa, 2014; Mitchell and Leopold, 2015),
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
FEF 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 the standard Rashbass step-ramp paradigm (Rashbass, 1961). 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 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 stabiliziation. All procedures with marmosets were performed in the
laboratory of Cory Miller under the approval of the Institutional Animal Care and Use
Committee (IACUC) 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, Liang, and
Wang, 2001a,b; Remington et al, 2012; Osmanski et al, 2013). 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 NIH guidelines. Both subjects were maintained on
food control to provide motivation in behavioral tasks with their weight ranging from 5-
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 squared error, ETL-200 ISCAN, Inc.). The camera was placed to the lower right visual field (12-15 degs 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 NIMH Cortex software. 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 over-sampled at 500Hz and stored digitally, with time-stamps for stimulus events, using the software package Cortex (http://dally.nimh.nih.gov/). Eye position was calibrated as described previously (Mitchell et al, 2014). First preferential looking towards 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 degrees 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 degree radius window at each of these positions. Position error at these eccentric locations was less than 10 percent.

Fixation stimuli for tracking tasks were presented on a computer monitor that was adjusted for a high background luminance to constrict the marmoset pupil. While 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, 1024x768 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 squared error less than 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 Figure 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 between 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 degrees per second). 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 which 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 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, Marmoset P completed on average 47.2 trials correctly (range 118 to 21 trials). Marmoset B completed on average 49 trials correctly (range 57 to 41 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 design (1961) 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 to 2 seconds 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 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. Though small in number, these trials were sufficient to evaluate the core features of their pursuit behavior. No
training was performed to shape marmosets towards 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 approximately 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 in order 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 to targets moving horizontally that varied in speed from 3 to 16 deg/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. 2A,E). Pursuit initiated relatively slowly in both subjects, beginning around 200ms 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. 2B,F). The gain for slow speeds nears 0.7 to 0.8, while for fast speeds it declines to 10% of the target speed (Fig. 2C,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 greater than 10 deg/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: 178ms, and marmoset B: 166 ms). We examined pursuit between 200-300 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
less than 30 deg/s (Lisberger and Westbrook, 1985). We found that initial eye acceleration was monotonically related to target velocity in both marmosets examined, but as with closed-loop eye velocity, only for slow moving targets (Fig. 2D,H). For slow speeds, 10 deg/s or slower, initial eye acceleration monotonically increases with target speed. For speeds faster than 10 deg/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. 2C,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 (12-15° 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, though pursuit was weaker for vertical motion (Fig. 3). Weaker pursuit for vertically-moving targets existed both for the initial eye acceleration
(Fig. 3B) as well as for closed-loop pursuit velocity (Fig. 3C). As in other primates, pursuit gain is higher for horizontally moving targets than for vertically-moving targets (Grass 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 (Schwartz and Lisberger, 1994; Churchland and Lisberger, 2002; Mahaffy and Krauzlis, 2011). 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. 4A), but when that same target motion is presented during pursuit, the changes in eye velocity are more dramatic (Fig. 4B). To isolate the response to the target perturbation during pursuit, we measured the pursuit response to constant target motion (Fig. 4C), and subtracted that from the response to pursuit that included the perturbation (Fig. 4D) as in previous studies (Schwartz and Lisberger, 1994; Churchland and Lisberger, 2002; Tavassoli and Ringach, 2009). While 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 deg/s to 10 deg/s) and found that similar eye movements evoked during pursuit were systematically greater than those during fixation (Fig. 4E). 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 movements evoked by target motion using the standard Rashbass 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 (Schwartz and Lisberger, 1994; Churchland and Lisberger, 2002; Mahaffy and Krauzlis, 2011).

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 (FPA), 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 micro-stimulation 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 to macaques, but in accord with our data from the marmoset, also reveal that pursuit gain drops for targets moving faster than 10-15 degs/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 this New World species when the head is fixed (McCrea and Gdowski, 2003; Heiney and Blazquez, 2011; 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 non-human 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. While 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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References


Figure Legends

Figure 1. The Rashbass step-ramp paradigm and typical single trial eye movement responses for horizontal pursuit. (A,B,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 seconds (horizontal stimulus position shown as discrete dots each video frame). Horizontal eye position traces are superimposed (solid line). (D,E,F) The eye and target velocity is 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 timescale is indicated by the calibration bar in panel B.

Figure 2. Dependence of pursuit velocity and acceleration with target velocity. (A,E) The mean horizontal 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, $\sigma=20\text{ms}$). The upward arrow indicates the beginning of target motion. Velocity and time calibration bars apply for both A and E. (B,F) The closed-loop pursuit velocity measured in the interval from 400-600 ms is shown as a function of target velocity averaged across sessions (+/- 1 std). The pursuit velocity shows a linear dependence for slower (<10 deg) 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,E) are labeled in green. (C,G) The closed-loop gain as a function of stimulus velocity reveals left and right asymmetries (black dashed line indicates the gain when camera position is swapped to the left eye). (D,H) The open-loop acceleration measured in the interval from 200-300 ms is shown as a function of target velocity averaged across sessions (+/- 1 std). Same conventions as in (B,F).

Figure 3. Velocity and acceleration for horizontal and vertical moving targets. (A) The mean horizontal (purple) and vertical (blue) velocity is shown for different cardinal directions of motion averaged over a single session (+/1 std) 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).

Figure 4. Smooth pursuit following brief motion perturbations depends on whether the perturbation occurs from fixation or during pursuit. (A) Left panels: 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 panels: Eye position and velocity (red traces) to the perturbation during pursuit of
a moving target. Right panels: 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 panels). (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. Symbol color indicates the subject and symbol shape indicates
the perturbation amplitude.