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Smooth pursuit of non-visual motion

Marian E. Berryhill, Tanya Chiu, and Howard C. Hughes

Dartmouth College, Hanover, NH

Corresponding Author:
Marian Berryhill
Department of Psychological & Brain Sciences
6207 Moore Hall
Hanover, NH 03755
Tel: (603) 646-0049
Email: marianb@dartmouth.edu
Abstract

Unlike saccades, smooth pursuit eye movements (SPEMs) are not under voluntary control and their initiation generally requires a moving visual target. However, there are various reports of limited smooth pursuit of the motion of a subject’s own finger in total darkness (pursuit based on proprioceptive feedback, e.g. Gertz 1916) and to the combination of proprioception and tactile motion as an unseen finger was moved voluntarily over a smooth surface (Watanabe and Shimojo 1997). In contrast, SPEMs to auditory motion are not distinguishable from pursuit of imagined motion (Boucher et al. 2004). These reports of smooth pursuit of non-visual motion cues used a variety of paradigms and different stimuli. In addition, the results have often relied primarily on qualitative descriptions of the smooth pursuit (see review by Ilg 1997). Here, we directly compare measurements of smooth pursuit gain (eye velocity/stimulus velocity) to visual, auditory, proprioceptive, tactile, and combined tactile + proprioceptive motion stimuli. The results demonstrate a clear and statistically reliable ordering of gain values according to stimulus modality (from lowest to highest gains): auditory, tactile, proprioceptive, proprioceptive + tactile and visual.
Introduction

Although most formal models of smooth pursuit eye movements consider retinal slip the controlling input to the smooth pursuit control system (Robinson 1965; Krauzlis and Lisberger 1994), it is known that other forms of input support some degree of smooth pursuit. Expectancies form one class of these non-visual inputs, since brief periods of pursuit can occur in anticipation of the movement of a stationary visual target (Kowler 1989), and smooth pursuit continues for brief time periods after a visual stimulus is extinguished (e.g. Becker and Fuchs 1985; Kveraga et al. 2001; Whittacker and Eholtz, 1982). This predictive ability helps overcome phase lags that would otherwise result from the relatively lengthy latencies of the visual control signals (e.g. Bahill and McDonald 1983; Deno et al. 1995).

Proprioceptive signals can also elicit smooth pursuit. Several studies have examined smooth pursuit eye movements as subjects follow the movement of their own hand in the dark (Gertz 1916, cited in Ilg 1997; Steinbach 1969, 1976; Gauthier and Hofferer 1976; Glenny and Heywood 1979), or in the light but with the hand remaining invisible (Watanabe and Shimojo 1997). In contrast, auditory signals are apparently unable to generate motion signals capable of supporting smooth pursuit eye movements; in fact, quantitative analyses indicate there is no difference between smooth pursuit to moving auditory stimuli and imagined moving stimuli (Boucher et al. 2004). Although the somatosensory system has access to cutaneous motion information through Meissner’s corpuscles (for a recent review see Johnson 2001) this information does not seem to be very effective either. Tactile information produced by tracking a hand as it slides across a stationary object did not support smooth pursuit eye movements (Watanabe and Shimojo 2004). To our knowledge, the ability to track motion across an extended area of the skin surface has not been investigated, but is explored in the present
experiments. The general pattern of results indicates that the smooth pursuit system has a very limited ability to utilize motion information from sensory modalities other than vision.

Previous studies of smooth pursuit of non-visual motion relied on qualitative descriptions of the quality of the pursuit eye movements, making direct comparisons between different non-visual modalities difficult. The goal of this study is to quantitatively compare smooth pursuit eye movements to several modalities of motion stimuli in the same participants and under the same conditions, thereby permitting an accurate assessment of the ability of the smooth pursuit control system to access motion signals from the following modalities: vision, audition, proprioception, tactile, and combination tactile + proprioception.

Methods

Participants: 7 participants contributed data (5 female). They ranged in age from 24 – 40 years, and were graduate students or former graduate students. The five naïve participants were paid $6 per session. All protocols were approved by the Dartmouth College Committee for the Protection of Human Subjects and each participant signed an informed consent document prior to participation.

Recording: A custom made pendulum (76 cm long) was equipped with a green LED, a Piezo speaker, and a rubber wheel at the base. The pendulum position was determined by the voltage across a potentiometer and was recorded simultaneously along with the eye movements. Eye movements were recorded using scleral search coils (Skalar Medical; Robinson 1963). The spatial resolution of the system is 2.0 min of arc. Eye position was digitized with 12 bit resolution at a sampling rate of 1000 Hertz and stored to disk for off-line analysis.
The pendulum was calibrated prior to experimentation and the correspondence between voltage output and degrees of eccentricity determined. Each session began with a calibration of eye position. During calibration, participants fixed their gaze at four stationary LEDs arrayed in a rectangle located at 30° horizontal eccentricity and 16° vertical eccentricity and a fifth LED on the pendulum located at the origin.

**Procedure:** Prior to each trial, the experimenter told the participant what type of trial was going to take place. For visual and audio trials, the experimenter raised the pendulum to a marked position to the right of the participant and released it when the Piezo speaker or LED turned on. For the proprioceptive trials the participant held the pendulum with their preferred hand and moved it right to left for the duration of the trial. In the tactile condition, the wheel at the base of the pendulum was placed on the dorsal surface of the participant’s forearm and the experimenter moved the pendulum back and forth along the participant’s arm while the participant tried to track this movement with their eyes. In the combination proprioceptive + tactile condition, the participant moved the pendulum along his/her own arm. In each session 5 - 10 trials of each condition were recorded. Each participant performed 2 sessions. Each subject contributed 10 trials per condition for a total of 50 trials per person.

**Data Analysis:** The saccades from each eye trace were removed using a saccade detecting algorithm and visually inspected to ensure accuracy. Saccades were identified as regions where the eye velocity exceeded 1.5 standard deviations of the mean velocity over a running 10 ms period. These samples were removed from both the eye and pendulum traces. Samples where the pendulum velocity exceeded $100 \, ^\circ \, s^{-1}$ were also excluded. Gain was calculated by dividing the horizontal eye velocity by the pendulum velocity for the saccade-free velocity traces. We also excluded the first 500 samples to
allow pendulum motion to be fully underway. Analyses were conducted using Matlab 6.5 (The MathWorks, Natick, MA).

Results

In Figure 1, the mean gain values per condition are presented. These data were subjected to a one-way analysis of variance (ANOVA) comparing gain values across the five conditions (visual, auditory, tactile, proprioceptive, and combined proprioceptive + tactile). There was a significant main effect of condition ($F_{4, 30} = 47.86, p < .001$, partial $\eta^2 = .95$). Pairwise comparisons use Tukey’s honest significant difference (HSD) to correct for multiple comparisons. Pairwise analyses revealed significantly greater gains for the visual condition than all other conditions (all $p < .001$). In addition, the smooth pursuit gain for the auditory condition was significantly smaller than all other conditions (all $p$’s < .04). There were no significant differences between the tactile, proprioceptive or combined proprioceptive + tactile conditions, although the difference between the tactile and the combination conditions is significant ($p = .01$) prior to correction for multiple comparisons ($p = .068$ after correction). Figure 2 demonstrates example traces from the visual (V), auditory (A), tactile (T), proprioceptive (P) and combination tactile and proprioceptive (T + P) conditions.

The motion paths in each of these experimental conditions were not really identical. The tactile condition had smaller pendulum amplitude, as the experimenter did was not able to slide the pendulum along the subjects’ arms to the same extent that the pendulum could freely swing. There were also some differences in the velocity of the pendulum motion in each condition, which were revealed by examination of velocity histograms of the pendulum trajectories in each condition. This analysis showed that the stimulus velocities for both the tactile and the tactile + proprioceptive combination trials
were on the average slower because, in these conditions, the pendulum was not swinging freely but was moved manually (by either the participant in the proprioceptive or combination condition or by an experimenter in the tactile condition). To control for this difference, we recalculated the gain values using only the samples with pendulum velocities of less than 50° s⁻¹. The statistics remained the same following this correction ($F_{4, 30} = 38.14, p < .001$, partial $\eta^2 = .89$), except that the difference between the tactile and auditory conditions fails to reach significance ($p = .46$).

![Figure 1](image.png)

**Figure 1.** The overall gain values per condition: A = auditory, T = tactile, P = proprioceptive, T+P = tactile and proprioceptive combination, V = visual. The error bars reflect the standard error of the mean.
Figure 2. Example eye traces from subject CG. Each panel (A. Visual, B. Tactile and Proprioceptive Combination, C. Proprioceptive, D. Tactile, E. Auditory conditions) includes the pendulum (gray) and horizontal eye trace (black).

Discussion

The present study compared ocular tracking of stimulus motion in four different modalities. After saccades had been eliminated, we determined the amount of smooth pursuit eye movements supported by visual and non-visual stimulus motion. We used a moving pendulum apparatus equipped with an LED and a speaker. Participants either
watched, listened, held, felt, or held and felt the pendulum moving back and forth in the frontal-parallel plane. The results confirm and extend previous findings and support the following conclusions: 1) visual input produces the highest gain values of smooth pursuit and 2) auditory input produces the least smooth pursuit, and 3) tactile, proprioceptive and combined tactile + proprioceptive signals support values of smooth pursuit gain that were intermediate between vision and audition.

Sustained, accurate smooth pursuit eye movements clearly require visual signals that specify the relative retinal motion of a visual target. Visual motion detectors are commonplace in the visual system, and provide a critical source of input to the smooth pursuit control system (e.g. Yamasaki and Wurtz 1991). It is therefore possible that measures of smooth pursuit of non-visual motion can serve as a behavioral index of motion detectors in non-visual sensory modalities. In this context, it is interesting to note that the very existence of auditory motion detectors remains unclear (Grantham 1986; Perrret and Marlborough 1989) since virtually no smooth pursuit is elicited by auditory motion alone (Boucher et al. 2004). Proprioception afferents also provide information concerning egocentric body position information over time, but it is not known whether the proprioceptive system contains motion detectors that are in any way comparable to visual motion detectors. The finding that proprioceptive signals support smooth pursuit eye movements that are superior to those using auditory motion suggests that the neural representation of body motion might be more robust than the neural representation of auditory motion. Similar considerations apply to tactile motion. The cutaneous system also provides motion information (Hagen et al. 2002), probably through stimulation of Meissner’s corpuscles (Johnson 2001). In addition, recent evidence indicates that tactile and visual information is processed in several common regions, including the superior colliculus (Maravita et al. 2003). Apparently, both the
cutaneous and the proprioceptive systems provide motion signals that are significantly more effective in supporting smooth pursuit than the auditory system.
References


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Email: marianb@dartmouth.edu
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Unlike saccades, smooth pursuit eye movements (SPEMs) are not under voluntary control and their initiation generally requires a moving visual target. However, there are various reports of limited smooth pursuit of the motion of a subject’s own finger in total darkness (pursuit based on proprioceptive feedback, e.g. Gertz 1916; Hashiba et al. 1996) and to the combination of proprioception and tactile motion as an unseen finger was moved voluntarily over a smooth surface (Watanabe and Shimojo 1997). In contrast, SPEMs to auditory motion are not distinguishable from pursuit of imagined motion (Boucher et al. 2004). These reports of smooth pursuit of non-visual motion cues used a variety of paradigms and different stimuli. In addition, the results have often relied primarily on qualitative descriptions of the smooth pursuit (see review by Ilg 1997).

Here, we directly compare measurements of smooth pursuit gain (eye velocity/stimulus velocity) to visual, auditory, proprioceptive, tactile, and combined tactile + proprioceptive motion stimuli. The results demonstrate high gains for visual pursuit, low gains for auditory pursuit, and intermediate, statistically indistinguishable gains for tactile, proprioceptive, proprioceptive + tactile pursuit.
Introduction

Although most formal models of smooth pursuit eye movements consider retinal slip the controlling input to the smooth pursuit control system (Robinson 1965; Krauzlis and Lisberger 1994), it is known that other forms of input support some degree of smooth pursuit. Expectancies form one class of these non-visual inputs, since brief periods of pursuit can occur in anticipation of the movement of a stationary visual target (Kowler 1989), and smooth pursuit continues for brief time periods after a visual stimulus is extinguished (e.g. Becker and Fuchs 1985; Kveraga et al. 2001; Whittacker and Eaholtz, 1982). This predictive ability helps overcome phase lags that would otherwise result from the relatively lengthy latencies of the visual control signals (e.g. Bahill and McDonald 1983; Deno et al. 1995).

Proprioceptive signals can also elicit smooth pursuit. Several studies have examined smooth pursuit eye movements as subjects follow the movement of their own hand in the dark (Gertz 1916, cited in Ilg 1997; Steinbach 1969, 1976; Gauthier and Hofferer 1976; Glenny and Heywood 1979; Hashiba et al. 1996), or in the light but with the hand remaining invisible (Watanabe and Shimojo 1997). In contrast, auditory signals are apparently unable to generate motion signals capable of supporting smooth pursuit eye movements; in fact, quantitative analyses indicate there is no difference between smooth pursuit to moving auditory stimuli and imagined moving stimuli (Boucher et al. 2004). Although the somatosensory system has access to cutaneous motion information through Meissner’s corpuscles (for a recent review see Johnson 2001) this information does not seem to be very effective either. Tactile information produced by tracking a hand as it slides across a stationary object did not support smooth pursuit eye movements (Watanabe and Shimojo 2004). To our knowledge, the ability to track motion across an extended area of the skin surface has not been investigated, but is explored in the present
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Methods

Participants: 10 participants contributed data (8 female). They ranged in age from 19 – 56 years, and were drawn primarily from the graduate community. The three authors participated and two (MB, HCH) had previous experience in smooth pursuit experiments. The 7 naïve participants had not participated in smooth pursuit eye movement studies although two participants were regular participants in saccade studies. Participants were paid $6 per session. All protocols were approved by the Dartmouth College Committee for the Protection of Human Subjects and each participant signed an informed consent document prior to participation.

Recording: A custom made pendulum (84 cm long) was equipped with a green LED, a Piezo speaker, and a rubber wheel at the base. The pendulum position was determined by the voltage across a potentiometer and was recorded simultaneously along with the eye movements. Eye movements were recorded using scleral search coils
(Skalar Medical; Robinson 1963). The spatial resolution of the system is 2.0 min of arc. Eye position was digitized with 12 bit resolution at a sampling rate of 1000 Hertz and stored to disk for off-line analysis.

The pendulum was calibrated prior to experimentation and the correspondence between voltage output and degrees of eccentricity determined. Each session began with a calibration of eye position. During calibration, participants sat at a viewing distance of approximately 20 cm and fixed their gaze at four stationary LEDs arrayed in a rectangle located at $85^\circ$ horizontal eccentricity and $45^\circ$ vertical eccentricity and a fifth LED on the pendulum located at the origin.

Procedure: Prior to each trial, the experimenter told the participant what type of trial was going to take place and when to start. Trial types were presented in pseudo-random order (random without replacement). For visual and audio trials, the experimenter raised the pendulum to a marked position to the right of the participant and released it when the Piezo speaker or LED turned on. For the proprioceptive trials the participant held the pendulum with their preferred hand and moved it right to left for the duration of the trial. In the tactile condition, the wheel at the base of the pendulum was placed on the dorsal surface of the participant’s bent forearm and the experimenter moved the pendulum back and forth along the participant’s arm while the participant tried to track this movement with their eyes. In the combination proprioceptive + tactile condition, the participant moved the pendulum along his/her own arm. In all but the visual condition, the experiment took place in the dark, and participants could not see the pendulum. In each session 5 - 10 trials of each condition were recorded. Each participant performed 2 sessions. Each subject contributed 10 trials per condition for a total of 50 trials per person.
Data Analysis: The saccades from each eye trace were removed using a saccade detecting algorithm and visually inspected to ensure accuracy. Saccades were identified as regions where the eye velocity exceeded 1.5 standard deviations of the mean velocity over a running 10 ms period. These samples were removed from both the eye and pendulum traces. Samples where the pendulum velocity exceeded 100° s⁻¹ were also excluded. Gain was calculated by dividing the horizontal eye velocity by the pendulum velocity for the saccade-free velocity traces. We also excluded the first 500 samples to allow pendulum motion to be fully underway. Reaction time was determined as the point at which eye movement velocity increased by more than .8 standard deviations over a 10 milliseconds. Root mean square error was calculated by first squaring the difference between the pendulum position and the eye position then taking the mean of the square root of these differences. Analyses were conducted using Matlab 6.5 (The MathWorks, Natick, MA).

Results

In Figure 1, the mean gain values per condition are presented. These data were subjected to a repeated measures analysis of variance (ANOVA) comparing gain values across the five conditions (visual, auditory, tactile, proprioceptive, and combined proprioceptive + tactile). There was a violation of homogeneity of variance, as determined by Mauchly’s test of sphericity (p = .03) which led us to use the Greenhouse-Geisser correction. There was a significant main effect of condition (F 2.1, 18.6 = 114.25, p < .001, partial $\eta^2 = .93$). Pairwise comparisons use Bonferroni corrections to correct for multiple comparisons. Pairwise analyses revealed significantly greater gains for the visual condition than all other conditions (all p < .001). In addition, the smooth pursuit gain for the auditory condition was significantly smaller than all other conditions (all p’s
There was no significant difference between the mean gain values in the tactile, proprioceptive or combination tactile and proprioceptive conditions. Additional repeated measures analyses of variance examined reaction time x condition and root mean square error x condition. There was no main effect of condition on reaction time and no significant differences between the reaction times for any of the conditions (all p > .1). The root mean square error revealed significantly higher accuracy for the visual traces than for the other conditions (all p’s < .01). Figure 2 demonstrates example traces from the visual (V), auditory (A), tactile (T), proprioceptive (P) and combination tactile and proprioceptive (T + P) conditions.

The motion paths in each of these experimental conditions were not really identical. The tactile condition had smaller pendulum amplitude, as the experimenter did was not able to slide the pendulum along the subjects’ arms to the same extent that the pendulum could freely swing. There were also some differences in the velocity of the pendulum motion in each condition, which were revealed by examination of velocity histograms of the pendulum trajectories in each condition. This analysis showed that the stimulus velocities for both the tactile and the tactile + proprioceptive combination trials were on the average slower because, in these conditions, the pendulum was not swinging freely but was moved manually (by either the participant in the proprioceptive or combination condition or by an experimenter in the tactile condition). To control for this difference, we recalculated the gain values using only the samples with pendulum velocities of less than 50° s⁻¹. The statistics remained the same following this correction (F₄, ₃₆ = 95.9, p < .001, partial η² = .91) and there was no violation of sphericity for these data.
Figure 1. The overall gain values per condition: A = auditory, T = tactile, P = proprioceptive, T+P = tactile and proprioceptive combination, V = visual. The error bars reflect the standard error of the mean.
Figure 2. Individual trial, example eye traces from subject CG prior to desaccading. Each panel (A. Visual, B. Tactile and Proprioceptive Combination, C. Proprioceptive, D. Tactile, E. Auditory conditions) includes the pendulum (gray) and horizontal eye trace (black). The respective gain values for each trace are the following: .82, .50, .46, .39, and .14.

Discussion

The present study compared ocular tracking of stimulus motion in four different modalities. After saccades had been eliminated, we determined the amount of smooth
pursuit eye movements supported by visual and non-visual stimulus motion. We used a moving pendulum apparatus equipped with an LED and a speaker. Participants either watched, listened, held, felt, or held and felt the pendulum moving back and forth in the frontal-parallel plane. The results confirm and extend previous findings and support the following conclusions: 1) visual input produces the highest gain values of smooth pursuit and 2) auditory input produces the least smooth pursuit, and 3) tactile, proprioceptive and combined tactile + proprioceptive signals support values of smooth pursuit gain that were intermediate between vision and audition.

It is possible that the nervous system possesses non-visual motion detectors but the outputs of these motion detectors simply do not gain access to the smooth pursuit system. However, it is also possible that smooth pursuit can serve as a behavioral index of motion detectors in non-visual sensory modalities. In this context, it is interesting to note that the very existence of auditory motion detectors remains questionable (Granatham 1986; Perret and Marlborough 1989). The apparent absence of auditory motion detectors might underlie the observation that auditory motion is virtually incapable of supporting smooth pursuit eye movements (Boucher et al. 2004, and the present results).

The saccadic system makes slower, less accurate saccades to auditory (see Zambarbieri 2002) and somatosensory targets (Groh and Sparks 1996). In contrast, sustained, accurate smooth pursuit eye movements clearly require visual signals that specify the relative retinal motion of a visual target. Visual motion detectors are commonplace in the visual system, and provide a critical source of input to the smooth pursuit control system (e.g. Yamasaki and Wurtz 1991). Although the possibility remains that non-visual motion signals cannot fully stimulate or initiate the smooth pursuit system, it is also possible that measures of smooth pursuit of non-visual motion can serve as a behavioral index of motion detectors in non-visual sensory modalities.
Proprioception afferents also provide information concerning egocentric body position information over time, but it is not known whether the proprioceptive system contains motion detectors that are in any way comparable to visual motion detectors. The finding that proprioceptive signals support smooth pursuit eye movements that are superior to those using auditory motion suggests that the neural representation of body motion might be more robust than the neural representation of auditory motion. Similar considerations apply to tactile motion. The cutaneous system also provides motion information (Hagen et al. 2002), probably through stimulation of Meissner’s corpuscles (Johnson 2001). Hashiba et al (1996) suggested that the smooth pursuit they observed in auditory and somatosensory conditions might be due to a common gating mechanism (see Krauzlis 2003 for a recent review). Our data suggest that if there is a single pursuit gating mechanism it is not efficiently accessed by all sensory modalities. Recent evidence indicates that tactile and visual information is processed in several common regions, including the superior colliculus (Maravita et al. 2003). Apparently, both the cutaneous and the proprioceptive systems provide motion signals that are significantly more effective in supporting smooth pursuit than the auditory system.


